



# Extrapair paternity as a cost of polygyny in the rock sparrow: behavioural and genetic evidence of the ‘trade-off’ hypothesis

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(Received 9 July 2001; initial acceptance 3 September 2001;

final acceptance 3 December 2001; MS. number: 6994)

We studied the association between extrapair paternity (EPP) rate and male mating status in the rock sparrow, *Petronia petronia*, a facultative polygynous species. Overall, 32.0% (58/181) of the chicks were not sired by the social father and 57.1% (24/42) of the broods contained at least one extrapair young. Polygynous males allocated less time to guarding their mate during her fertile period than monogamous males but did not differ in the time spent guarding their nest. Polygynous males were cuckolded more frequently than monogamous males (50.5 and 6.6% of the young, respectively) and their paternity loss was positively correlated with the degree of overlap between the fertile periods of their primary and secondary females. Paternity loss did not differ between primary and secondary broods of polygynous males and acquiring a second mate was possible only at the expense of paternity in both broods. Late broods contained fewer extrapair young, despite no significant seasonal trend in the time allocated by the male to guarding his mate. Male yellow badge size was not associated with paternity. Old males were cuckolded less frequently than first-year males, but male age had a minor effect on paternity compared with male mating status. Reproductive success (number of young fledged/year) did not differ between monogamous and polygynous males once paternity was accounted for. Together, these results suggest that mate guarding can be efficient in preventing cuckoldry, and that there is a trade-off between attracting an additional mate and protecting paternity in the rock sparrow, whereas male age and phenotype were, at best, fair predictors of paternity.

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Molecular paternity tools have revealed that extrapair paternity is widespread among birds (Birkhead & Møller 1992; Owens & Hartley 1998; Hasselquist & Sherman 2001). Behavioural and experimental studies have shown that females often actively seek extrapair copulations (EPCs; Birkhead & Møller 1993; Gowaty 1994). However, males counter the risk of being cuckolded by adopting strategies that maximize their paternity, namely mate guarding and frequent copulation (Birkhead & Møller 1992). In those species in which some males are polygynous, one may expect males to face a trade-off between paternity assurance and acquiring more than one mate. However, any prediction about the paternity level associated with a male's mating status will rest on (1) the degree to which the female is constrained by her access to extrapair males by her social mate, and (2) the (main) benefit the female stands to gain through her extrapair

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strategy (Gowaty 1996). If females paired to a low-quality male mate with an extrapair male to upgrade the quality of their offspring, we would expect females who are paired with polygynous males to be more faithful than those with monogamous males, since polygynous males are usually the most preferred males in the population (the so-called ‘female choice’ hypothesis, Kempenaers 1994). Evidence that polygynous males are cuckolded less frequently than monogamous males has been reported in the Savannah sparrow, *Passerculus sandwichensis* (Freeman-Gallant 1997). Other studies have shown that polygynous males do not lose paternity more often than monogamous males (e.g. Westneat 1993; Hasselquist et al. 1995; Kempenaers et al. 1995). Comparative evidence suggests that this may be a common pattern among passerines (Hasselquist & Sherman 2001), but a study based on a different methodological approach reached opposite conclusions (Møller & Ninni 1998).

In contrast, if all females are expected to look for extrapair copulations, for example to insure against the infertility (temporary or permanent) of their social

partner, the pattern of the extrapair fertilizations (EPFs) should depend on the different ability of males when guarding their mates. In particular, polygynous males should be less effective in guarding their mates than monogamous males, since they have to divide their time between two mates. Under this scenario, males face a trade-off between acquiring a second mate and protecting their paternity. Tentative support for the so-called 'trade-off hypothesis' (Birkhead & Møller 1992; Soukup & Thompson 1997) has been found in a few bird species, in which socially polygynous males are cuckolded more frequently than monogamous males (Bollinger & Gavin 1991; Dunn & Robertson 1993; Freeland et al. 1995; Soukup & Thompson 1997).

