COMMENTARY

Did Tree Swallows Cross a Polygyny Threshold?

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Recently, Quinney (1983) demonstrated that female Tree Swallows (*Tachycineta bicolor*) involved in bigamous relationships had poorer reproductive success than monogamous females. Despite this, he entitled his paper "Tree Swallows cross a polygyny threshold." Because Quinney did not assess the reproductive success of polygynous females (those females choosing already-mated males), a comparison between concurrently settling females was not made, as is usual in assessments of polygyny threshold models (Garson et al. 1981). Quinney's conclusions therefore are premature.

Quinney couched his arguments in terms of the Verner-Willson-Orians (VWO) model for the evolution of polygyny (Verner 1964, Verner and Willson 1966, Orians 1969). This model assumes that polygyny is adaptive and will evolve if a female mating with an already-mated male has a reproductive success equal to or greater than that of a female mating with a bachelor male. However, tests based on this premise often are invalid due to the potential depressing effects of beta females on alpha females (Altmann et al. 1977) or the effects of discontinuous habitat or male quality on female success (Simmons MS). Using the VWO model as his criterion, Quinney showed that monogamous females were significantly more successful in fledging young than were alpha and beta females (4.7 vs. 2.1, $P < 0.01$) and that monogamous females raised slightly heavier young. Assuming that alpha plus beta (= "polygynous," Quinney 1983) productivity is equivalent to the (more correct) beta female productivity, then polygyny according to the VWO model appears maladaptive for polygynous females. However, Quinney states that "polygyny is advantageous to secondary [beta] females at the Sewage Lagoon if these females could not breed otherwise." First, it is possible that the beta females could have bred at Backus Field (or other nearby sites), since not all of the nest boxes were occupied there. Second, if a lack of males was preventing nesting at alternate sites, Quinney is invoking the "desperation" hypothesis (Simmons 1983), which assumes that polygyny arises from a forced choice among females who cannot breed without choosing a mated male. This should not be confused with models based on resource-defence polygyny, because no monopolizable resource is necessarily at stake, and a female may well breed with the first mated male who will accept her. This confusion appears to have arisen from Quinney's misinterpretation of Emlen and Oring's (1977) review of factors affecting mating systems. As Quinney (1983: 750) assumed, polygyny does not occur "only when the operational sex ratio [OSR] . . . deviates from unity in conjunction with some minimum degree of inequity in territory quality." Rather, Emlen and Oring (1977) stress that the "prerequisite for a polygynous mating system is the economic monopolizability of several mates" and that "where the OSR is skewed toward males, polygyny is expected." That a skewed OSR is not required for polygyny to occur has been shown by Willson and Pianka (1963) and Orians (1972).

Having implied that desperation is the cause of polygyny in Tree Swallows, Quinney does not test the hypothesis. A simple test would be to calculate the laying sequences of all females and determine whether each bachelor male defending a nest box was mated prior to polygynous situations arising. If bachelors remained unmated during the establishment of polygynous associations, a polygyny threshold situation is likely. It may be that the laying sequences of female Tree Swallows were impossible to measure in Quinney's study, but without this test no conclusions can be drawn.

Quinney further suggested that food quality was a mitigating factor in the advent of polygyny: ". . . and a superior supply of food [relative to the Backus Field site] apparently has led to the appearance of polygyny at the Sewage Lagoon." However, differential food quality (e.g. between male Tree Swallows) is required before any mated male is likely to be chosen in preference to a bachelor (cf. Altenburg et al. 1982 for a good example). This was not tested. There is no reason to believe that polygyny could not arise as easily in a poor environment (such as Backus Field) with one good "breeding situation" (Wittenberger 1976) as it could in a rich environment with no variation in breeding situations.

As presented, Quinney's results and interpretation cannot be used to test the idea that Tree Swallows practice resource-defence polygyny and that this is adaptive for polygynous females. Because Tree Swallows do not defend feeding territories and presumably have identical nest boxes, there is no resource that is both defendable and of differential quality. Therefore, unless the males themselves differ in reproductive quality (such as in food-provisioning rate),

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a female has nothing to choose between and thus no polygyny threshold to cross. Two alternative hypotheses that have been associated with poor reproductive success in polygynous females are the "sexy son" hypothesis (Weatherhead and Robertson 1979, Heisler 1981) and male cheating (Alatalo et al. 1981, 1982; Simmons 1983). Either alternative is as plausible as female desperation in Quinney's population, but Quinney's data do not distinguish between them.

In summary, Quinney (1983) (a) did not or could not distinguish truly polygynous (beta) females from alpha females, (b) did not or could not compare the productivity of concurrently settling monogamous and polygynous females in order to test a resource-defence polygyny threshold model, (c) implied that desperation was responsible for the polygyny seen but did not test the hypothesis, and (d) implied that food contributed to a polygyny threshold but did not demonstrate any differential food supply between males and/or nest boxes. I believe, therefore, that his implication that a polygyny threshold was crossed by Tree Swallows is misleading and possibly inaccurate.

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