Female Extra-Pair Behaviour and Environmental Quality in the Serin (Serinus serinus): A Test of the 'Constrained Female Hypothesis'

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Female extra-pair behaviour and environmental quality in the serin (*Serinus serinus*): a test of the 'constrained female hypothesis'

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Recent behavioural and molecular studies have shown that in most monogamous bird species extra-pair copulations and fertilizations outside the pair bond occur routinely. The consequences of female extra-pair behaviour might comprise effects on important life-history traits, such as the extent of male parental care. In this study we test the assumption that, within a species, females' options for extra-pair mating depend on female quality and the environments that females occupy. This 'constrained female hypothesis' predicts that females in good environments or high-quality females are able to resist males' control efforts better than females in poor environments or low-quality females. We test the idea in the socially monogamous serin. We found that the likelihood of extra-pair paternity is significantly higher in territories with high availability of food. There was a negative relationship between environmental quality (food availability) and paternity both in natural and in experimentally manipulated habitats. Male feeding rates were negatively related to food availability and positively related to paternity. These data and the additional result that in better environments all of a females' offspring were sired by one extra-pair male provide support for Gowaty's 'constrained female hypothesis'.

Keywords: extra-pair paternity; DNA fingerprinting; food availability; environmental quality; parental care; 'constrained female hypothesis'

1. INTRODUCTION

Recent behavioural and molecular studies (reviewed in Birkhead & Møller 1992; Birkhead 1998) have defeated the assumption that monogamy implies an exclusive mating relationship between two individuals. In most bird species extra-pair copulations and fertilizations outside the pair bond can be observed regularly (Birkhead & Møller 1996). In most bird species, females seem to control the success of a copulation attempt and it is obvious that females seek extra-pair fertilizations for different reasons, namely to improve the genetic quality of their offspring, to reduce the costs of mate loss or to gain direct benefits (see Petrie & Kempenaers 1998). The occurrence of extra-pair fertilization depends on the costs and benefits of this female behaviour and on the efficiency of male counter-strategies to avoid losing paternity. An outcome of this female extra-pair behaviour might comprise consequences for important life-history traits, such as the extent of male parental assistance (Birkhead & Møller 1992; Møller & Birkhead 1993; Birkhead 1998). A positive relationship between male parental care and paternity depends on the costs and benefits of reducing parental care and the availability of reliable paternity cues to the male. So far, paternity cues have been found in only a few cooperatively breeding species (Davies 1992; Hartley *et al.* 1995). Furthermore, the effect of male parental care on female reproductive success is variable both within most

populations (see, for example, Duckworth 1992; Dunn & Hannon 1989, 1992) and between populations (see, for example, Beletsky & Orians 1990); therefore the male parental care hypothesis (meaning that females always fail without male assistance) is probably not a sufficient explanation for the occurrence and distribution of extra-pair young in socially monogamous birds (Gowaty 1996). This also applies to the two other main hypotheses, the resource distribution hypothesis (Orians 1969) and the female–female aggression hypothesis (Gowaty 1980) explaining the evolution of social monogamy in birds (Gowaty 1996). The resource distribution hypothesis states that when resources necessary for reproduction are distributed so that it is impossible for one male to defend adequate resources for more than one female, males are constrained to social monogamy. This idea has been tested in socially polygynous species (see, for example, Björklund & Westman 1986), elaborated to explain other mating systems besides social monogamy and social polygyny (Davies 1991; Bensch & Hasselquist 1991), and tested also in typically socially monogamous species (see, for example, Gowaty 1980; Veiga 1992). The female–female aggression hypothesis states that males might be constrained to social monogamy because any additional females attracted to a male's territory might be inhibited from settling by the aggression of an already resident female (see also Slagsvold *et al.* 1992; Veiga 1992).