Both the female choice and the trade-off hypotheses make distinct predictions. In particular, the female choice hypothesis predicts that (1) polygynous males should have higher paternity, in both their primary and secondary nests, than monogamous males; (2) EPFs are expected to be more frequent late in the season when the majority of the low-quality males breed; mate guarding should also be more intense late in the season, at least for monogamous males (e.g. Saino et al. 1999); (3) paternity should be unrelated or negatively related to male mate guarding (Møller 1994); and (4) paternity should be independent of the degree of overlap between the fertile periods of the two females paired to a polygynous male (e.g. Møller & Tegelstrom 1997). Using the same line of reasoning, we expect under the female choice hypothesis (5) males with more developed secondary sexual characters (ornaments) to be cuckolded less frequently than males with underdeveloped ornaments (e.g. Saino et al. 1997), and (6) old males to be cuckolded less frequently than young males (e.g. Dunn & Robertson 1993).

In contrast, the trade-off hypothesis predicts that (1) polygynous males are cuckolded more frequently than monogamous males, (2) within polygynous males, paternity decreases with the degree of overlap between the fertile periods of primary and secondary female, and (3) mate guarding should be less intense in polygynous males than in monogamous males. Furthermore, if there is a trade-off between protecting paternity and looking for additional mates (Hasselquist & Bensch 1991), males are expected to invest more time in guarding their mate when the probability of attracting a new mate is low. Since remating opportunities for males are lower late in the breeding season, we can additionally predict that (4) within-pair paternity should be lower at the beginning of the breeding season and increase with the season as remating opportunities decrease. Accordingly, (5) mate guarding should increase late in the season, because polygynous males should allocate more of their time budget to protecting paternity rather than looking for new mates. With respect to age and ornamentation, if old and ornamented males are more likely to be polygynous than first-year and less ornamented males, then (6) we expect a negative effect of age and ornament size on paternity. However, (7) within monogamous and polygynous males old and ornamented males should be cuckolded less frequently, if their ability to guard their mates increases with age and phenotypic quality.

We tested these predictions in an alpine population of rock sparrows, *Petronia petronia*, breeding in nestboxes. In this population, about one-third of the males are polygynous (Pilastro et al. 2001a). Polygyny ranges from perfect contemporary polygyny (i.e. the two females paired to the same male start to lay their eggs on the same day) to successive polygyny, in which primary and secondary female breeding attempts are temporally separated. Males are territorial only at the nest (Cramp & Perrins 1994), and defend one or two nestboxes, by singing and displaying to females. Male rock sparrows have a yellow breast badge, which varies between individuals and does not correlate with age. Correlative evidence suggests that it may signal phenotypic quality. In particular, early breeders and polygynous males have larger badges than late breeders and monogamous males (unpublished data). So this species is an ideal model to test the predictions of the two hypotheses.

## METHODS

### Study Area and Field Methods

Since 1991, a rock sparrow population breeding between 1550 and 1800 m a.s.l. in the Western Alps has been studied using nestboxes and individual colour ringing (Mingozzi et al. 1994; Pilastro et al. 2001a). Nestboxes (11 × 12 cm and 50 cm high) were set up in three small villages. The distance between the two furthest villages was about 2 km. Nestboxes were designed also to work, when necessary, as trapping devices. When such operation did not interfere with nest building or egg laying, we trapped adults within the nestboxes and marked them with aluminium rings and with a unique combination of plastic colour rings. Similarly, chicks were individually marked with colour rings at an age of about 14 days.

Age (first-year or older) was known for those males that were ringed, as young or adults, in previous years. The capture-recapture pattern suggests that adult males are highly philopatric (Tavecchia et al., in press). Since virtually all young are ringed at the nest each year, we assumed that unringed birds that were found breeding were all first-year immigrants. We measured the badge size of males by placing a strip of transparent acetate over the breast, holding the bird on its back, with bill and head perpendicular to the body, and drawing the contour of the yellow patch. We then measured the major and minor axes of the outline by laying the transparent strip on millimetre graph paper. We used the length of the major axis as a measure of badge size. We measured the badge width of 20 individuals twice. The mean difference between the two measures ± SE was  $8.5 \pm 1.92\%$  ( $N=20$ ). Badge width in this rock sparrow population ranges between 9.5 and 17.0 mm (A. Pilastro, unpublished data). As not all males could be captured to measure badge size, sample size varies between analyses.

Capture, ringing and blood-sampling procedures were carried out under permit from the INFS and the Regione Veneto. Disturbance to the adults and nestlings was kept to a minimum (for example in bad weather we avoided capturing the adults) and did not cause any nest failures.

