COMMENTARY

Condor, 82:476–477

TO THE EDITOR

The evolution of lek and communal courtship behavior in some tropical frugivorous passerines has long puzzled ecologists and behavioral biologists. A key to the problem is to understand how monogamy can be transformed by natural selection into promiscuity, with the attendant loss of male parental investment. A recent article by D. W. and B. K. Snow (Condor 81:286–292, 1979) and Commentary by E. O. Willis (Condor 81:324, 1979) again raise this issue.

Most hypotheses concerning the evolution of promiscuous mating are based upon the premise that the fecundity of neither the female nor the male would be enhanced by male parental investment. Specifically, fecundity is thought to be limited by some factor other than a resource provided to the offspring potentially by both parents.

The Snows and Willis both suggested that in promiscuous, tropical, frugivorous passerines, fecundity is limited by adaptations to reduce predation on their eggs and young. Willis suggested that predation may be more intense upon the offspring of fruit-eating species than upon those of insectivorous species. He reasoned that fruits support larger populations of birds than do insects and that high population density in turn attracts more predators and enhances their efficiency by facilitating the formation of search images for nests. Adaptations to reduce predation may include smaller broods if predation rate increases in direct relation to brood size (A. F. Skutch, Ibis 91:430–455, 1949), and smaller nests, hence smaller broods indirectly, if predators find large, conspicuous nests more readily than small, cryptic nests (B. K. Snow, Ibis 112:299–329, 1970). I believe that the hypothesis relating male emancipation to predation is inadequate. I shall state my reasons for this opinion briefly and then propose an alternative.

First, one result of a model relating predation and brood size to each other and to breeding productivity is that predation upon eggs and nestlings does not likely limit brood size in tropical passerine birds (R. E. Ricklefs, pp. 193–214. *In* B. Stonehouse and C. M. Perrins [eds.], Evolutionary ecology. Macmillan, London, 1977). The conditions under which predation might be a major factor in the evolution of brood size are unrealistic with respect to predator behavior, as I understand it, and are inconsistent with measured rates of predation. Second, many promiscuous species rear two nestlings per brood, which is the typical number for the majority of monogamous passerines in humid, tropical regions, or even three (E. O. Willis, D. Wechsler, and Y. Oniki, Auk 95:1–8, 1978). Although some promiscuous species rear only one chick, there appears to be no general trend towards reduced brood size in such species, an enigma clearly recognized by Skutch (1949).

I suggest here that the prevalence of promiscuous mating systems in certain groups of tropical passerines can be related to special attributes of their food supplies and to general mechanisms of population regulation, according to the following propositions.

(1) In general, the densities of breeding birds are determined more by the capacity of the environment to support populations during the nonbreeding season than by territorial behavior of individuals during the breeding season. That is, territory or home range size is compressible and determined by the number of conspecific individuals vying for space at the beginning of the breeding season. For a particular food resource and population, one pair of a monogamous species cannot defend a larger territory than a single female of a promiscuous species, provided males and females do not defend territories against each other.

(2) The distribution of some kinds of food resources, especially certain types of fruits, can be so perfectly known that the supply within a territory can be harvested completely by a single individual. A pair can provide no more to their brood than can a single female.

If propositions (1) and (2) are correct, a male would not be able to enhance his fecundity by enlarging his territory to include more food resources or by searching for them himself. Indeed, a male might reduce his fecundity by competing with his mate for a fixed food supply (Willis et al. 1978). In insectivorous birds, harvesting rate is probably directly proportional to the combined search time of the pair and, therefore, male parental investment can enhance breeding productivity.

Propositions (1) and (2) can account for the emancipation of males from parental care and the fact that they require a small proportion of the day to feed themselves. These ideas allow no prediction about the relative sizes of broods of promiscuous and monogamous species because each would be limited by qualitatively different resources. I have argued elsewhere that brood size is determined by the availability of food to breeding adults, which is regulated through density-dependent factors by the seasonality of food resources (R. E. Ricklefs, Auk 97:38–49, 1980). According to this hypothesis, monogamous and promiscuous species would rear broods of similar size if their resources exhibited similar seasonal fluctuations. Proposition (1) addresses an issue, the compressibility of breeding territories, that is not fully resolved (J. Brown, Wilson Bull. 81:293–329, 1969; cf. J. P. Myers, P. G. Connors, and F. A. Pitelka, Auk 96:551–561, 1979). This is not the proper forum for detailed discussion.

Proposition (2), that some kinds of food resources can be fully harvested, might be investigated by detailed studies of the relationship of frugivores to their food supply. I would predict that the fruits eaten mainly by promiscuous species and those eaten by monogamous frugivores (mainly tanagers among passerines in the New World tropics) have distinctively different patterns of dispersion, availability, and, perhaps, nutritional value.

Data collected by the Snows on Trinidad demonstrate that different species of frugivorous birds may have very different diets. Of records of the promiscuous Black-and-White Manakin (*Manacus manacus*) feeding at fruiting plants, 47% were from the family Melastomaceae, primarily *Miconia*, and 14% were Rubiaceae (D. W. Snow, Zoologica 47:65–104, 1962). Of 350 seeds collected below one nest of the promiscuous Bearded Bellbird (*Procnias averano*), 74% were of Lauraceae (*Cinnamomum* 19%, *Ocotea* 55%), and 15% Burseraceae (*Protium*) (B. K. Snow 1970). Of 1680 records of feeding by 9 species of monogamous tanagers (Thraupidae), 32% involved Melastomaceae (mostly *Miconia*), 19% Moraceae (*Ficus* and *Cecropia*), and 6% Araliaceae (*Didymopanax*) (B. K. and D. W. Snow, Auk 88:291–322, 1971). While these data cannot be used to test the ideas outlined above, they do indicate food specialization among frugivores at the level of plant families.

Our inability to resolve the various explanations proposed for promiscuous mating systems in tropical fruit-eating birds by the Snows, Willis, and myself, emphasizes how little we know about these species, their food resources, and the factors that regulate population density and reproductive success. Clearly, future work on these birds should include a more detailed characterization of their food resources. I thank E. O. Willis and D. W. Snow for comments.—ROBERT E. RICKLEFS, *Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104.*

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NEWS AND NOTES

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The Wilson Ornithological Society announces the availability of three awards for 1981. Louis Agassiz Fuertes Awards are available to all ornithologists, although graduate students and young professionals are preferred. Margaret Morse Nice Awards are intended for independent researchers without access to funds and facilities available at colleges and universities and thus are restricted to amateurs and students at high school and undergraduate levels. Any type of research may be funded by both Fuertes and Nice Awards.

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Requests will be considered only for manuscripts that have been accepted for publication by an established scientific series or publisher of recognized standing in scholarly circles. Preference will be given to the highest caliber monographs for which alternative publication fund searches have been documented and for those for which only partial or matching funds are being requested.

Awards will be limited to the difference between estimated production expense and anticipated income from sales, with appropriate provisions for recovery of profit to NSF. Six to nine months should be allowed between submission of the proposal and the requested effective date of the grant. For additional information, write to James C. Tyler, Program Director, Biological Research Resources Program, National Science Foundation, Washington, DC 20550.

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