Female brood desertion increases with number of available mates in the Rock Sparrow

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We studied the reproductive strategy of a Rock Sparrow Petronia petronia population, breeding in nest boxes in the Western Alps (Italy). Over seven years of study (1991–1997) 19% of the females laid second clutches after successfully fledging the first one. Among these, about 50% deserted the first nest when nestlings were 14.3 d old (range 8–19 d), 3.6 d before fledging (range 1–8 d). In all these cases the primary male mate took over all parental duties and successfully reared the young. Inter-clutch time of deserting females was 8.1 d shorter than that of non-deserting double-brooded females. The breeding success of deserting females was significantly greater than that of both single-brooded females and double-brooded females that did not desert their first brood. The fledging success of the second clutches depended on the status of the secondary male: females paired with previously unpaired males had a higher fledging success than those that paired with a polygynous male. The frequency of deserting females varied among years from 0 to 16%, and was significantly and positively correlated with the frequency of males available as mates at the time of desertion. In this study we showed that sequential polyandry with brood desertion is a regularly occurring strategy in the female Rock Sparrow.

Among birds, the most common mating system is monogamy, and usually both parents take care of the young (Lack 1968). However, whenever ecological conditions allow the offspring to be raised by a single parent, selection may favour clutch or brood desertion by one of the parents, if this enhances its opportunity to find a new mate and increases its reproductive success (Lack 1968, Pitelka et al. 1974, Oring 1986, Székely and Williams 1995, Székely et al. 1996). In birds, the usual pattern is that the male deserts the offspring, and looks for a second female. In far less numerous cases, the deserting gender is the female. Consequently, polyandry is less common than polygyny (Reynolds and Székely 1997).

Female clutch or brood desertion, associated with male uniparental care and sequential polyandry (i.e. the female lays separate, successive clutches with different males in the same breeding season), occurs mainly in shorebirds (Székely et al. 1996). It is commonly thought that polyandry and exclusive paternal care in shorebirds have evolved as a consequence of ecological conditions characterised by short breeding seasons, abundant food, and strongly male-biased operational sex ratio late in the breeding season (Whitfield and Tomkovich 1996). Another characteristic of shorebirds is that they have precocial young. Comparative analysis suggests that female brood desertion and exclusive male parental care are significantly associated with young precociality (Temrin and Tullberg 1995).

Among passerines, which all have altricial young, although mate switching is frequent in several species (Black 1996), female brood desertion and male uniparental care are very rare (Lack 1968, Oring 1986). One special case is the Penduline Tit Remiz pendulinus, a species with uniparental care, where either the male or the female deserts the brood soon after the eggs have...
been laid (Persson and Öhrström 1989). Female brood desertion has been described in detail in another two species (Middleton 1988, Hasselquist and Langefors 1998). We report here the case of a fourth passerine, the Rock Sparrow Petronia petronia, in which females, the gender which usually carries out most or all parental care, adopt brood desertion and sequential polyandry as a regularly occurring strategy. In the course of a study on the ecology and breeding biology of a northern, alpine population (Mingozzi et al. 1994), we gathered information on the occurrence of female brood desertion over seven years. In this paper we describe the modality of clutch desertion, and analyse the reproductive success of females adopting alternative mating strategies. We then relate the yearly frequency of female brood desertion in our study population to the availability of males not engaged in mate guarding or feeding young at the time females desert their brood, in order to see whether the decision to desert is influenced by the availability of male mates.

Materials and methods

Since 1991, a Rock Sparrow population breeding between 1550 and 1800 m a.s.l. in the Western Alps has been studied using nest boxes and individual colour ringing (Mingozzi et al. 1994). A total of 39 nest boxes (11 × 12 × 50 cm) were set up in three small villages. The distance between the two furthest villages was about 2 km. Nest boxes were designed also to work, when necessary, as trapping devices. Adults trapped within the nest boxes were marked 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 13 days. Boxes were checked every 2–3 days, during all stages of the breeding season. Observations were made at each nest box to determine pair bonds and the feeding activity of parents (Mingozzi et al. 1994). In total, 77 females and 66 males were ringed and observed during their breeding attempts. During seven breeding seasons (1991–1997), we recorded 212 breeding attempts (at least one egg laid). In 139 of these the identity of the female was known. Clutches were classified as first, second (i.e. clutches laid after the first brood fledged successfully) or replacement clutches (i.e. clutches laid after the first or the second clutch failed). We did not measure quantitatively the extent of parental care carried out by each parent for the entire study period. However, because nests were checked every 2–3 days, we could record which parent was observed to feed the young in the nest.