## Behavioural Observations

We checked boxes every 2–3 days, at all stages of the breeding season, to determine pair bonds and the date laying started (Mingozzi et al. 1994). Additional observations were carried out at the nest during early morning and late afternoon in two breeding seasons (1999–2000). We recorded the time spent at the nest (min/h) by the male and female, male song rate (min singing/h), male solicitation rate (solicitations/h) and copulation rate (copulations/h). A mate-guarding index was calculated as the proportion of arrivals to and departures from the nest in which the male was following the female. We assumed that the female's fertile period starts 6 days before the first egg is laid (Birkhead et al. 1989). During this period, we carried out observations on 48 nests, 21 in 1999 and 27 in 2000. Mean observation time per nest  $\pm$  SD was  $2.88 \pm 1.16$  h (range 1–5), for a total of 138 h. Thirty nests belonged to monogamous males, and 18 to polygynous males ( $N=9$  males). The nests of polygynous males were temporally separated (difference in date of start of laying) by on average 16.5 days (range 1–29 days). In the analyses, for polygynous males we used the average values of the behaviours recorded at the two nests.

## DNA Fingerprinting and Paternity Exclusion

In 1997–1999, we took blood from birds by draining 50–100  $\mu$ l from the brachial vein using disposable eparinysed capillaries. In most cases, adults were sampled when feeding young at nest, and the chicks when about 14 days old. The blood samples were each transferred from the capillary into 1.5 ml of buffer solution (0.15 M NaCl, 15 mM sodium citrate pH 7, 10 mM EDTA pH 7.4) and stored at  $-20^{\circ}\text{C}$  until analysed.

We did the paternity analysis according to previous studies (Galeotti et al. 1997; Pilastro et al. 2001b). In brief, total genomic DNA was extracted from blood samples. The blood suspension was incubated overnight with proteinase K at  $55^{\circ}\text{C}$  and RNase at  $36^{\circ}\text{C}$  for 2 h, DNA was extracted with phenol:chloroform and digested with Hae III (New England BioLabs, Beverly, MA, U.S.A.). About 8  $\mu$ g of digested DNA were electrophoresed through a 1.0% agarose gel in  $1 \times$  TBE buffer at 36 V for 120 h. Gels were washed in a denaturing solution (0.5 M NaOH, 1.5 M NaCl) for 30 min and in a neutralizing buffer (0.5 M Tris-HCl, 3.0 M NaCl, pH 7.5) for 30 min. DNA was then Southern blotted on to nylon hybridization transfer membranes (Hyperbond N+, Amersham Biosciences, Uppsala, Sweden). Membranes were hybridized with the Jeffreys' 33.15 probe (Jeffreys et al. 1985), using alkaline phosphatase-labelled oligonucleotide (NICE, Cellmark Diagnostics, Abingdon, U.K.) and a chemiluminescent substrate (Lumi-Phos 530). Membranes were then exposed to standard X-ray films for 24–36 h at  $30^{\circ}\text{C}$  without an intensifying screen.

Bands were scored by two independent observers, one of whom was unaware of the identity of the individual fingerprints. Bands were scored in the 2–23 kb size range. We compared fingerprinting profiles by marking all bands on a transparency film overlay with four

permanent coloured ink pens denoting paternal bands, maternal bands, shared bands and nonattributable (novel) bands. Novel bands are the bands in the offsprings' fingerprinting that are absent in the mother and in the putative father. We considered mismatching bands those that were at a distance of more than 0.5 mm. Band sharing between two individuals was then calculated as  $2b_s/(b_a+b_b)$ , where  $b_s$  is the number of shared bands, and  $b_a$  and  $b_b$  are numbers of bands scored in individuals a and b, respectively (Lynch 1988).

