OLDER MALES HAVE BIGGER KNOBS: CORRELATES OF ORNAMENTATION IN TWO SPECIES OF CURASSOW

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ABSTRACT.—I examined the correlation between the size of male facial ornamentation and three measures of viability in the polygynous Yellow-knobbed Curassow (*Crax daubentoni*) and the relationship between age and knob size in the monogamous Great Curassow (*C. rubra*), to determine which of three sexual selection models could account for the maintenance of these anomalous structures. Field studies of both species suggest that these ornaments are not used in intrasexual signaling. The data for the Yellow-knobbed Curassow support the "good genes" model of sexual selection, although not the Hamilton and Zuk (1982) model of extravagant characters as indicators of male resistance to parasites. Ornament size was not associated with body size or coccidian load, although the latter was negatively correlated with tarsus length. No hematozoa were found in blood smears. Knob height, wattle height, and wattle width were reliable indicators of age in this species and may be used by females in mate choice. Because older males have demonstrated their presumably heritable ability to survive, female preference for males with big ornaments is consistent with the "good genes" model. The absence of a correlation between knob size and age in male Great Curassows supports the hypothesis that age-character relationships will be strongest in long-lived polygynous species. *Received 14 February 1990, accepted 30 July 1990.*

EXTRAVAGANT characters are morphological or behavioral traits that may be maladaptive under natural selection but provide a differential mating advantage under sexual selection (Nur and Hasson 1984). Both intrasexual and intersexual roles have been proposed for these traits. In Borgia's (1979) War Propaganda model a male assesses the competitive abilities of other males by examining the quality of their extravagant characters. By clearly and honestly signaling their status (Kodric-Brown and Brown 1984), high-quality males avoid energetically costly battles with weaker males. In addition to or instead of intrasexual signaling, female assessment of male extravagant characters may occur.

There are three major schools of thought on the adaptive function of female choice (Johnson and Marzluff 1990). The first holds that female choice is based on the ability of males to provide immediate benefits to her and their offspring (e.g. courtship feeding, foraging areas). However, extravagant characters are most elaborate in mating systems where males provide little or no paternal care (Sigurjønsdøttir 1981, Payne 1984, Björklund 1990). This suggests that these traits are not used to assess parental abilities. Therefore in this paper I concentrate on models of extravagant character evolution that address the nondirect benefits most likely associated with ornamentation.

The "good genes" hypothesis proposes that extravagant characters reflect the genetically based ability of a male to survive, gain access to essential resources, and reproduce (Trivers 1972, Zahavi 1975, Kodric-Brown and Brown 1984, Andersson 1986). Females could increase their reproductive success if their offspring carried such "good genes," and they should prefer those males with the biggest, brightest, or most intense characters. A study of mate choice in *Drosophila* provides the only direct empirical support for this model (Partridge 1980).

The third hypothesis for the evolution of extravagant characters, first proposed by Fisher (1930), implies that, although females may have initially chosen males for a specific adaptation that promoted survival under natural selection, this adaptive reason for choice has been lost in a "runaway process." In the process he described, a genetic correlation evolves between the male character and the female preference for that character. Once the female-choice gene is established, female preference for the male character may continue under sexual selection alone, which would cause exaggeration of the trait until countered by natural selection (i.e. when the cost in decreased survival due to the

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character is greater than the benefit it provides in mate attraction) or until additive genetic variance for the male character is exhausted. Genetic models support the runaway process and demonstrate that it can be initiated by stochastic factors such as genetic drift (O'Donald 1980; Kirkpatrick 1982, 1985; Lande and Arnold 1985; but see Nichols and Butlin 1989).

Heisler et al. (1987) have proposed a methodology for distinguishing between the end products of these two intersexual processes at evolutionary equilibrium. Variance in an extravagant character that evolved via the good genes process must be positively associated with measures of individual viability (*sensu* Andersson 1986), whereas a nonpositive relationship with viability should be found for characters that are the result of runaway selection. The "runaway" hypothesis is not falsified, however, until all the possible viability correlates of ornamentation have been tested; a difficult task if selection is episodic or the species' natural history is not well known. Clearly most short-term studies will not be able to disprove this model convincingly. In any case isolating the mechanisms underlying phenotypic variation in extravagant characters remains the first step in determining how these traits are maintained (Zeh and Zeh 1988).

