

supposition is contradicted by recent theoretical models that show intersexual selection can favor elaborate ornaments in monogamous species, where both sexes provide parental care, and even in sexually monomorphic species (Kirkpatrick et al. 1990), and by many examples of monogamous species with brighter plumage and more elaborate ornaments than curassows (e.g. tropicbirds, *Phaethon*; egrets, *Egretta*; parrots, *Platycercus* and *Trichoglossus*; some auks, *Aethia*; puffins, *Fratercula* spp.; bee-eaters, *Merops*; sunbirds, *Nectarinia*; kingfishers, *Tanysiptera*; jays, *Calocitta* and *Cyanocorax*; and tyrant flycatchers, *Muscivora*). Elaborate traits expressed in males and females may be the result of mutual sexual selection related to variation in mating success of both sexes (Kirkpatrick et al. 1990). Thus, the logic of good-genes, runaway, and direct-benefits models may apply to ornaments of monogamous nonlekking species, but understanding of which model best explains evolution of extravagant traits will depend on carefully designed field experiments on a variety of species with different mating systems. Eventually we may find that all three models may work in nature, perhaps even simultaneously.

Finally, data indicating a lack of correlation of curassow ornaments with parasite prevalence is not consistent with good-genes models of sexual selection. It is more consistent with Buchholz's (1991) depiction of the runaway model, or with the idea that knob ornaments are arbitrary with respect to viability. Successful evaluation of these sexual-selection models awaits derivation of testable mutually exclusive predictions, and on field studies that experimentally measure active mating preferences and intrasexual competition, while controlling for confounding factors such as age.

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Received 25 April 1991, accepted 26 April 1991.

The Auk 109(1):199-201, 1992

Confusing Models with Tests in Studies of Sexual Selection: Reply to Jones

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Jones' (1992) thought-provoking commentary points to some statistical issues and intricacies of sexual-selection theory not discussed in my original paper. However, I believe that some of the "pitfalls" he describes are moot in the empirical realm.

In the major thrust of his commentary, Jones

wrongly contends that the predictions of the "good-genes" and "runaway" models for the evolution of ornaments are not exclusive. He hypothesizes that runaway traits may become good indicators of the bearer's fitness as they become more burdensome. This scenario is not unreasonable. Nevertheless, once

a runaway-derived character becomes indicative of viability, it becomes a good-genes trait. One has no way of testing the frequency with which runaway characters became good-genes indicators, because there is no time machine that allows us to document past selective pressures. (Although it is sometimes possible to infer past selective factors from comparative studies of the ecological correlates of the character across species, ecological correlates of runaway selection are not expected.) Therefore, the question of how an extravagant trait evolved in the past is inferable only by investigating why that costly trait is maintained in the present! Unless new predictions of these models become apparent, we have no other option. In evaluating the adaptive significance of curassow knobs, I can rely only on my evidence from the present, which suggests that knob size is maintained because it is used by conspecifics as a reliable indicator of age.

Jones correctly pointed out that I do not provide direct evidence showing that bigger knobs are actually preferred by females, or that they are not used in male-male interactions. This certainly is a valid critique of a study of sexual selection. However, I believe the evidence I did provide (i.e. the sexually dimorphic nature of fleshy ornamentation in curassows, a strong correlation between ornament size and size dimorphism across *Crax* species, and male behavior during courtship displays) strongly suggests a sexually-selected function for knobs. In light of the difficulty of studying these animals and the paucity of information on their biology, I have no qualms about placing the data I was able to collect into a theoretical framework. If future research finds that females select mates based on knob size, we will have some notion of the adaptiveness of that preference.

Several authors (Halliday 1983, Manning 1985, 1989) have suggested that females should prefer to mate with older males, because those individuals have demonstrated their ability to survive despite predators, parasites, and intraspecific competition. I concluded that knobs were good indicators of age in Yellow-knobbed Curassows (*Crax daubentoni*) and that females may use male knob size to assess male age. Jones (1992) countered that knob size may not be due to age per se, but rather due to the "nongenetic" benefits accrued with age (such as increased dominance status or more efficient foraging). This would not pertain to the curassows I studied, because these birds were maintained in captivity as single pairs with ample food and no opportunity for direct interaction with conspecifics. His alternative suggestion that a correlation between knob size and age occurs for "developmental reasons" is exactly my point. If knob size is dependent on development, it is an uncheatable indicator of male age. Thus, the next step in testing the "female-choice-for-male-age" hypothesis, presuming that females do prefer bigger knobs, is to determine if the offspring of older males are genet-

ically more viable than offspring of younger males. Examining the correlation between knob size and viability correlates within age classes, as Jones suggested, provides data to test other equally important explanations for the evolution of extravagant characters, such as the Hamilton and Zuk (1982) hypothesis, but does not directly test the female-choice-for-male-age hypothesis. This is critical because, if age is a good indicator of the overall genetic quality of males, and if a female's ability to detect various categories of male quality is limited (by sensory systems, Cohen 1984; or time, Janetos 1980), it would seem that one is more likely to find that females of long-lived species are choosing mates based on age than for any other reason.