Two criteria are usually adopted for paternity exclusion: a father–offspring band-sharing coefficient value lower than those observed between mother and offspring, and a number of unattributable bands exceeding those expected by mutation alone (e.g. Westneat 1990; Lifjeld et al. 1993; Westneat 1993; Burley et al. 1996; Pilastro et al. 2001b). On average, the number of bands scored per individual  $\pm$  SD was  $23.9 \pm 3.96$ . The mean band-sharing coefficient between mother and offspring  $\pm$  SE was  $0.587 \pm 0.007$  (range 0.278–0.824,  $N=178$ ). One young had a band-sharing coefficient with her mother (0.278) that was distinctly lower than the others. The band sharing with the father was also low (0.286), and could represent a possible case of brood parasitism. Excluding this latter case, the lower first percentile of the mother–offspring band-sharing distribution was 0.371 ( $N=177$ ). Overall, we found 474 unattributable bands, 32 of which were in young with one novel band. We assumed that all novel bands belonging to these young were mutations (Westneat 1993). The probability that a nestling had at least one novel band can then be calculated as 0.33, which in turn gives an estimate of a mutation rate/band=0.014 per generation. With this estimate, the expected probability of observing three novel bands from mutation alone is 0.036, four novel bands 0.012 and five novel bands 0.004. On the basis of these results, we excluded paternity when there were (1) more than two novel bands and (2) a band-sharing coefficient lower than 0.371 with one of the parents.

## Statistical Procedures

To analyse data we used parametric tests when distributions were normal and variances were homogeneous. Proportions were arcsine transformed when used in parametric tests (Sokal & Rohlf 1995). When these assumptions could not be met even after transformation, corresponding nonparametric tests were used. Where not otherwise stated, means  $\pm$  SE are given, and all probabilities are two-tailed. Analyses were performed with SPSS 9 statistical package (Norusis 1993). For nonparametric tests, exact probabilities were calculated with the SPSS /Method=Exact procedure. As some behaviours were not observed in some of the nests (e.g. mate guarding), sample sizes vary between analyses.

## RESULTS

### Mate Guarding, Copulation Rate and Singing Rate

Table 1 summarizes the behaviour of the male and female. Overall, males and females spent  $8.35 \pm 7.56$  min

**Table 1.** Behaviour of male and female rock sparrows at the nest during the female's fertile period

	Monogamous	Polygynous†	<i>U</i> ‡	<i>P</i>
Male at nest (min/h)	8.01±8.06 (30)	9.49±5.83 (9)	109.0	0.40
Female at nest (min/h)	6.36±7.90 (30)	5.47±5.49 (9)	124.0	0.73
Copulation rate (copulations/h)	0.60±0.89 (30)	0.64±0.60 (9)	108.0	0.35
Singing rate (min/h)	3.89±5.25 (29)	7.12±6.66 (9)	79.0	0.08
Mate guarding*	0.64±0.29 (28)	0.33±0.28 (9)	58.5	0.02

Details of behavioural measurements are given in the Methods. Means are given±SD, with sample size in parentheses.

\*Proportion of flights (arrivals to and departures from the nestbox) initiated by the female that were followed by the pair male.

†Data from the two nests averaged.

‡Mann-Whitney *U* test.

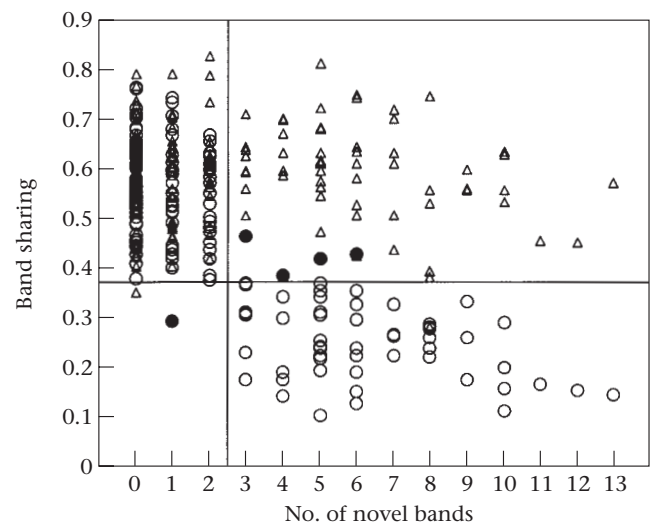
and 6.15 ± 7.36 min at the nest, respectively. Copulation rate was 0.61 ± 0.82 copulations/h and males uttered territorial song at a rate of 4.65 ± 5.69 min/h. On average, 57 ± 31% of the movements were initiated by the female and immediately followed by the pair male (for sample sizes, see Table 1). Behaviour of monogamous and polygynous males did not differ in any respect (Mann-Whitney *U* test: all  $P > 0.3$ ) with the exception of mate guarding, whereas singing rate was only marginally significant. In particular, polygynous males sang at a higher rate and guarded less intensely than monogamous males (Table 1). Mate guarding did not change significantly as the breeding season advanced (Spearman rank correlation: monogamous males:  $r_s = -0.210$ ,  $N = 28$ ,  $P = 0.28$ ; polygynous males:  $r_s = -0.336$ ,  $N = 9$ ,  $P = 0.38$ ; pooled:  $r_s = -0.294$ ,  $N = 37$ ,  $P = 0.08$ ).