I examined age, size, and parasite load as correlates of an extravagant character in captive Yellow-knobbed Curassows (*Crax daubentoni*), and I examined age in Great Curassows (*C. rubra*; Galliformes: Cracidae). Males of both of these strikingly sexually dimorphic species have yellow "fleshy" knobs—absent in females—on the maxilla. In addition the male Yellow-knobbed Curassow has two pendant wattles on the mandible. Although the adaptive significance of this ornamentation is not known, sexually selected functions have been proposed for "fleshy" ornaments in this species (Delacour and Amadon 1973, Buchholz 1989) and have been described in related species (Brodsky 1988, Zuk et al. 1990). My goal was to determine which sexual selection model might account for the evolution of curassow knobs and wattles. Across curassow species, male ornament size is correlated positively with sexual size dimorphism, a measure of male-male competition in other Galliformes (Spearman rank correlation, $r_s = 0.97$, $n = 7$, $P < 0.02$; Fig. 1; Payne 1984). However an absence of any direct male-male combat in field studies of the Yellow-knobbed and Great curassows does not support the "intrasexual signaling" hypothesis (Sermeno 1986, Buchholz 1989). Sexual dimorphism in curassows may be the result of female choice or alternative processes (Hedrick and Temeles 1989). Because courtship displays appear to emphasize the size and color of the ornamented head by placing it against the black back of the animal (Delacour and Amadon 1973), it seems likely that female choice has played the predominant role in the evolution of knobs and wattles.

Both the "good genes" and the "runaway" hypotheses predict that females will prefer to mate with males with the biggest knobs. Only the "good genes" theory predicts that males with big ornaments are older or healthier than their small-knobbed conspecifics (Heisler et al. 1987). If curassow ornaments evolved via the Fisherian runaway process, big-knobbed males should be no more likely to survive than small-knobbed ones.

METHODS

The study species.—Curassows are elusive and occur at low population densities. Little is known of their natural history. Based primarily on observations of captive pairs, Delacour and Amadon (1973) asserted that all curassows are monogamous. However, considerable fieldwork provides contrary evidence (Schaefer 1954, Gines and Aveledo 1958, Buchholz 1989, Strahl et al. in press). Male Yellow-knobbed Curassows do not appear to defend feeding territories or care for chicks (Schaefer 1954, Buchholz 1989). The dispersion and calling behavior of Yellow-knobbed Curassow males most closely resembles that of the "exploded lek" (Buchholz 1989, Strahl et al. in press) described for birds of paradise, some grouse, and parasitic widow-birds (Gilliard 1969, Wittenberger 1978, Payne and Payne 1979, Beehler and Pruett-Jones 1983). On my study area in Venezuela, males displayed within earshot of one another from calling trees on the edge of the gallery forest. Females, which otherwise spend most of their time in the forest, visited these calling sites singly or in groups, and they were courted by the resident male (Strahl et al. in press). Based on this evidence, I think it likely that this species is polygynous. The Great Curassow, on the other hand, is probably monogamous, with the male helping in nest construction and care of the brood (Quinto Adrian 1981, Sermeno 1986). The Great Curassow has a less exaggerated knob than the Yellow-knobbed Curassow and no wattles.