Wittenberger & Tilson's (1980) original hypotheses for social monogamy provide a good condition for making assumptions about why males and females should alter

their choice of partner. If the parental assistance of both male and female is essential to rear any offspring, each sex has similar interests and therefore the costs of extra-pair copulations for females outweigh any possible benefits. Although sexual and social monogamy correspond in those species, observational evidence for a conflict of interests between males and females concerning female copulation behaviour can be observed in other species. Females seem to be able to balance costs and genetic benefits by controlling the paternity of their offspring (Birkhead & Møller 1993; Birkhead *et al.* 1993; Lifjeld *et al.* 1994). In a few species males seem to be able to control females by making extra-pair copulation too costly for females to initiate, but resulting in a situation in which forced extra-pair copulation by males occurs routinely (see, for example, McKinney *et al.* 1983).

A theory of coevolutionary selective pressures acting on males for the control of females' reproductive capacities and on females for resistance to males' efforts to control them proposes that social monogamy will often be genetic polyandry (Gowaty 1996). This 'constrained female hypothesis' is in line with initial studies of sperm competition (see, for example, Parker 1970) and subsequent studies (see, for example, Briskie & Montgomery 1992). However, it is Gowaty's assumption that it is female quality, or the quality of the environment that females are in, that determines levels of extra-pair paternity that is new and unique to this hypothesis. The 'constrained female hypothesis' predicts genetic mating patterns of socially monogamous females and describes the relationship between female fitness as a function of interactions between female quality and environmental quality. The model says that females of poorer quality or in less permissive environments are more vulnerable to manipulation by male helpful coercion than are females of higher quality or those in highly permissive environments. In other words, low-quality females have more to lose if male help is withdrawn and females with the most to lose from the withdrawal of male help should be the most highly constrained and, thus, are coerced by males. Specific predictions of the hypothesis are (i) that high-quality females or females in good environments are more likely to produce extra-pair offspring, and (ii) that higher-quality females or females in better environments will be more likely to be genetically monogamous, whereas lower-quality females or females in poor environments who have extra-pair offspring will be genetically polyandrous.

Here we test these specific predictions in the socially monogamous serin, *Serinus serinus.* In the study area, which is outside the main spreading area, this passerine breeds in a situation amenable to studying the following relationships: (i) male parental feeding rates and paternity, (ii) environmental quality (food availability) and paternity, and (iii) environmental quality and male parental feeding rates. Because male serins try to become polygynous (J. C. Senar, personal communication), we would further predict that they adjust their parental care in relation to their need against further mating opportunities (Hoi-Leitner *et al.* 1999).

2. METHODS

(a) *Study area and species*
We conducted the study during the 1995, 1996 and 1997 breeding seasons in the province of Jaén (37°52′ N, 3°55′ W), in southern Spain. The study sites are intensively cultivated olive orchards of a very uniform structure, interrupted only by some gravel roads and small patches of dry herbaceous and shrub vegetation. Olive trees are planted at regular intervals of 10 m; vegetation cover on the ground is very low. Depending on cultivation intensity and technique the vegetation cover on the ground can be evenly distributed as well as clumped (Valera 1992). This herbaceous layer consists mainly of weeds, dominated by *Diplotaxis virgata, Erodium malacoides* and *E. cicutarium*, which are the basis of the diet of serins in this area (Valera 1992; Valera *et al.* 1997).

The serin is a socially monogamous passerine that in its breeding distribution shows a marked preference for mosaic patterns of vegetation of diverse spacing and composition (Cramp 1985). Nest-building is performed mainly by the female, which also incubates and broods (Cramp 1985). Both sexes feed the young and the male feeds the female during incubation (M. Hoi-Leitner, H. Hoi and F. Valera, unpublished results). In the study area the distances between nests averaged 87 m. We chose a circle of 300 m around each nest site for the estimation of habitat quality, because in poor-quality territories parental foraging ranges are not restricted to the immediate area around the nest site.