### Extrapair Paternity

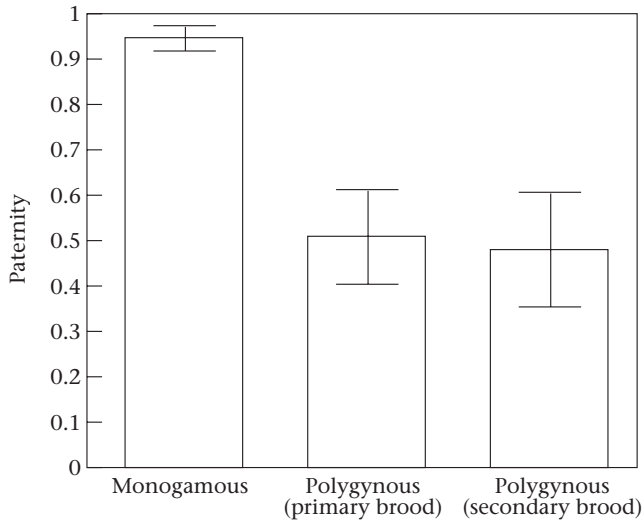
We fingerprinted 42 broods (16 in 1997, 16 in 1998 and 10 in 1999), for a total of 186 young with their social parents. The mean band sharing between father and offspring was 0.460 ± 0.012 (range 0.122–0.764,  $N = 186$ ; Fig. 1). Ten males had two nests within the same year (three in 1997, six in 1998 and one in 1999), whereas only one female had two broods, with two different males in 1998. In two cases we could not capture the female and for these two broods (of four young each) we could only calculate the band-sharing value between the father and the young. In both cases, the father-offspring band sharing was well above the threshold value adopted for paternity exclusion (0.581 ± 0.060, range 0.435–0.638,  $N = 8$ ). We therefore considered these young to be sired by the social father. Overall, 123 young were sired by the social father, 58 were not, and five were not assigned (Fig. 1). Two of the nonassigned young belonged to the same nest, which was therefore excluded from the subsequent analyses. Considering only the young that fully met the paternity inclusion/exclusion criteria, 32.0% (58/181) of the young were extrapair (EPY). Considering the broods, 18 contained no EPY, whereas 24 (57.1%) contained at least one EPY.

Polygynous males suffered a higher proportion of EPY in their broods than monogamous males (Mann-Whitney *U* test:  $U = 64$ ,  $N_1 = 17$ ,  $N_2 = 25$ ,  $P < 0.001$ ; Fig. 2).