Based on measurements on nine birds, I concluded that there is no relationship between age and knob size in the Great Curassow (*C. rubra*). Jones (1992) correctly asserted that the risk of a Type II error at this sample size is high. Unfortunately, Jones' reanalysis of my data duplicates my error, incorrectly using an ANCOVA to compare the data in figures 3 and 5 of Buchholz (1991), when those figures do not share the same independent axes (fig. 3 utilizes an actual measurement, whereas fig. 5 uses a ratio derived from photographs of birds), and violating the assumption of a continuous distribution underlying analyses of variance (male age was measured in intervals of one year). The *P*-value associated with the original Great Curassow data (0.28) does not suggest a trend in the data. Recently, with support from the Cracid Breeding and Conservation Center in Lanaken, Belgium, I obtained knob height and age data on two additional Great Curassows. Despite a sample size ($n = 11$) now approaching that available for Yellow-knobbed Curassows, the significance of the association between knob height and age is lower ($P = 0.73$). Although my original data are not numerous enough to be strongly confident that age and knob size are not positively correlated in the Great Curassow, there is no additional evidence that my conclusions were incorrect. Thus, while awaiting further data, I maintain that Great Curassow knobs are probably not a reliable indicator of male age.

Clearly, monogamy does not preclude the operation of sexual selection (O'Donald 1980). This does not mean that sexual selection in polygamy and monogamy are equivalent, as Jones (1992) opined. Mathematical models of ornament evolution via sexual selection under monogamy have shown it to be slower and less stable than in polygynous systems (Kirkpatrick et al. 1990). Therefore, when comparing two closely-related species, such as the Great and Yellow-knobbed curassows, it is perfectly reasonable to expect a sexually-selected trait to evolve more quickly and become more exaggerated in the polygynous species. What is important is that male Yellow-knobbed Curassows are markedly more ornamented than male Great Curassows, even if both species are relatively

somber in plumage. Jones (1992) provided examples of monomorphic, monogamous species that are brightly colored as support for sexually-selected extravagance in monogamy. However, it is important to remember that there also are nonsexual explanations for the evolution of bright plumage (West-Eberhardt 1983, Baker and Parker 1979) and that these selective conditions are particularly likely to occur in monogamous systems.

Jones (1992) also lamented the neglect shown the direct-benefits hypothesis in studies of sexual selection in polygynous species. I rejected this hypothesis in my study of the Yellow-knobbed Curassow because males do not provide obvious direct benefits to females, such as feeding territories and paternal care. Jones suggested that polygynous males may provide less-obvious benefits to the female, such as avoidance of predation, injury, and contagion (Reynolds and Gross 1990). Nevertheless, it seems that the reason few authors have addressed the direct-benefits hypothesis is that there is little reason to believe, with the exception of the contagion-avoidance theory, it is an important mechanism in polygynous systems. Unfortunately, despite the applicability of the contagion-avoidance theory, testing it requires basic etiological information not yet available, technology not often used by field biologists (e.g. ELISA techniques) and restrictions incongruent with remote field conditions. It appears likely that these barriers to testing the contagion-avoidance hypothesis will soon be surmountable for a few select species of direct economic importance.

Lastly, Jones (1992) contended that my data are inconsistent with the good-genes model, because I found no effect of coccidia load on male ornamentation. The model of Hamilton and Zuk (1982) of parasite-driven sexual selection is but one good-genes scenario. The exclusion of this hypothesis, especially in captive animals with relatively low parasite loads and minimal parasite diversity, does not eliminate the entire idea of good genes.

Jones (1992) has identified gaps in my evaluation of the adaptive significance of fleshy ornamentation in curassows. Clearly, he and I have different, though not incompatible, philosophies of ornithology. Jones called for experimental field studies that control for "confounding factors." I agree that manipulation provides us with the best chance of testing these models. I am presently conducting such experiments in Wild Turkeys (*Meleagris gallopavo*) and Sandhill Cranes (*Grus canadensis*). However, the relative ease with which some common "weedy" species are manipulated does not exclude the need for studies of rarer species in a theoretical framework, even if they do not meet all the criteria for a perfect and complete analysis of the

question. Ornithologists are interested not only in sexual selection, but in the behavioral, morphological and physiological diversity of the class Aves. The reasons a large-bodied, late-maturing, small-clutched, elusive curassow is brightly ornamented may provide a very different view of the evolution of sexual ornamentation than that provided by experimental studies of Zebra Finches (*Taeniopygia guttata*), widow-birds, swallows or junglefowl. Thus, in order to begin to understand the breadth of avian ornamentation, I believe we need to encourage study of the "difficult" species, as well as the "easy" ones.

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Received 14 June 1991, accepted 27 June 1991.