(b) *Fieldwork*
Starting at the end of February we systematically searched the study sites for nests, which were mapped; we noted the breeding states of the different pairs. Adult birds were provided with an aluminium ring and individually colour-ringed, blood-samples were taken and the birds were followed up over the rest of breeding. We provided nestlings with an aluminium ring and took blood samples when nestlings were eight days old. For the investigation of chick development we measured several morphological variables including weight, tarsus length and wing length at the age of four, seven and ten days. We collected data on parental feeding frequencies and paternity from 17 pairs in 1995, ten pairs in 1996 and 20 pairs in 1997. We measured parental care using focal sampling during 1 h periods on a daily basis throughout the feeding phase. This yielded information on the absolute rate at which males and females brought food to the nestlings. Because we also measured the number of feeding visits of the female, the feeding frequency of the male could additionally be expressed as a percentage of the total number of feeding visits. We did behavioural observations during the morning hours (08.00–11.00) and changed the order of observations on the various individuals from day to day. We gathered between three and four sampling periods per nest starting at a nestling age of four days. We found no significant variation in feeding rates between sampling periods for each nest (repeated measurements analysis of variance: $F = 1.6, p > 0.2$, d.f. $= 2{,}92$), which suggests that there is no relationship between nestling age and feeding rate.

Because serins feed their chicks exclusively with fresh seeds of mainly *Diplotaxis* sp. and *Erodium* spp. (Valera 1992; Romero Pujante 1995; Valera *et al.* 1997), we measured food plant abundance around nest sites at two times (during nest building and during chick feeding). Information about differences in food plant abundance was obtained by the line intercept method (Smith 1984). Eight 300 m transects were laid in different directions starting from the nest site. The first transect was established at random and the rest were each separated by 45°. We recorded the expanse of the different plant species along the transects. For calculation of the cover by the food plants we summarized the number of metres for each species over all transects of a nest site. From these data we calculated

the following food plant index: $100 \times$ (total intercept length of food plants)/(total transect length). We found no relationship between habitat quality and the density of bird nests (serins: $r_S = 0.14$, $p > 0.5$, $n = 22$; other species: $r_S = 0.25$, $p > 0.2$, $n = 22$).

We performed habitat manipulations during the fertile phase of the females (i) by offering food plants (*Diplotaxis* sp. kept fresh in water containers) within a circle of 10 m around the nest site in territories with low availability of food plants, and (ii) by removing (mowing) all food plants within 300 m around nest sites in territories with high availability of food plants. A total of 20 territories were manipulated in this way (11 experiments with food decrease: five in 1995 and six in 1997; and nine experiments with food increase: four in 1995 and five in 1997). A total of 25 unmanipulated nests were chosen at random. For the experimental treatments particular territories were chosen as stated above. We found no significant difference in egg-laying dates between nests in the two experimental treatments and in the unmanipulated controls (Mann–Whitney *U*-test: $z = 0.87$, $p > 0.4$, $n = 11,9$). Breeding synchronization index (see Kempenaers 1993) was calculated for females within a radius of 300 m around the focal female. There was neither a difference in laying dates in each of the three years (Kruskal–Wallis test: $T = 1.4$, d.f. $= 2$, $p > 0.1$) nor in breeding synchronization between years ($T = 1.2$, d.f. $= 2$, $p > 0.4$).

(c) *DNA fingerprinting*

Our fingerprinting analyses followed standard techniques described by Epplen & Zischler (1990). DNA was digested with *Hae*III, separated by agarose gel electrophoresis, transferred to a nylon membrane by Southern blotting and hybridized with a digoxigenin-labelled oligonucleotide $(GATA)_4$ probe. We scored an average $\pm$ s.d. of 21 ± 2.3 bands in the 3.0–23 kb range. For parentage assignment we used the procedure described by Westneat (1990). For each family we assessed the proportion of band sharing between the adults and between putative mother–young and putative father–young, respectively. For each young we also measured the number of novel bands (bands found in the nestlings' DNA profile but not found in the DNA profile of putative parents). We followed the method of Westneat (1993) to set a statistical limit to the number of novel bands that has arisen from mutations or scoring errors and to set 99% confidence limits to band sharing between parents and offspring. The estimated probability of finding one novel band per individual was 0.092 (14 of 153 individuals). The probability of finding two novel bands per individual from random processes alone was therefore 0.0084, three novel bands 0.00076 and four novel bands 0.00007. For a sample size of 153 the expected number of individuals with two, three and four novel bands was 1.3, 0.1 and 0.01, respectively. We found similar values in the serin (one individual with two novel bands and zero with three and more novel bands). Nestlings with zero or one novel band shared, on average (s.e.), 0.61 ± 0.06 of their bands with each parent. The lower 99% confidence limit of this distribution was 0.49, whereas the upper 99% confidence limit for unrelated parents ($n = 74$) was 0.48. Therefore 0.48 was used as the expected upper limit for band sharing between illegitimate offspring and mismatched parents.

