



High frequency of extrapair fertilization in a plural breeding bird, the Mexican jay, revealed by DNA microsatellites

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We used tetra-nucleotide microsatellite DNA typing to estimate the frequency of extrapair fertilization (EPF) in a plural breeding species, the Mexican jay, *Aphelocoma ultramarina*, in Arizona. We found EPF in 32 of 51 complete broods (63%) and 55 of 139 nestlings (40%) for which the putative father had been identified (one of the highest rates of EPF known for birds). At least 96.1% of EPF fathers came from within the group. This is by far the highest known within-group EPF rate among socially monogamous, communally rearing species. Most (70%) males of breeding age (3+ years) had no genetic paternity in a given year. Social fathers (i.e. those with nests and mated females) rarely obtained EPFs; of 25 social fathers, 23 had young in only one nest and only two had young in two nests by virtue of EPF. Of the 27 males known to be EPF fathers without a nest of their own, none had young in more than one nest. Only 7% of EPF fathers had their own broods reaching banding age (day 14), compared with 29.7% of social fathers. The proportion of EPF young was significantly larger in smaller broods. Breeding females in all age classes were equally likely to have EPF young.

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Communal rearing of young (or cooperative breeding) is a system in which individuals other than the parents provide care to the offspring together with the parents. Indirect fitness has been considered as an important factor for the evolution of this behaviour in nonbreeders (Reyer 1980; Brown 1987; Emlen & Wrege 1988, 1989, 1994; Emlen 1997), although not without controversy (Cockburn 1998). For helpers of breeding age, multiple paternity is another plausible evolutionary factor for communal rearing: feeding might be provided by males within the group that share paternity of young, as in the dunnock, *Prunella modularis* (Burke et al. 1989) and other polyandrous species with breeding helpers (Brown 1987). However, in the many communally rearing species in which genetic parentage been examined, only in fairy-wrens (*Malurus* spp.) is there a high level of extrapair fertilization (EPF) of offspring (less than 15%; Rabenold et al. 1990; Poldmaa et al. 1995; Haydock et al. 1996; Waite & Parker 1997). Even in fairy-wrens, most EPF offspring are not sired by males from the same group (Mulder et al. 1994; Green et al. 1995; Dunn & Cockburn 1996). These results seem to reject the hypothesis that within-group

extrapair copulations (EPCs) might serve mainly to recruit helpers at the nest. However, most of these studies were done on singular breeding species that live in small, nuclear family groups formed usually by a single breeding pair with its offspring and sometimes a few immigrants. In these circumstances EPCs within the group would cause a high degree of inbreeding, which is not generally favoured by natural selection. EPFs in these species tend to require a step-parent within the group (Koenig & Pitelka 1979; Mumme et al. 1985; Haydock et al. 1996) or individuals from another group. Therefore, it is not surprising to observe a low level of EPF in most species that live in nuclear family groups. Plural breeding species, which have multiple females breeding simultaneously (Brown 1978), are, therefore, more promising for the study of extrapair copulation in relation to helping behaviour.

The Mexican jay, *Aphelocoma ultramarina*, provides a favourable system in which to examine the potential complexity of mating behaviour in a plural breeding species. It lives in groups of 5–25 whose territory locations remain stable across years (behaviour reviewed by Brown & Brown 1990; Brown 1994). About half the group members are in one or more extended families; the other half are immigrants from neighbouring groups (Brown & Brown 1981). During the breeding season (mid-March to June, Brown & Li 1996), two or more females nest

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