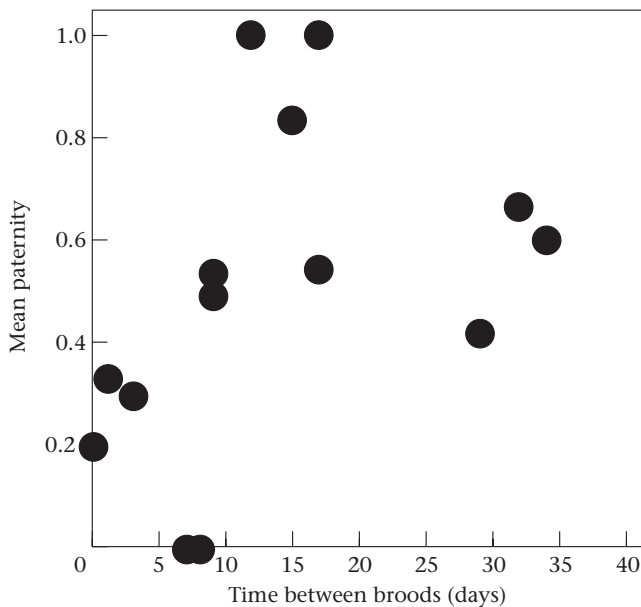
The difference remains significant when only one (primary) brood was considered for polygynous males ( $U = 38$ ,  $N_1 = 17$ ,  $N_2 = 14$ ,  $P < 0.001$ ). For 10 males we had paternity data on both primary and secondary broods. Paternity in the two nests was not correlated ( $r_s = 0.06$ ,  $N = 10$ ,  $P = 0.87$ ) and the difference in paternity between first and second brood was not significant (first: 0.483 ± 0.126; second: 0.448 ± 0.133; paired *t* test:  $t_9 = 0.24$ ,  $P = 0.82$ ). For the six males whose mating status differed between years, paternity was always equal to 1 when they were monogamous, whereas it was on average 0.475 ± 0.097 when they were polygynous (Wilcoxon paired test:  $T = 0.0$ ,  $N = 6$ ,  $P = 0.031$ ). The mean proportion of EPY in polygynous nests was correlated with the degree of overlap of the fertile periods of primary and secondary females (Spearman rank correlation:  $r_s = 0.67$ ,  $N = 14$ ,  $P = 0.008$ ; Fig. 3). Similar results were obtained using the paternity in the first of the two broods ( $r_s = 0.55$ ,  $N = 14$ ,  $P = 0.044$ ), but not in the second ( $r_s = 0.41$ ,  $N = 11$ ,  $P = 0.22$ ).



**Figure 1.** Band-sharing coefficients between parents and offspring ( $\Delta$ : mother-offspring;  $\circ$ : social father-offspring) in relation to the number of unattributable bands. Young in the top-left sector of the plot are classified as legitimate offspring, and those in the bottom-right sector as illegitimate. Five young that did not meet both paternity inclusion criteria were excluded from the analyses ( $\bullet$ ).



**Figure 2.** Mean paternity  $\pm$  SE according to mating status in monogamous ( $N=17$ ) and polygynous (primary broods,  $N=14$ , secondary broods,  $N=11$ ) rock sparrows (1=all young sired by the putative father; 0=all young illegitimate).



**Figure 3.** Mean paternity (1=all young sired by the putative father; 0=all young illegitimate) in broods of polygynous males according to the degree of temporal overlap between primary and secondary brood (days between start of laying of the two broods).

Total paternity loss was observed only in the nests of polygynous males (eight broods). Even if we conservatively assumed that all cases of 100% paternity losses were due to errors of social father assignment, and exclude them from the comparison, polygynous males would still have had significantly lower paternity than monogamous males (Mann-Whitney  $U$  test: monogamous broods:  $0.94 \pm 0.12$ ,  $N=17$ ; polygynous broods:  $0.73 \pm 0.22$ ,  $N=17$ ;  $U=64$ ,  $P=0.002$ ; two broods for the same polygynous male averaged:  $0.69 \pm 0.28$ ,  $N=14$ ;  $U=52$ ,  $P=0.002$ ).

Badge size did not differ between monogamous and polygynous males that were fingerprinted (Student  $t$  test: monogamous:  $13.1 \pm 6.5$  mm,  $N=15$ ; polygynous:  $13.8 \pm 4.6$  mm,  $N=14$ ;  $t_{28}=0.79$ ,  $P=0.44$ ). Paternity did not correlate with male badge size (monogamous:  $r_s = -0.08$ ,  $N=15$ ,  $P=0.78$ ; polygynous:  $r_s = 0.17$ ,  $N=14$ ,  $P=0.54$ ; pooled:  $r_s = -0.05$ ,  $N=39$ ,  $P=0.78$ ). Within monogamous males, first-year birds had a mean paternity of  $0.84 \pm 0.08$ , versus  $0.99 \pm 0.01$  of adult males ( $U=13$ ,  $N_1=5$ ,  $N_2=12$ ,  $P=0.015$ ). Within polygynous males, old males were also cuckolded less frequently (mean paternity  $0.55 \pm 0.09$ ,  $N=13$ ) than first-year males ( $0.0$  and  $0.54$ ,  $N=2$ ). In a two-way ANOVA, the ranks of mean paternity values were significantly associated with male mating status ( $F_{1,31}=39.4$ ,  $P<0.001$ ) and age ( $F_{1,31}=5.70$ ,  $P=0.024$ : model,  $F_{3,31}=20.4$ ,  $P<0.001$ ), but this result is only indicative, since the variances were not homogeneous even after transformation.