Parametric tests were used only when assumptions for normality were met. Tests were two-tailed throughout.

3. RESULTS

(a) *Paternity*

DNA fingerprinting analysis revealed that 19.2% of all nests ($n = 47$) contained at least one nestling not related to the attending male. In 14.9% of all nests at least one chick
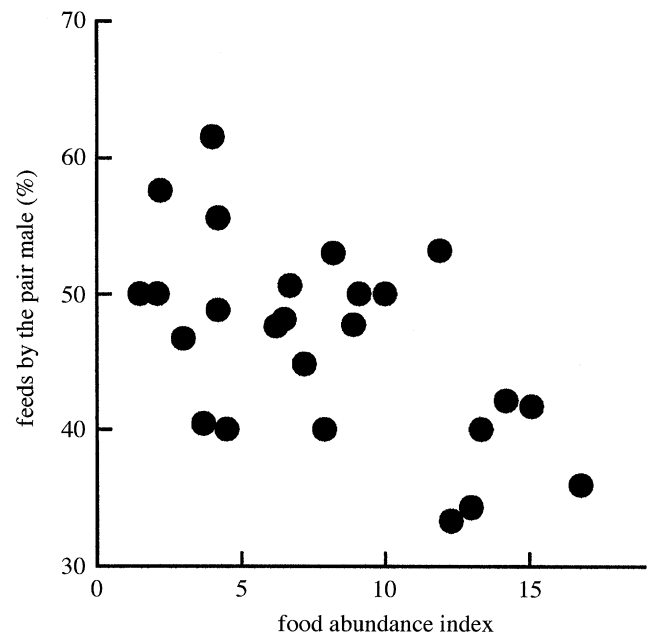
Figure 1. Relation between food availability (expressed as food abundance index) around the nest site, and percentage of feeds by the male of each pair.

was fathered by an extra-pair male and an additional 4.3% of all nests contained nestlings resulting from intraspecific brood parasitism; 9.4% of all nestlings ($n = 139$) were fathered by an extra-pair male and 1.4% of all nestlings were cases of intraspecific brood parasitism. Five nests contained one extra-pair fathered young and in two nests, four out of four nestlings resulted from extra-pair paternity.

(b) *Parental effort and food availability*

There was no significant relation between food availability and clutch size ($r = 0.34$, $p > 0.08$, $n = 25$) as well as number of fledglings ($r = 0.26$, $p > 0.1$, $n = 25$). Male feeds were related neither to clutch size (male feeds per nest, $r = -0.17$, $p > 0.3$, $n = 25$; percentage of feeds by the male of each pair, $r = -0.02$, $p > 0.9$, $n = 25$) nor to brood size (male feeds per nest, $r = -0.02$, $p > 0.9$, $n = 25$; percentage of feeds by the male of each pair, $r = 0.09$, $p > 0.6$, $n = 25$). However, we found a negative relationship between food availability in the territory and male and female absolute feeding rates (number of feeds per chick by male, $r = -0.7$, $p < 0.0001$, $n = 25$; by female, $r = -0.5$, $p < 0.004$, $n = 25$) as well as between food availability and percentage of feeds by the male of each pair ($r = -0.5$, $p < 0.02$, $n = 25$) (figure 1). This relation was also significant when excluding nests with cases of extra-pair paternity and intraspecific brood parasitism (with male absolute feeding rates, $r = -0.62$, $p < 0.001$, $n = 18$; with percentage of feeds by the male of each pair, $r = -0.43$, $p < 0.03$, $n = 18$). Furthermore, the results of the habitat manipulation experiments revealed that males seem to adjust their feeding effort in relation to food abundance. Although not significantly different, male feeding rates tended to be higher when food abundance was decreased and lower in cases of increase in food abundance (Mann–Whitney *U*-test: $z = -1.2$, $p > 0.1$, $n = 9,11$) (figure 2a). This relation was even significant when examining the percentage of feeds by the male of each pair (Mann–Whitney *U*-test: $z = -2.78$, $p < 0.006$, $n = 9,11$) (figure 2b).
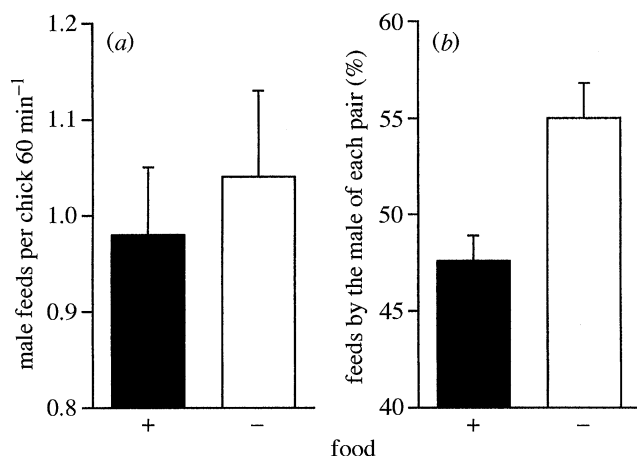
Figure 2. Relationship between experimentally manipulated food availability and (*a*) male absolute feeding rates, (*b*) percentage of feeds by the male of each pair. (Plus symbol refers to increase, minus symbol refers to decrease in food.) Results are means ± s.e.m.

