

Mate choice by female red junglefowl: the issues of multiple ornaments and fluctuating asymmetry

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Abstract. The significance of multiple ornaments of male birds and other animals is currently not well understood. Male red junglefowl, *Gallus gallus*, possess a number of morphological traits that appear to be ornamental in nature. These traits include components of the colourful plumage and fleshy structures on the face and head, the single, medially-located comb, paired wattles and ear lappets. Some studies have implicated the comb in the mate choice decisions of female junglefowl, and some have also indicated that plumage of males is not important in this regard. To test for a possible role of other male morphological ornaments in female mate choice, and to evaluate the earlier counterintuitive findings concerning male plumage, we controlled comb size, and experimentally manipulated plumage, wattles and ear lappets of male red junglefowl. We also tested responses of female junglefowl to asymmetry of bilaterally paired male ornaments by manipulating the symmetry of the paired wattles, ear lappets and the ornate hackle feathers of the neck. None of these manipulations provided evidence that female red junglefowl are sensitive to asymmetry of paired ornaments of males. A series of tests involving a male with pronounced body asymmetry likewise produced negative results. In contrast to some other studies on birds, we obtained no evidence that female red junglefowl use symmetry of either ornamental or non-ornamental traits in mate choice decisions. Comb size, the only male trait shown to be used by females, both in the present study and in some earlier ones, did not correlate significantly with natural asymmetry in any of several measured traits.

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Males of most species of birds have more than one kind of morphological ornament thought to be used in sexual selection. Ornaments of birds take many forms. In addition to colourful and structurally modified plumage, species from many orders have bare skin on the face or head, which is often colourful and structurally specialized (e.g. the cock's comb). Although male birds typically have more than one display trait, consideration of multiple ornaments has only recently begun to be incorporated into models of sexual selection (e.g. Zuk et al. 1992; Møller & Pomiankowski 1993a; Hill 1994; Johnstone 1995; Andersson & Iwasa 1996).

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Møller & Pomiankowski (1993a, p. 167) offered three hypotheses to explain multiple ornaments. (1) The multiple message hypothesis '... proposes that each display reflects a single property of the overall quality of an animal. This is likely to be the case for ornaments that respond to condition on different time scales.' (2) The redundant signal hypothesis '... suggests that each ornament gives a partial indication of condition ...', and that 'females pay equal attention to the expression of all the secondary sex traits in order to obtain an estimate of overall male condition'. (3) The unreliable signal hypothesis '... argues that some ornaments are unreliable indicators of overall condition and are only maintained because they are relatively uncostly to produce and there is a weak female preference for them. This predicts that multiple sexual ornaments should be particularly common in taxa with the most intense sexual selection (i.e. lekking and other polygynous taxa).'

In the polygynous red junglefowl, *Gallus gallus*, males have multiple ornaments. In an earlier study of male ornaments and female mate choice in this species, Zuk et al. (1992) reported that females tended to ignore the comb when it was experimentally manipulated (covered with a latex false comb), and appeared to focus instead on plumage traits, such as hackle colour. These results led Zuk et al. (1992, p. 1005) to suggest that (1) '... the various male secondary sex characters may be redundant, so that the same information is conveyed by several characters presented simultaneously', and (2) 'Alternatively, the various traits may be additive, with representatives needed from several areas for the hen to respond to the whole.' These suggestions correspond to the redundant signal and multiple message hypotheses, respectively, both of which were rejected by Møller & Pomiankowski (1993a) in favour of the unreliable signal hypothesis. The conflicting conclusions of Zuk et al. (1992) and of Møller & Pomiankowski (1993a) provided the impetus for the study of multiple ornaments presented here.

Another popular aspect of female mate choice is based on the phenomenon of fluctuating asymmetry (Van Valen 1962; Palmer & Strobeck 1986; Parsons 1990; Watson & Thornhill 1994). Fluctuating asymmetry is a population phenomenon and is defined as small, random deviations from perfect bilateral symmetry in a morphological trait. Fluctuating asymmetry, measured as the numerical difference in length between the two sides of a morphological trait (Thornhill 1992), occurs when a bilaterally symmetrical trait (e.g. left and right outer tail feathers) is under the control of the same gene or genes, and when an individual is unable to undergo identical development of the trait on both sides of its body. Failure to produce perfect symmetry indicates an inability to cope with stress (environmental or genetic) during development of that trait (e.g. Leary & Allendorf 1989; Parsons 1990; Nilsson 1994). Diverse factors, such as nutrition and level of inbreeding may contribute to fluctuating asymmetry.

