



## Mate Choice in Avian Polygyny: Why Do Females Prefer Older Males?

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## MATE CHOICE IN AVIAN POLYGYNY: WHY DO FEMALES PREFER OLDER MALES?

Several recent studies of polygynously breeding birds have found that older males attract more mates on the average than younger males. Both Picman (1980) and Yasukawa (1981) reported that male red-winged blackbirds (*Agelaius phoeniceus*) returning to the same territories in successive years became increasingly successful in recruiting females. Järvi et al. (1982) reinterpreted the data reported by Alatalo et al. (1981) for pied flycatchers (*Ficedula hypoleuca*) and suggested that older males can be recognized as such by females and are preferentially chosen as mates. Because these results clearly show that females use male quality as a criterion in selecting mates they are of critical importance to the debate over whether or not females prefer certain males because they sire genetically superior offspring and thereby enhance the females' inclusive fitness (Weatherhead and Robertson 1979, 1981; Searcy and Yasukawa 1981; Wittenberger 1981). Specifically, the question that needs to be answered is whether females prefer older males because they are superior phenotypic fathers (i.e., they provide better parental care allowing the female to fledge more young) or whether they are superior genotypic fathers (i.e., they provide better genes such that even if a female suffers an immediate reduction in reproductive success, the higher quality of her offspring will ultimately provide her with higher inclusive fitness). In the case of the genotypic argument, the usual connection suggested between male age and genotypic quality is that by surviving longer the male has proven his superiority (Halliday 1978; Weatherhead and Robertson 1981; Järvi et al. 1982).

In a recent review, Searcy (1982) concluded that the evidence for red-winged blackbirds indicated that females choose older males because they provide superior parental care and that overall the evidence in favor of parental care is much more compelling than that for superior genes. Here I demonstrate that neither of these conclusions is warranted and that the best evidence, albeit indirect, supports the genotypic quality hypothesis.

Searcy (1982) draws his main support from Yasukawa's (1981) study of an Indiana population of red-winged blackbirds which showed that older males obtain more mates and spend proportionately more of their on-territory time courting females and assisting females in feeding nestlings. Females, therefore, can recognize older males by their courtship behavior and preferentially choose them because they spend more time feeding nestlings. Yasukawa (1981) presented these data in the form of rank correlation analyses which preclude the determination of absolute feeding rates, the number of males that fed and, most importantly, how much assistance individual females can expect when choosing an older male and the implications thereof for her expected reproductive success. The latter point is crucial to assessing the data since a proportionately high rate of feeding by an older male means nothing to a female if she does not benefit from it.

Fortunately, Patterson (1979) studied male parental care for 3 yr in the same Indiana red-winged blackbird population and provides the data necessary to assess the role of that care in female mate choice. While her data clearly show that it is advantageous to a female to be helped by a male, they also show that the majority of females receive no help whatsoever. Over 3 yr, only 20 of 34 (59%) males assisted females at all and within the territories of those 20 males, their feeding was restricted to only 32 of a total of 94 (34.4%) nests. Also, there was no difference in the number of mates obtained by feeding and nonfeeding males, indicating that the preference for older males is independent of the fact that some older males spend proportionately more time feeding. Thus, feeding is neither something that affects most females nor is it apparently important in determining harem sizes.

Two possibilities remain that might salvage part of the parental care hypothesis. First, if females are unable to predict which of them a male will assist then a female may preferentially choose an older male just on the chance that he will be one of those that assists females and that her offspring will be the lucky recipients. This idea must be rejected, however, since Patterson (1979) showed that it is highly predictable that if a male feeds he will favor the first female to settle in his territory (19/20 times). The second possibility is that the territories of feeding males are superior so that females fledge more young in spite of not being one of those getting assistance. In 2 of the 3 yr of Patterson's (1979) study there was no difference in reproductive success of unassisted females on territories of males that fed and those that did not feed. In the remaining year, however, unassisted females on territories of feeding males fledged significantly fewer young than females rearing young on territories of males that fed no young at all. Thus, if anything, later settling females on territories of feeding males do worse than females on territories of nonfeeding males. A final point to make is that Picman (1980) found the same pattern as Yasukawa (1981) of older males recruiting more mates in a population in which there was essentially no feeding of nestlings by males (J. Picman, personal communication) and for which, therefore, the parental care argument is obviously untenable.

Given the failure of the hypothesis that females prefer older males because they are phenotypically superior fathers, one is left with two alternatives. Either females prefer older males because they are genotypically superior, or the mating preference is a nonadaptive artifact of some other phenomenon. Although no direct evidence is available with which to judge the relative merits of these two alternatives, indirect support for the genotype quality hypothesis is provided by the data for pied flycatchers. Secondary females fledge substantially fewer young than primary females (Alatalo et al. 1981) even though Järvi et al. (1982) suggest that these females have the option of themselves becoming primary females. Therefore, for this mate choice not to be maladaptive (as opposed to nonadaptive) one must invoke an inclusive fitness advantage from mating with a genotypically superior male. Although Alatalo et al. (1981) felt the reduced reproductive success of secondary females was too great to be overcome by producing reproductively successful sons (see Weatherhead and Robertson 1979), Järvi et al. (1982) point out several reasons why the reproductive deficit may be less substantial than it

appears. They go on to suggest that if older males sire offspring that are more fit, the deficit may be overcome. From an inclusive fitness standpoint, the reproductive success of the male offspring will contribute most to eliminating the deficit (given that they become polygynous) and this would therefore be a case in which older was "sexier" (Weatherhead and Robertson 1981).

In summary, therefore, there is no evidence to support the hypothesis that most females in polygynously breeding species prefer older males because they provide better parental care. On the contrary, there is evidence to indicate that for some females there is a cost associated with choosing an older male such that only enhanced inclusive fitness of the female resulting from that male's higher genetic quality is consistent with that choice of mate not being maladaptive.

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