(c) *Paternity and food availability*

We found no relationship between food availability and start of egg-laying (*r* = −0.15, *p* > 0.5, *n* = 22) nor between food availability and breeding synchronization index (*r* = 0.09, *p* > 0.6, *n* = 22). There was also no relationship between start of egg-laying and percentage of extra-pair paternity (*r*$_S$ = −0.16, *p* > 0.4, *n* = 25) and we found no difference in start of egg-laying between nests with and without extra-pair chicks (Mann–Whitney *U*-test: *z* = 0.42, *p* > 0.6, *n* = 5,20).

A relationship between the occurrence of extra-pair paternity and habitat quality is evident from different points of view.

(i) Food abundance was on average significantly higher in territories with nests containing extra-pair chicks (Mann–Whitney *U*-test: *z* = −3.2, *p* = 0.0012, *n* = 5,18) (figure 3). The two cases of intraspecific brood parasitism also originated from territories with high abundance of food (food plant indexes 16.8 and 13.3, respectively; values varied from 1.5 to 16.8 in this study).

(ii) Cases of extra-pair paternity occurred in territories in which food abundance was experimentally increased (two out of nine nests), whereas no extra-pair chick was found in territories with experimentally decreased food abundance (*n* = 11) (exact binomial test: *p* = 0.08). We found no association between food availability and the number of fledglings (see above), but a significant positive relationship between food availability and chick development (expressed as (i) weight increase per day (*r* = 0.83, *p* < 0.0001, *n* = 25), and (ii) chick weight at nine days (*r* = 0.76, *p* < 0.0001, *n* = 25)).

(iii) There was variation in habitat quality between years. Food abundance (mainly *Diplotaxis* sp.) was lower because of bad weather in 1996 compared with the breeding seasons 1995 and 1997 (M. Hoi-Leitner, H. Hoi and F. Valera, unpublished data). This was reflected in breeding success (figure 4). We found a significant variation in reproductive success between years (analysis of variance: *F* = 3.3, *p* = 0.04,
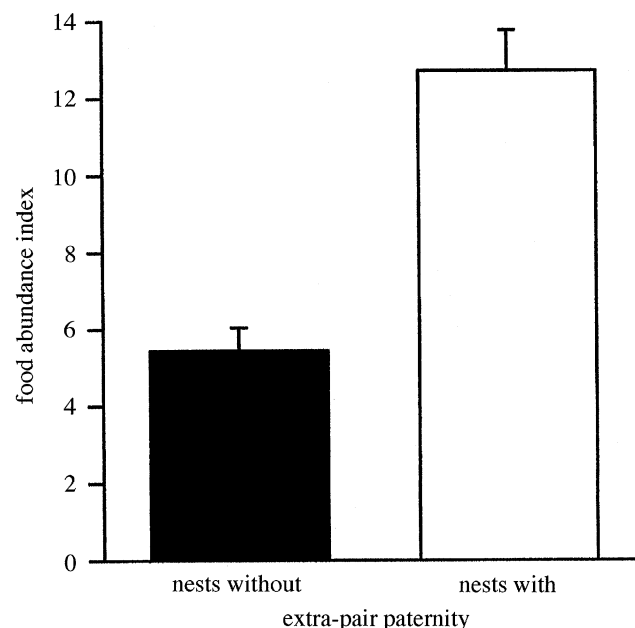

