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## Parental Role-reversed Polyandry and Paternity

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Male birds may desert their mates whenever they benefit more by deserting and remating than by sharing in the care of their young (Ridley 1978, Wittenberger 1979). In a few species, females desert and remate and males care alone (Emlen and Oring 1977, Ridley 1978, Wittenberger 1979, Erckmann 1983, Oring 1982, 1986). Such a reversal in parental roles is central to the evolution of avian polyandry, and polyandrous mating systems in general.

Theoretical studies suggest that polyandry through female desertion can only occur when there is strong selection against desertion by males (Trivers 1972, Williams 1975, Boucher 1976, Dawkins and Carlisle 1976, Maynard Smith 1977, Graul et al. 1977, Lazarus 1990). Three general hypotheses have been proposed to explain the reversal of parental roles among polyandrous birds (see reviews by Ridley 1978, Wittenberger 1979, Erckmann 1983, and Oring 1982, 1986): (1) remating opportunities are greater for deserting females than for deserting males (Maynard Smith 1977); (2) females are less able than males to raise the offspring alone because of the stress of egg laying (Grafen and Sibly 1978); and (3) males benefit from female emancipation from parental care because it enables the female to double clutch or to replace a failed clutch for her mate (Jenni 1974). Recent studies suggest that sex-ratio biases may favor mate desertion by the rarer sex in some facultatively polygamous fish (Keenleyside 1983) and some birds (Beissinger 1987, 1990, Beissinger and Snyder 1987, Benkman 1989, Fujioka 1989), including one species of polyandrous shorebird (Oring et al. 1983).

Evidence for these hypotheses is largely inconclusive for most polyandrous shorebirds, the avian group in which polyandry is most prevalent (Jenni 1974, Pitelka et al. 1974, Ridley 1978). The idea that male desertion is constrained by advantages of territoriality (Gross and Sargent 1985) may not apply to polyandrous birds because often they are not territorial, or both sexes may defend all-purpose breeding territories (Oring 1986). In a few cases females may be less able than males to raise the young unaided (Brunton 1988). However, parental constraints are unlikely to be a general explanation for polyandry in shorebirds, because females tend to be larger and more aggressive than males (Jenni 1974, Erckmann 1983). Thus, females should be better at protecting the young than males.

Here I suggest that the reversal of parental roles and polyandry in birds may also be favored if males gain a benefit by inseminating the female before she

deserts, thus siring at least part of the subsequent brood she lays for another male. Moreover, if the benefit the male expects from inseminating the deserting female is greater than the benefit he expects from deserting and remating, parental role reversal may arise because polyandry is in the male's interest. This could be the case when deserting males have a low probability of remating, when insemination of deserting females results in a high probability of paternity, and when any increase in parental effort caused by the female's desertion has little cost to the male's survival. The feasibility of this hypothesis relies on the ability of female birds to store viable sperm for days or weeks (e.g. Birkhead and Møller 1992). Moreover, the cost of uniparental care, in terms of the male's survival, appears to be low (e.g. Oring et al. 1983, Oring 1986, Valle 1994).

This hypothesis implies that the benefit some males gain through the insemination of their deserting mate will result in decreased paternity for later nesting males, which in turn may decrease a male's willingness to provide parental care (e.g. Trivers 1972, Houston and Davies 1985, Winkler 1987, Richardson and Coetzee 1988, Whittingham et al. 1992, Xia 1992). However, if all males experience a relatively constant average reduction in certainty of paternity in the brood for which they care, decreased certainty of paternity per se may not affect the male's willingness to care (Maynard Smith 1978, Grafen 1980, Werren et al. 1980). This may be the case in populations that breed more or less continuously throughout the year, such as tropical jacanas. However, among populations that breed seasonally, such as the polyandrous arctic shorebirds, males breeding earlier may not only ensure high paternity in their first brood, but also gain extra offspring at the expense of later breeders. Therefore, males that do not mate until later in the season should attempt to improve paternity by mating with previously unmated females and discriminating against formerly mated ones (Whitfield 1990). However, any male breeding late may have little choice of partners. Such males are likely to be younger or of lower quality, and perhaps cannot afford to be too choosy about their mates (but see Whitfield 1990). Furthermore, in arctic shorebirds because rapid reproduction is at a premium due to the shortness of the breeding season, and because unmated females may be in short supply late in the season, late-nesting males may be forced to accept previously mated females. Moreover, high rates of nest failure, weak pair bonding, and recurrent opportunities for reneating

(Erckmann 1983, Oring 1986) increase the likelihood that, later in the season, most or all unpaired females are carrying sperm from previous matings. Therefore, later breeding males may have only limited opportunities for improving paternity through active mate choice.

DNA paternity studies in polyandrous birds are still scanty. However, these analyses have shown that deserted males sired offspring in broods of deserting females in the Spotted Sandpiper (*Actitis macularia*; Oring et al. 1992) and Wattled Jacana (*Jacana jacana*; Emlen and Wrege unpubl. data). Evidence from heritability estimates in Darwin's finches (*Geospiza*) also suggests that males deserted by their mate sired a proportion of the deserting female's subsequent brood produced with another male (Boag 1983). Among shorebirds, deserting females remate relatively quickly, within a week after completing the first clutch in some species (Johnsgard 1981), and this may enhance the first male's probability of siring offspring in the second clutch. This suggests that males gaining such a genetic side benefit through insemination of deserting mates may be widespread among polyandrous shorebirds. Behavioral studies have paid little attention to the pattern of rate of copulations, a possible indicator of the occurrence of males inseminating deserting females. Copulations near the time females deserted were rare in Flightless Cormorants (*Phalacrocorax harrisi*; Valle 1994), and apparently they do not occur in Snail Kites (*Rostrhamus sociabilis*; Beissinger, pers. comm.) either. Valle (1994) has discussed the possible reasons as to why in some populations males do not attempt to copulate with their mates shortly before desertion and, thus, do not gain the extra genetic benefit discussed here.

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## Gut Passage of Insects by European Starlings and Comparison with Other Species

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Digestive processes influence a bird's net rate of energy gain and its utilization efficiency of food (Karasov 1990, Place and Stiles 1992). These factors, in turn, can influence feeding behavior and possibly constrain rates of growth and reproduction (Karasov et al. 1986, Tiebout 1989, Levey and Grajal 1991).

Retention time is a key feature of digestive processing, rarely studied in nondomesticated birds (Warner 1981). When reported, the data are often difficult to compare or interpret in an ecological context because animals were held under stressful conditions, fasted for an unnaturally long period of time, or fed a large dose of nonnutritive marker (e.g. barium suspensions). Even disregarding such problems, retention-time data are especially scarce for passerines eating insects; we know of only three published reports (Stevenson 1933, Dykstra and Karasov 1992, Levey and Karasov 1992).

Here we report retention times of crickets (*Acheta domestica*) in European Starlings (*Sturnus vulgaris*) feeding continuously under unstressful conditions. With these data and those from published studies we then address a fundamental question about gut processing: To what extent is retention time determined by diet, as opposed to vice versa? More specifically, is there an "ideal" retention time for an insectivore or frugivore and, if so, how fixed is it within a species? This issue is ecologically relevant since, if food processing is largely invariable, a bird may be unable to switch diets, or may be less effective using an alternative diet than a more specialized bird. The former result constrains niche width directly, and the latter may do so indirectly via competition.

We compare: (1) retention times in starlings on fruit and insect diets to determine if they can modulate retention time; and (2) mass-normalized retention