Curassow knobs and wattles are thought to increase in size with age, but they probably do not change in size or color seasonally or during courtship (Delacour and Amadon 1973). It has been suggested that "fleshy"

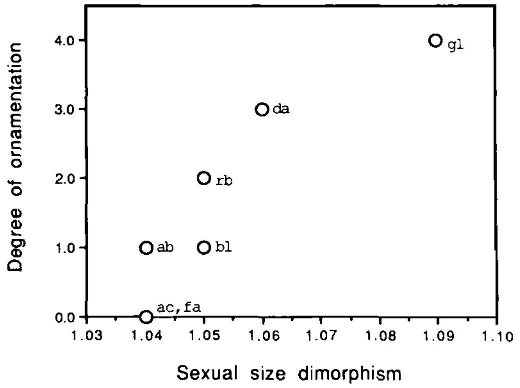

Fig. 1. Maximum degree of fleshy ornamentation increases with sexual size dimorphism (male wing chord/female wing chord) across curassows in the *Crax rubra* superspecies group (r_s = 0.97). Size data from Blake 1977. ab = alberti; ac = alector; bl = blumenbachii; db = daubentoni; fa = fasciolata; gl = globulosa; rb = rubra.

facial ornaments in birds, which are often highly vascularized (Lucas and Stettenheim 1972), are used by females to assess the blood parasite load of prospective mates (Hamilton and Zuk 1982). Cracids are known to be very susceptible to protozoan (Phylum Apicomplexa, Subclass Eucoccidiida) infections of the blood (*Haemoproteus, Plasmodium, Trypanosoma*) and gastrointestinal tract (coccidia of the genus *Eimeria*), thus they may provide a good test of this hypothesis (Todd and Hammond 1971, White et al. 1978, Bennett et al. 1982).

The study area and methods.—A unique living collection of nearly all species of the family Cracidae are kept by Jesús Estudillo L. in Mexico (described by Winckler 1988). The majority of the curassows were hatched and raised on the premises, and thus they were of known age and history. Additional data on the Yellow-knobbed Curassow came from two captive specimens in San Fernando de Apure, Venezuela. In Mexico, 11 separately housed male Yellow-knobbed Curassows were captured, and I measured wing chord and tarsus length with a tape measure. Six measures of ornament size were taken in this species with calipers (Fig. 2). I measured knob height from the dorsalmost part of the knob to the constriction at the maxilla, and I measured wattle height from the dorsalmost colored part of the wattle integument (the upper edge of the mandible) to the ventralmost part of the pendant wattle. Knob and wattle width was the thickest diameter of these structures in the lateral plane. I measured ornament depth from the anteriormost projection to the posterior limit.

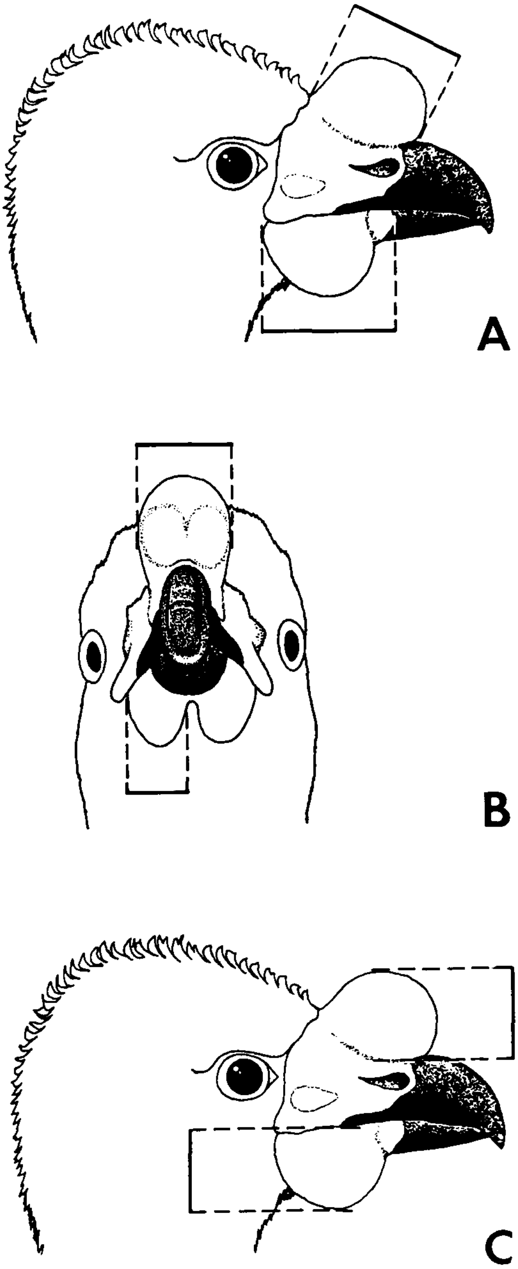

Fig. 2. Ornament measurements taken from the Yellow-knobbed Curassow: (A) knob and wattle depth, (B) knob and wattle width, (C) knob and wattle height.