Figure 3. Food availability (expressed as food abundance index) around nests without extra-pair paternity (*n* = 18, filled bar) and nests with extra-pair chicks (*n* = 5, open bar). Results are means ± s.e.m.
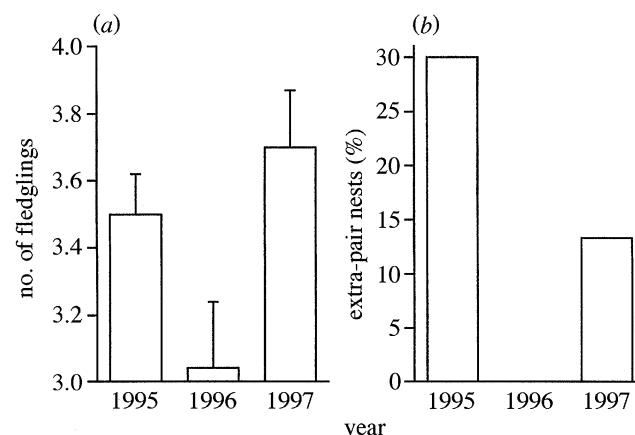

Figure 4. Breeding success (number of fledged chicks per nest) (*a*) and occurrence of nests with extra-pair paternity (*b*) in the breeding seasons 1995–1997. Results are means ± s.e.m.

d.f. = 2.51). Post-hoc comparisons within this model suggest that this difference is due mainly to a significantly lower reproductive success in 1996 compared with 1997 (Duncan's range test: *p* < 0.05). The reproductive success was also mediated by the occurrence of extra-pair paternity revealing extra-pair chicks in good years and no extra-pair chicks in the bad year (figure 4). However, the variation was not significant (exact binomial test: *p* > 0.1 for comparisons between all pairs of years), which might have been due to the small sample size for this low extra-pair paternity rate in the serin.

4. DISCUSSION

This study has shown that in serins the likelihood of extra-pair paternity is significantly higher in territories with a high availability of food. We found a negative relation between environmental quality and paternity (figure 3),

both in unmanipulated and manipulated habitats. Second, male parental assistance was related to food availability. In effect, the higher the food abundance was, the lower were the male absolute feeding rates as well as the percentage of feeds by the male of each pair, which is true for natural situations (figure 1) as well as for experimentally manipulated situations (figure 2). Because females also reduce the number of feeding trips with food abundance we cannot assume that they compensate for male reduction, at least in terms of feeding trips. However, there was no effect of reduced male feeding rates on either the number of chicks or chick development. Alternatively, food abundance around nest sites seems to influence chick development positively and hence to have more than a compensating effect for male parental reduction. The reduction of feeding trips with increasing food availability suggests that birds use different foraging strategies. High abundance of food might facilitate more efficient food exploitation. Birds can store a large quantity of seeds in their oesophageal pouches and they have 'to waste time' to fill them up completely, because even when food supply is high they have to look for intact fruits. One can imagine that places with poor food supply are depleted more quickly and birds have to move more frequently with less food. There is no obvious difference in pouch size between sexes (F. Valera, unpublished data), which would explain a stronger reduction in males apart from the need for male help.