To test the hypothesis that the females’ decision on whether to desert or not depends on the number of available partners, we calculated the yearly number of potential male mates available at the time of desertion, divided by the total number of territorial males. We considered as potentially available mates, territorial males that had not yet been able to attract a mate, those that had lost their first brood, and those that had already completed their first brood and were not engaged in a second breeding attempt. We excluded floaters, since females never nest in boxes not occupied by a territorial male (T. Mingozzi, pers. obs.). All desertions occurred between 12 and 25 July. The proportion of males potentially available as mates was calculated as the mean proportion observed in the period comprised within ± 1 s.d. of the mean desertion date (200.9 ± 4.38 d; 1 January = 1). This choice was based on the following assumptions: (a) the proportion of available mates varies unpredictably over a few days, being influenced by nest failure; (b) the females that are going to lay a second clutch evaluate whether to desert or not, once young are able to thermoregulate, since males never brood either eggs or young (T. Mingozzi, pers. obs.). We may therefore reasonably expect that females assess the opportunities of remating at, or just before, the developmental stage at which young could be raised successfully by their deserted male alone.

Where necessary, homogeneity of variances was attained by log transformation (Levene test for homogeneity of variance, p < 0.05). In a few cases, nests were found when the female had already completed egg laying, or the exact number of young that had successfully left the nest was unknown. Therefore, sample sizes varied according to the analyses. If not otherwise stated, means ± s.d. are given. All probabilities are two-tailed.

Results

Of the total 139 breeding attempts of known females, 100 (71.9%) were classified as first clutches, 17 (12.2%) as replacements of a first clutch, 19 (13.7%) as second clutches, and 3 (2.2%) as replacements of a second clutch. The difference in laying date between the earliest and the latest clutch was 68 days, and 50% of the first clutches were laid between 12 and 20 June. Among the 19 second clutches, 18 were laid after a successful first brood, and one after a successful replacement of a very early clutch deserted at the stage of two eggs. Overall, 87 first clutches and 13 replacements of the first clutch were successful. Thus, 19% of the females were able to lay a second clutch after successfully rearing a first brood. In 10 of the 19 second clutches, the females abandoned the young in their first nest and re-mated with another male. In all these cases the deserted male took full care of the young, all of which left the nest successfully. In the remaining 9 second clutches, the female did not desert the brood but shifted mate be-
tween the first and second breeding attempt in five cases and re-nested with the same male in four cases.

Females that deserted their first brood stopped feeding their young 3.9 ± 1.8 d before the young left the nest (range = 2–7 d) and started laying the second clutch 0.5 ± 3.9 d before the young of the first brood fledged (range from 8 d before to 4 d after they fledged). Age of young at desertion was 14.3 ± 3.5 d (range 8–19 d). For deserting females, inter-clutch time (i.e. days elapsed between start of laying of first and second clutches) was 36.9 ± 9.1 d (range 29–44 d), 8.1 d shorter than that for non-deserting double-brooded females (45 ± 5.3 d, range = 39–55 d; t_{16} = 3.53, p = 0.003).

Breeding success of first and second clutches

Clutch size varied significantly between groups (ANOVA, F_{2,116} = 5.47, p = 0.005). Second clutches of non-deserting females contained fewer eggs than first clutches, whereas second clutches after desertion were intermediate (Scheffé test for multiple comparisons, p < 0.05, Fig. 1a). There was also significant variation between groups in number of young fledged (ANOVA, F_{2,116} = 6.93, p = 0.001), with significantly fewer young fledging from second clutches of non-deserting females than from both first clutches and from second clutches of deserting females (Scheffé test for multiple comparisons, p < 0.05 in both cases, Fig. 1b). In contrast, there was no difference in number of young fledged between first clutches and second clutches after desertion. Similarly, the frequency of successful broods (i.e. broods that fledged at least one young) differed significantly among clutches (\( \chi^2 = 11.39, df = 2, p = 0.004 \)). In particular, the frequency of successful broods in first clutches was significantly higher than in second clutches (\( \chi^2 = 11.09, df = 1, p = 0.001 \)), but not higher than in second clutches after desertion (\( \chi^2 = 1.05, df = 1, p = 0.31 \), Fig. 1c).

Breeding success of second clutches was associated with the status of the new male mate. Seventy percent of the second clutches laid by females in the nest of a previously unmated male were successful (n = 10); this proportion dropped to 22% in second clutches laid in the nest of an already mated male (Fisher exact test, p = 0.02). Similarly, considering only clutches of deserting females, these proportions were 100% (n = 5) and 20% (n = 5), respectively (Fisher exact test, p = 0.048).

The groups of females also differed in the number of young fledged per year (one-way ANOVA on log-transformed values, F_{2,85} = 7.75, p = 0.001). In particular, females deserting their first brood reared more young per year (8.50 ± 2.95, n = 10) than both successful single-brooded (4.97 ± 1.49, n = 69) and non-deserting double-brooded females (5.33 ± 2.45, n = 9), whereas the latter two groups did not differ from each other (Scheffé post hoc test, p < 0.05).