To assess parasite load, three or four blood smears were made from each bird with blood taken by syringe from the wing vein. Smears were air-dried, fixed in 100% methanol, stained with Giemsa following standard methods, and examined for hematozoa. Fresh fecal samples were preserved in 10% formalin and "floated" for collection of coccidian oocysts (Todd and Hammond 1971). Species identification of fixed coccidian oocysts is not possible, and thus the data represented a general measure of infestation by the Eucoccidia. The curassows had not been treated for

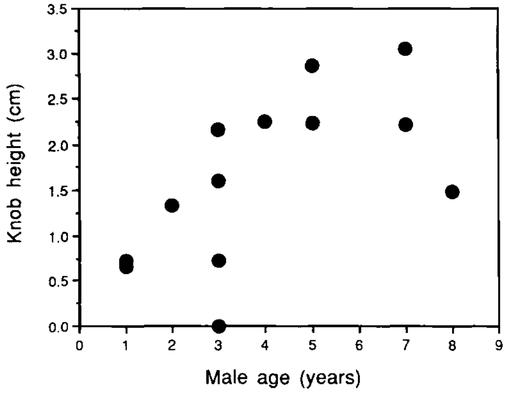

Fig. 3. Knob height of male Yellow-knobbed Curassows in relation to their age in years ($r_s = 0.67$).

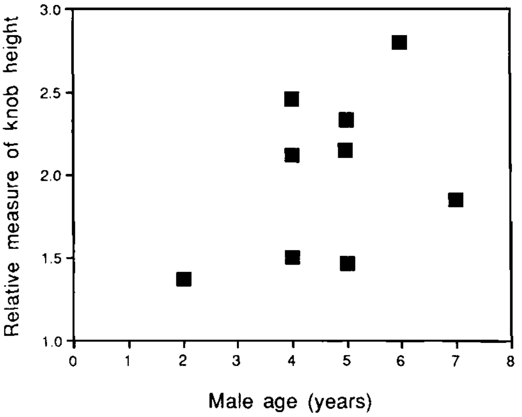

Fig. 5. The relative knob height of the Great Curassow is not significantly correlated with age.

hematozoan or coccidian infection (E. Appelaniz and M. Merino pers. comm.).

Rather than handling nine Great Curassows of known age, we used photographs to measure knob height. Knob height relative to eye diameter (presumed constant across individuals) was measured from a projection of an Ektachrome slide of each male. In Yellow-knobbed Curassows direct measurement of knob height was highly correlated (Spearman rank correlation, $r_s = 0.82$, n = 12, $P < 0.01$) with photographic measurements, so this method should be similarly accurate for the Great Curassow. The Spearman rank correlation test was used to determine the significance of associations between viability correlates and ornamentation.

RESULTS

There was no significant relationship between body size, as measured by tarsus and wing chord length, and age ($r_s = -0.18, -0.09$, $n = 13$, $P > 0.05$) in the yellow-knobbed species. Similarly, body size was not significantly associated with ornament size parameters (all $P > 0.05$). Knob height was highly correlated with age ($r_s = 0.67$, $n = 13$, $P = 0.02$; Fig. 3), but knob width and depth were not ($r_s = 0.54, 0.45$, $n = 13$ $P > 0.05$). Wattle height and width were highly correlated with age ($r_s = 0.64, 0.77$, $n = 13$, $P = 0.03$, $P = 0.008$; Fig. 4) but not wattle depth ($r_s = 0.82$, $n = 13$ $P > 0.05$). The height of the knobs of the Great Curassow, the only ornament variable measureable from photographs, was not significantly correlated with age ($r_s = 0.47$, $n = 9$, $P > 0.05$; Fig. 5).