These results suggest that females in good environments are less vulnerable to manipulation through male help than females in poorer-quality situations. Male help apparently does not strongly influence female reproductive success in good habitats. Females in good environments seem to resist male control efforts better than females in poor environments, which in turn might cause females to engage in extra-pair copulations. Hence this result is consistent with one of the main predictions of the 'constrained female hypothesis' (Gowaty 1996), which states that female options for extra-pair matings depend on the intrinsic quality of a female or, as here, the environment that the females occupy. These two factors might be coupled in many bird species. Here we have been able to uncouple them by means of the habitat manipulation experiments; we have strong evidence that there is an effect of habitat quality on female extra-pair behaviour. That females really seek extra-pair copulations is suggested by earlier findings. Hoi-Leitner *et al.* (1999) could show that fertile females visit male lek sites and solicit extra-pair copulations. However, there are potentially confounding factors such as the time of the season (the best territories with high abundance of food are occupied earlier in the same year). Another confounding factor might be nesting synchronization (Stutchbury & Morton 1995). If there is a possible trade-off between male mate guarding, extra-pair activity and parental care then these might depend critically on whether the females in a population were fertile at the same time and whether there was any overlap between fertile period and chick feeding. We did not find any relation between territory quality (food availability) and egg-laying date or nesting synchronization. We further found no relationship between the occurrence of extra-pair paternity and time of the season. Furthermore, our results do not support the idea that different levels of nesting synchronization or the

timing of breeding explain any of the year-to-year differences. In our study population, serins starting to breed early in the season might therefore have no advantage.

If females try to parasitize conspecifics, they should try to give their eggs the best chances of survival. It is therefore not surprising that the two cases of intraspecific brood parasitism also occur in high-quality habitats. This is not contradictory to the 'constrained female hypothesis', although females in high-quality habitats might have to take a higher risk of intraspecific brood parasitism into account when evaluating the importance of their male for their own reproductive success.

A second assumption of the 'constrained female hypothesis' is that females in better environments will be more consistent in their choice of an extra-pair male. If females seek extra-pair matings they should go for genetic quality of the extra-pair father; hence the extra-pair father should be of higher quality (Gowaty 1996). We do not have sufficient data to test this, but our results show that in cases with more than one extra-pair chick, all of them are fathered by one extra-pair male.

Paternity has been thought to be related to parental care either because males should be selected to reduce investment in brood care with uncertain paternity, or because male extra-pair activity is traded against parental care (Møller 1999). In serins there is an obvious decrease in male parental care in relation to food abundance (figure 1). However, because food abundance is also positively coupled with female extra-pair behaviour it is unclear at this stage whether the decrease in paternal care is due to one of these two alternative possibilities, namely a consequence of increased paternity uncertainty or a consequence of a male increase in extra-pair behaviour in better environments. It seems likely that male serins trade their own extra-pair activities against parental care. This is suggested by the fact that the relationship between paternal care and food abundance holds also for nests without extra-pair chicks. However, this is not necessarily conclusive because we do not know anything about the availability of reliable paternity cues that males use in this species. If males were to use food abundance as a paternity cue one would expect a general decrease in paternal care just as a response to the higher risk in general of extra-pair paternity in good environments, but this might also depend on other costs and benefits of reducing parental effort (Gowaty 1999). Additional evidence that males adjust parental care to food abundance is that they made short-term adjustments by reducing their parental care immediately after we increased food abundance around the nest site during chick feeding (M. Hoi-Leitner, unpublished data). J. C. Senar (personal communication) reported cases of polygyny in serins, which also suggests that males trade paternal care against further matings. We found that males frequently join lek sites and fertile females visit these 'leks' to engage in extra-pair copulations (Hoi-Leitner *et al.* 1999).

Furthermore, there is recent discussion on whether and how males should invest in parental care (Wright 1998; Gowaty 1999). There is little evidence that males really adjust their parental effort to the risk of extra-pair paternity (Dixon *et al.* 1994; Weatherhead *et al.* 1994; Sheldon & Ellegren 1998). However, one recent study shows that there

is a negative relation between paternal care and extra-pair paternity at the interspecific level (Møller 1999). Paternity cues have been found in only a few cooperatively breeding species (see, for example, Hartley *et al.* 1995). Gowaty (1999) argued that this positive relation between paternity and parental care is not necessary at all. However, it is still possible that in serins male parental reduction is a consequence of paternity uncertainty.

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