Frequency of female brood desertion in relation to the proportion of available male mates

The proportion of available mates at the time of desertion ranged over the seven years of study between 19 and 43.2% of the territorial males (mean = 26.6 ± 9.0). The number of deserting females relative to the total number of females that successfully raised their first brood ranged between 0 and 16% (mean = 10.6 ± 5.7). The frequency of deserting females was strongly and positively correlated with that of males available (\( r_s = 0.88, p = 0.008, n = 7 \), Spearman rank correlation). An equivalent result was obtained using the absolute numbers of deserting females and available male mates (\( r_s = 0.86, p = 0.013 \), Fig. 2).
Discussion

In this study we showed that sequential polyandry with brood desertion is a regularly occurring strategy in the female Rock Sparrow. In six of the seven years of the study we observed at least one case of female brood desertion. Considering only females that laid a second clutch, about 50% deserted their first brood and social mate. females adopting brood desertion had a much higher yearly breeding success (expressed as number of young fledged) than non-deserting females. Despite being cared for by the male alone, the survival rate of female-deserted young after fledging was not lower than that of young not deserted by their mother. Local recruitment rate was 30.4% for young of deserting females, 18.2% for successful single-brooded females and 22.7% for double-brooded non-deserting females (T. Mingozzi et al. unpubl. obs.). The greater annual reproductive success of deserting females may be due to several factors. First, deserting females start to lay their first clutch about one week later than non-deserting double-brooding females, when environmental conditions are probably less harsh. A slightly delayed start of breeding may result in deserting females having to invest less to successfully raise their first brood. They may therefore be in better condition when raising their second brood. A second reason for their greater overall success may be better physical condition when raising their second brood resulting from reduced parental investment in young of their first brood. Finally, deserting females may be mated to males whose condition is higher than average, and which are able to fully compensate for female desertion. The role of the male in determining the fledging success of second broods seems evident, since male mating status was significantly associated with nesting success in second broods.

Our observed frequency of brood desertion was intermediate between that reported for the American Goldfinch Serinus tristis (Middleton 1988) and the Sedge Warbler Acrocephalus schoenobaenus (Hasselquist and Langefors 1998), two other passerine species in which females may desert their first brood before laying a second clutch (71% and 33% of double-brooded females, respectively). In these three species, the male does not incubate eggs or brood young, and desertion apparently occurs only when the nestlings are well developed (in the Rock Sparrow when they are at least 8 days old). These three species have in common a relatively low proportion of double-brooding females (6.4% in the Sedge Warbler and about 20% in the American Goldfinch and Rock Sparrow). Remating opportunities for early breeding females that desert their first brood are therefore expected to be higher than for males. This scenario is similar to that commonly thought to underlay the evolution of sequential polyandry and male uniparental care in shorebirds. In the Kentish Plover Charadrius alexandrinus, removal experiments have shown that remating opportunities are higher for females, since the operational sex ratio (OSR) is male-biased in this species (Székely 1996, Székely et al. 1996). This result led Székely et al. (1999) to suggest that the high remating opportunities for females might have favoured the evolution of male uniparental care in shorebirds. However, several studies of sequentially polyandrous shorebird species have found either no bias or a female-biased OSR (reviewed in Balshine and Blomqvist 1999). Thus, the role of the OSR in the evolution of the breeding system in birds remains debated. Our observations on the Rock Sparrow support Székely et al.’s (1999) view that a male-biased OSR promotes this alternative female breeding strategy. The female-biased OSR observed in some polyandrous bird species may be a condition derived, over evolutionary times, from an originally male-biased OSR, as the frequency of deserting females increases.

Female brood desertion in the Penduline Tit, the third passerine species where females are known to desert their clutch because the male can take over all parental duties (Persson and Öhrström 1989), has probably evolved in another context. This species shows exclusively uniparental care, and either the male deserts the clutch after the female starts to lay the eggs, or the female deserts when the clutch is completed. Time and energy investment for the construction of the nest, carried out by the male only, is very high and probably matches the female’s investment for producing the clutch. Moreover, the species has a rather prolonged breeding season, which increases the opportunity for a female to lay several clutches and for a male to find a new mate. Thus, the sexes probably have similar opportunities/costs for desertion (Valera et al. 1997). Another passerine species which has been reported to show sequential polyandry is the White-plumed Antbird...
*Pithys albifrons*, where the female leaves her mate, who, unaided, cares for the single young while she searches for a new mate (Campbell and Lack 1985). Unfortunately, quantitative information on the breeding biology of this species is lacking.

The conditions that probably promoted the evolution of female brood desertion in the Rock Sparrow are widespread among passerines, in particular among long-distance migrant species and species/populations living in northern latitudes or at high altitudes. We would not be surprised if a more thorough examination of breeding systems of other passerine species will reveal this female reproductive strategy to be more common than previously thought.

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**References**


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