We did not find any significant correlation between laying date and paternity in monogamous males ( $r_s = -0.13$ ,  $N=17$ ,  $P=0.62$ ). In contrast, we found an effect of the season on paternity in polygynous males where earlier broods had higher levels of EPP ( $r_s = 0.58$ ,  $N=15$ ,  $P=0.025$ ). The relation remained significant when the overlap between the fertile periods of primary and secondary females and date were entered in a multiple regression analysis where the ranks of the original variables were used (multiple regression:  $F_{2,13}=10.8$ ,  $R^2=0.60$ ,  $P=0.003$ ; date:  $\beta=0.66$ ,  $P=0.003$ ; overlapping:  $\beta=0.49$ ,  $P=0.018$ ).

Polygynous males had a higher annual fledging success ( $7.20 \pm 0.66$ ,  $N=13$ ) than monogamous males ( $4.53 \pm 0.35$ ;  $U=52$ ,  $N=17$ ,  $P=0.003$ ). Once corrected for paternity, within-nest yearly reproductive success (number of young sired/year) did not differ significantly with male mating status (monogamous males:  $4.27 \pm 0.35$ ,  $N=17$ ; polygynous males:  $3.42 \pm 0.31$ ,  $N=13$ ;  $U=80$ ,  $P=0.07$ ).

## DISCUSSION

The pattern of EPP we found is consistent with the trade-off hypothesis (Soukup & Thompson 1997), since four out of five predictions that can be made under this hypothesis were met. First, polygynous males were cuckolded more frequently than monogamous males. This was confirmed in the six cases in which we could compare the paternity of the same male between years in which he had different mating status. In eight nests, all of them belonging to polygynous males, all young were EPY. We are confident that these were not due to an erroneous assignment of the brood to the social father or to rapid mate switching. Males were considered to be the social father of a brood when they were observed to sing and defend the nestbox in which the clutch was laid, during the fertile period of the female. In this respect, monogamous and polygynous males did not differ in the time spent on the nestbox during the fertile period (Table 1). In any case, polygynous males had significantly lower paternity even excluding broods with total paternity loss.

Second, within polygynous males, paternity decreased significantly as the overlap between the fertile periods of their females increased. Total loss of paternity in at least one of the two broods was observed only when the fertile period of primary and secondary females overlapped to some extent. Third, behavioural observations indicate that monogamous males guarded their mates more intensely than polygynous males. This pattern is similar to that found, for instance, in the great reed warbler, *Acrocephalus arundinaceus*, in which polygynous males guard their mates less intensely (Hasselquist & Bensch 1991). However, in that species, polygynous males do not lose more paternity than monogamous ones (Hasselquist et al. 1995).

During the fertile period, male rock sparrows spent on average 8–9 min/h at the nest, most of the time singing, and polygynous and monogamous males did not differ in this respect. A trade-off between mate guarding and nest guarding has been shown in other passerines (e.g. Schleicher et al. 1993; Meek & Robertson 1994). In the rock sparrow, however, territorial activity was not reduced in polygynous males, possibly because of the risk of being replaced by another male. Polygynous males apparently did not compensate for their reduced mate guarding by copulating more frequently (Birkhead & Møller 1992), since copulation rate at the nest did not differ with mating status. This is the first time, to our knowledge, that an evidence of a trade-off between paternity and mate guarding has been found.

The fourth prediction of the trade-off hypothesis, that early broods have lower paternity because mating opportunities for males are higher at the beginning of the season, was also confirmed, but only in polygynous males. This implies that polygynous males invested less in mate guarding early in the season. However, this does not seem to be the case, since mate guarding was not significantly correlated with date, and the tendency, if any, was for it to decrease as the breeding season advanced. Thus, the seasonal pattern of EPP was apparently not due to males trading guarding their mates against attracting additional mates (e.g. defending additional nestboxes). A possible explanation may be that females have fewer opportunities to engage in EPCs late in the season and males consequently allocate less effort to guarding their mates.