I detected blood parasites in 43 blood smears from 12 males sampled. Coccidian oocysts were present in low numbers (1-3) in 3 of the 11 birds sampled and were numerous (10) in 2 of the birds. A negative relationship between coc-

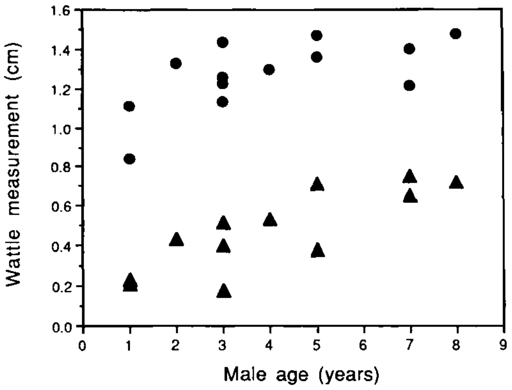

Fig. 4. Wattle height (●) and width (▲) of male Yellow-knobbed Curassows in relation to their age in years ($r_s = 0.64$ and $r_s = 0.77$, respectively).

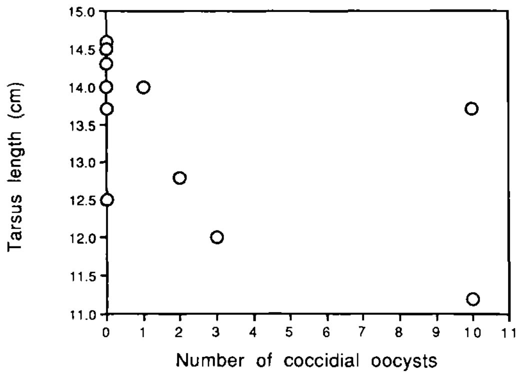

Fig. 6. The number of coccidial oocysts per fecal sample is negatively correlated with male tarsus length in the Yellow-knobbed Curassow ($r_s = -0.64$).

cidian load and tarsus length was significant ($r_s = -0.64$, $n = 11$, $P < 0.05$; Fig. 6). Wing chord was not significantly correlated with coccidian load ($r_s = 0.13$, $n = 11$; $P > 0.05$). Coccidian count had no correlation with any aspect of ornament size (all $P > 0.05$) and did not account for ornament variability within age classes (Kendall partial correlation coefficient, all $P > 0.05$; Siegel and Castellan 1988).

DISCUSSION

The size of ornaments on male Yellow-knobbed Curassows are accurate indicators of male age. Because older age demonstrates general viability (Halliday 1983), the data support the "good genes" model of sexual selection for the Yellow-knobbed Curassow. Big knobs may indicate that males have survived despite parasitic diseases and limited resources. However, these results do not specifically support the Hamilton and Zuk (1982) model of ornamentation as an intraspecific indicator of resistance to parasites. Although the reduced tarsus sizes for infected curassows suggests a deleterious effect of coccidian infection, this was not correlated with ornament size. Thus resistance to coccidia, which are common and damaging parasites in many Galliformes (Ruff et al. 1988, Schmidt and Roberts 1989), could not be assessed by females on the basis of male knob or wattle size in this population. Females may assess coccidian load based on some unmeasured ornament characteristic, such as pigmentation, although no variation in ornament coloration was evident. An unlikely alternative possibility is that this species is not normally infected by coccidia in the wild, and thus advertisement of coccidian load has not been favored through female choice.

