

dak 4" × 5" type 4162), and thermoprints (Sony 110 mm × 20 mm) to document plumulaceous structures. We use an alphanumeric generator to label the face of photomicrographs using species codes from Edwards (1982, 1986). Each photomicrograph is labelled with species, tract, vane, vanule, and position of the barbules along the rachilla or ramus. We include technical information, such as the type of SEM, working distance, and magnification (if not shown on the face of the photograph). The photomicrographs are stored in file-card boxes or notebooks (in systematic order) following alphanumeric codes developed by Edwards.

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Sexual Selection and the Evolution of Extravagant Traits in Birds: Problems with Testing Good-genes Models of Sexual Selection

IAN L. JONES

Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, United Kingdom

The evolution of extravagant traits that may be favored by sexual selection has received much attention in recent literature. Empirical studies have focused on attempts to test alternative sexual-selection mechanisms, using ornaments of some birds as examples of such elaborate traits. However, the interpretation of empirical evidence has been controversial, and recent papers have pointed out numerous difficulties in testing these models (Read 1990, Kirkpatrick and Ryan 1991). Here, I reevaluate some findings of a recent paper on ornaments of curassows (Buchholz 1991) to point out some pitfalls to consider in inter- and intraspecific tests of sexual-selection hypotheses. Buchholz (1991) pointed to a correlation between knob-ornament size and age of Yellow-knobbed Curassows (*Crax daubentoni*) as evidence for "good-genes" models of sexual selection. The interpretations presented in his study illustrate several perceptions of

sexual selection in general, and "good-genes," "run-away" and "direct-benefits" models (references in Kirkpatrick and Ryan 1991) in particular, that merit further discussion

Buchholz (1991) suggested that direct-benefits models to explain the evolution of mating preferences do not apply to Yellow-knobbed Curassows, because males "do not appear to defend territories or care for chicks." Even if this were true, it should not eliminate this model from consideration, because direct benefits (e.g. involving parasite, predator, or harassment avoidance; Reynolds and Gross 1990) could favor evolution of female preferences for extravagant male traits in lekking species, or others where males provide no care. Ornaments could be favored by sexual selection if they reflect nongenetic phenotypic differences among males that involve these mating advantages to females. Tests of the direct-benefits hypothesis seem

to have been lost in a rush to verify good-genes models, while the former remains a plausible alternative (Kirkpatrick and Ryan 1991). Further empirical work will need to address whether mating preferences relate to extravagant traits that indicate direct benefits, and/or to the much more difficult to evaluate good-genes model.

A second problem of interpretation concerns supposed exclusive predictions of good-genes and runaway models of sexual selection. It has been suggested that a positive relationship between an extravagant character and viability is an exclusive prediction of a good-genes model, and that a runaway model predicts no relationship between ornaments and viability (Heisler et al. 1987, Buchholz 1991). This may be an oversimplification of predictions of these models. Because both models explain evolution of costly traits that seem to be maladaptive with respect to natural selection, a correlation between expression of an extravagant trait and individual viability is expected regardless of whether the trait has evolved by runaway or as a signal of good genes (Read 1990). Imagine an ornament that has evolved through the hypothetical runaway process. Female preferences may drive evolution of this trait until its expression is limited by natural selection, potentially leading to an extravagant and costly ornament. Any differences in health or viability among individuals are then likely to be reflected in ornament expression, because healthy individuals will be able to afford greater costs. Thus, a correlation between viability and ornament size could result from a runaway process without any selection for a signal of good genes. Furthermore, such correlations are likely to be consistent with a direct-benefits model. Thus, simple correlations between extravagant traits and viability should not be taken alone as support exclusive to a good-genes model. The search for testable predictions of these sexual-selection models clearly has just begun. Buchholz (1991) suggested that the runaway model is not falsifiable until all possible correlates with viability have been tested. If this is the case, then it must also be true for good-genes models, because lack of correlation between ornament and one aspect of viability may inevitably lead to a search for other measures of viability, rather than rejection of this hypothesis.

Another question arises over the presence or absence of intrasexual selection favoring ornaments on Yellow-knobbed Curassows. We are told that no male-male combat was observed in Yellow-knobbed Curassows or Great Curassows (*C. rubra*), so curassow ornaments are unlikely to be favored by intrasexual selection. Lack of male-male combat does not rule out occurrence of intermale competition, nor does it rule out intrasexual selection favoring curassow ornaments. Male-male interactions that determine, for example, favored positions in an exploded lek may be extremely subtle. Observations that curassow ornaments do not change seasonally or during courtship (Delacour and Amadon 1973) suggest that knobs could

have a signal function outside the context of active female choice. However, no evidence presented by Buchholz (1991) establishes whether curassow ornaments have been favored by either inter- or intrasexual selection. Without such evidence, the appropriateness of good-genes, runaway, and other models involving intersexual selection to curassow knobs is doubtful. In general, careful observation and experiments must show that ornamental traits are favored by active mating preferences, while controlling for intrasexual competition (e.g. Höglund et al. 1990), before proceeding to test intersexual selection models.

Another source of difficulty in interpretation of sexual-selection models concerns whether a correlation between an extravagant trait and age represents evidence that the trait signals good genes. Buchholz (1991) suggested that only good-genes theory predicts that males with big ornaments are older or healthier than their small-knobbed conspecifics. However, such relationships are not exclusive properties of a good-genes mechanism; they are likely to appear under other sexual-selection models, or even in the absence of sexual selection. Measures of viability are known to correlate with age within individuals, either for developmental reasons or because older individuals are more experienced. For example, individuals may become better foragers (e.g. Greig et al. 1983), or increase in dominance status (e.g. Ekman and Askenmo 1984) with age, either of which could lead to a correlation between age and viability. Expression of a costly ornament could reflect these nongenetic differences among individuals, or the ornament might itself be constrained by developmental processes related with age. Female preferences could then be favored by direct benefits associated with mating with older, more ornamented males. Thus, the only unequivocal evidence consistent with ornaments even correlating with good genes would be if ornament size remains correlated with viability within age groups (i.e. after controlling for age in a longitudinal study). Ultimately, we would need to know if these individual differences in viability are heritable.

Buchholz (1991) contended that size of Great Curassow knobs is not an accurate indicator of age. However, this was not properly tested because, with a sample of only nine birds, correlation between age and knob would have to be overwhelmingly strong to be significant (see Forbes 1990). Based on data presented in figures 3 and 5 of Buchholz (1991), there is no significant difference in strength of the relationship of knob height and age between Yellow-knobbed and Great curassows (ANCOVA of standardized data extracted from figs. 3 and 5; species-by-age interaction term is nonsignificant, $F_{1,18} = 0.03, P = 0.9$). There are simply insufficient data to indicate whether the relationships are different.

Buchholz (1991) suggested further that, because the Great Curassow is monogamous, sexual selection cannot favor evolution of an extravagant ornament. This

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

RICHARD BUCHHOLZ

Department of Zoology, 223 Bartram Hall, University of Florida, Gainesville, Florida 32611, USA

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