Whereas male mating status was a strong predictor of cuckoldry rate, male phenotype (badge size) was not associated with EPP, even when controlling for male mating status. This is similar to what has been reported for the house sparrow, *Passer domesticus*, where either male bib size does not predict EPP (Wetton et al. 1995; Cordero et al. 1999; Whitekiller et al. 2000) or large-bibbed males are cuckolded more frequently than small-bibbed males (Griffith et al. 1999). Rock sparrow males that were at least 2 years old were cuckolded less frequently than first-year males. However, the effect of male age on EPP was minor compared with the effect of social status. In both monogamous and polygynous groups, older males had an EPP rate that was about 10% lower than that of first-year males, whereas male social status accounted for a difference of EPP of about 45%. This

result may be because older males are better at protecting their paternity than first-year males (Møller 1987; Grant & Grant 1989). The pattern of EPP in relation to male badge size is in agreement with the trade-off hypothesis whereas both hypotheses predict that paternity should increase with age.

We are aware of three other studies in which EPP has been suggested as a cost of polygyny, but the evidence is either incomplete (e.g. mate-guarding data are lacking) or not fully supported from a statistical point of view (Bollinger & Gavin 1991; Freeland et al. 1995; Soukup & Thompson 1997). Bollinger & Gavin's (1991) study on bobolinks, *Dolichonyx oryzivorus*, did not give any measure of mate guarding. In the house wren, *Troglodytes aedon*, secondary, but not primary, nests of polygynous males are cuckolded more frequently than those of monogamous males (Soukup & Thompson 1997). This could be influenced by secondary females that engage more frequently in EPC to obtain benefits from neighbouring males and not by a trade-off between mate guarding and acquiring a second mate. Furthermore, a trade-off would exist only if males acquiring a second mate risked losing paternity in both broods. In a third study on willow ptarmigan, *Lagopus mutus* (Freeland et al. 1995), although the data presented were in agreement with the trade-off hypothesis, they were statistically significant only when the young (and not the broods) were taken as statistically independent observations, which is clearly not the case.

The bird species for which the strongest association between polygyny and paternity loss has been found is the tree swallow, *Tachycineta bicolor* (Dunn & Robertson 1993). In this species, polygynous males have a breeding success that is about a third that of monogamous males, but the estimate of EPP rate of polygynous males was based on five males only and may need to be confirmed on a larger sample.

Our results leave two questions unanswered: what are the benefits of EPC for rock sparrow females, and why should rock sparrow males engage in polygyny if their breeding success is no greater than that of monogamous males? Several direct benefits have been proposed for female EPC in birds (Westneat et al. 1990; Birkhead & Møller 1992; Jennions & Petrie 2000). Our results suggest that female rock sparrows are not engaging in EPC to upgrade their social mate choice, but we did not have any evidence of direct benefits. From a male's perspective, polygyny may not be adaptive, but instead may be the result, for instance, of an unnaturally low density of suitable nesting sites which allows competitive males to exclude other males from reproduction and forces females to mate polygynously (polygynously mated females have a lower breeding success, T. Mingozzi, unpublished data); polygyny may also be facilitated by the synchronous breeding season in this alpine population (Pilastro et al. 2001a). Alternatively, polygynous males may be more likely to sire young in other males' nests than monogamous males, as shown in the starling, *Sturnus vulgaris* (Smith & Sandell 1998). An inclusion paternity study is needed to improve our estimate of male reproductive success.

## Acknowledgments

We thank Guglielmo Marin for allowing us to use his laboratory for paternity analyses. Jonathan Evans, Guglielmo Marin, Giuliano Matessi, Wolfgang Forstmeier and an anonymous referee made constructive comments on the manuscript. We thank Anna Pagliani, Laura Senese and Claudia Callegarin for their help with the paternity analyses, and Nicoletta Fedreghini and Cristina Terzolo for their help in the field. We thank Luigi Poncet for his kind hospitality during the fieldwork. This study was partly supported by grants from the University of Padova (Ex60% 1999, 2000) and the MURST (Cofin1999).

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