The absence of blood parasites in the blood smears is frustrating in light of the high infection rates normally seen in the Cracidae (ca. 30%; White et al. 1978). The aviaries in which these birds were kept are at a relatively high altitude and are not within the normal range of any cracid species. Nevertheless, several hundred cracids are maintained in close quarters in these aviaries, and because many were wild caught, they should provide an adequate inoculum and population size for blood parasites and their insect vectors. A better understanding of the life cycle of the parasites and their vectors is necessary to clarify this result (Endler and Lyles 1989). Alternatively, some blood parasites, such as *Plasmodium*, may remain dormant after the initial infection, only to again manifest their haemolytic effects when the host is stressed (Hayworth et al. 1987). The birds were sampled near the end of their long breeding period in captivity and thus were probably in the most stressful period of their yearly cycle, but with unlimited food and no opportunities for intrasexual interaction, stress was minimized. It remains possible that my sampling technique may not have actually determined the infected state of these males. Repeated sampling over time would provide a better assessment of parasite levels.

Although there is often a marked change in the plumage of birds when they reach sexual maturity, data on the accuracy of male sexual characters for assessing age are sparse (Manning 1985). Precise age-graded changes in the plumage of some birds have been documented, for example, in Long-tailed Manakins (*Chiroxiphia linearis*; McDonald 1987) and Satin Bowerbirds (*Ptilonorhynchus violaceus*; Borgia 1986). In addition, ornament-specific changes with age have been described in the tail feathers of male lyrebirds (*Menura* spp.; Smith 1965) and in the number of ocelli on the trains of Common Peafowl (*Pavo cristatus*; Manning 1989). Data from the present study shows that the knobs and wattles of Yellow-knobbed curassows are accurate indicators of male age, but that the knobs of the Great Curassows are not.

Male age was the only significant correlate of ornament size found in the Yellow-knobbed Curassow. Females and other males could assess the general viability of the ornament bearer by examining his knob height and wattle height or width. Curassows have a small clutch size (2 eggs), take up to 3 yr to mature, and can live longer than 20 yr in captivity (Estudillo 1977). They are probably also long-lived in the wild. This life-history pattern places a premium on long survival, and female choice of male age might be especially advantageous under these conditions. The mechanisms of mate assessment may not be fine-tuned enough to detect small differences in parasite load or other aspects of viability (Cohen 1984). However, age subsumes most other correlates of fitness and should be chosen for by mate seekers, provided the older individual has not deferred possible matings in order to attain a greater age. Male-male interaction (Rohwer 1982; Borgia 1979, 1987; Petrie

1988) or resource limitation (Kodric-Brown 1989) may be other means of insuring that ornaments are honest advertisements of age.

The impact of different life histories and mating systems on the shape of the age-character relationship will reveal the relative, and perhaps conflicting, forces of natural and sexual selection on ornamentation. First, age-graded growth of extravagant characters should be most common in species with very long life spans. One would not expect to find age-graded growth in relatively short-lived species (e.g. <5 or 6 yr), in which yearly fecundity rather than longevity is the most important factor determining lifetime reproductive success. Ornaments in short-lived species may instead indicate more immediate attributes of viability, such as parasite resistance (Hamilton and Zuk 1982) and foraging ability (Kodric-Brown 1989). Second, because greater size or elaboration of ornaments may allow finer detection of male age by females (Cohen 1984), one would expect the more greatly exaggerated sexual characters found in polygynous species to be relatively better indicators of age than those of smaller size found in monogamous species. In addition, as demonstrated by the absence of a correlation between age and ornament size in the monogamous Great Curassow, the overwhelming constraints of natural selection on sexually selected extravagance in species that provide paternal care (Lande 1987, Kirkpatrick 1985) may limit ornament size and age-indication.

I suggest that male ornamentation in the Yellow-knobbed Curassow is the evolutionary result of female choice for older males and is not due to a Fisherian preference for mates with the biggest character. The runaway process may still have been an important force in the evolutionary history of the trait, or it may presently serve as a selective pressure on some other unstudied aspect of the character's appearance (e.g. its color or use in display). Unfortunately for researchers the "runaway" hypothesis is a default hypothesis that can never be proven experimentally, it can only be accepted as the unique selective pressure maintaining a trait after all other possibilities have been excluded.

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