Møller and colleagues have examined fluctuating asymmetry with regard to sexually selected ornaments in birds (e.g. Møller 1991; Møller & Hoglund 1991; Møller & Pomiankowski 1993b). In birds, sexual ornaments are usually bilaterally symmetrical. Often the paired ornaments are expressed or presented such that any deviation

from a high degree of symmetry should be readily apparent (Møller & Hoglund 1991). That is, the males' mode of presentation of certain paired morphological ornaments often appear to provide a means by which females could readily assess the degree of deviation of the ornaments from perfect bilateral symmetry. To date, female preference for males with the most symmetrical bilateral ornaments have been described in three bird species. First, female barn swallows, *Hirundo rustica*, prefer males with the longest and most symmetrical outer tail feathers (Møller 1992; but see Balmford & Thomas 1992; Balmford et al. 1993; Evans et al. 1994). Second, female domestic zebra finches, *Taenopygia guttata*, preferred symmetrically colour-banded males and males with symmetric chest plumage (Swaddle & Cuthill 1994a, b). Third, in the peafowl, *Pavo cristatus*, symmetry and degree of ornamentation are correlated (Manning & Hartley 1991) and peahens prefer males with more elaborate trains (Petrie et al. 1991). Other studies of the possible role of fluctuating asymmetry of male ornaments in sexual selection, however, have failed to demonstrate a preference by females for the more symmetrical male (e.g. Oakes & Barnard 1994).

Male red junglefowl have a number of ornamental characteristics, most of which are paired and bilaterally symmetrical, including certain groups of paired feather ornaments, such as the saddle of the lower back and the fleshy red wattles and ear lappets of the head. In contrast to these paired structures, the comb is a single structure atop the male's head.

Mate choice by female red junglefowl is influenced by the colour and size of the males' comb (e.g. Ligon & Zwartjes 1995; Zuk et al. 1995). Testosterone level directly affects comb size (e.g. Domm 1939; Ligon et al. 1990) and is negatively related to immune system activity (Zuk et al. 1995). The comb therefore appears to be a condition-dependent trait. In contrast, normal male-type plumage develops in the absence of testosterone (Domm 1939), which suggests that plumage probably cannot provide precise, current information about male condition (Ligon et al. 1990; Ligon & Zwartjes 1995).

The goal of the present study was to clarify the proximate basis of mate choice decisions by female red junglefowl with regard to the issues of multiple ornaments and the symmetry of paired ornamental male traits.

METHODS

The Study Species

The red junglefowl is the conspecific ancestor of the domestic fowl (Stevens 1991; Fumihito et al. 1994). Like most other pheasants, males are elaborately ornamented. Males have colourful orange, red and black plumage, and a fleshy red comb and paired wattles and ear lappets on the head. The plumage of females is drab and cryptic. Red junglefowl are polygynous and males typically provide no parental care. Free-ranging males routinely assist females in choosing a nest site, however, and during the period of egg laying males often provide high-quality (high protein) food items and protection, by serving as sentinels while the gravid females forage (J. D. Ligon, unpublished observations). Thus, unlike lekking species, free-ranging female junglefowl receive some direct (non-genetic) benefits from the male with which they associate.

The origin and general maintenance of the red junglefowl used in this study have been described (e.g. Ligon et al. 1990; Zuk et al. 1990, 1992). Briefly, we obtained junglefowl from the San Diego Zoo in 1984 and 1985. Subjects were reared in brooders until they were about 6 weeks old, after which rearing was completed in large outdoor pens containing birds of both sexes. We fed the birds commercial chicken feed (21% protein), later supplemented with scratch, and provided water *ad libitum*. We performed mate choice trials in the following spring, after the junglefowl were sexually mature, starting at 9–10 months of age.

Subjects

Females

All female subjects ($N=56$) were about 1 year old and had no prior breeding experience. Although they had not seen any of the male subjects for several months prior to the tests, they had been exposed earlier to immature males. In each experimental manipulation, females saw the same pair of males only once; however, most females were used in more than one set of trials. We tried to ensure that the hens tested were in the process of producing a clutch of eggs, which both increased their interest in mating and maximized the importance of their mate choice decisions.

Males

Roosters ($N=19$) were the same age as the females. As they reached sexual maturity, each male was penned individually. Such isolation from other males ensured that all test males behaved in a dominant manner. Matched pairs of test males were drawn from the pool of subjects.

Mate Choice Trials

Our test design allowed a female junglefowl to choose between two males and to mate with one of them without the complicating issue of male–male competition (Ligon & Zwartjes 1995). During each trial, we recorded behaviours of the test males.

Tests were run in outdoor enclosures (about $5.3 \times 5.3 \times 2.4$ m). For each trial, we tethered two test males in the centre of individual sections of the enclosure separated by a wood partition, and placed a female in a wire observation pen that ran the length of the enclosure. The males' tethers were long enough to permit the roosters to reach the corner or edge of their section of the enclosure, but stopped them just short of the partition between the sections. Both males were thus visible to the female but not to each other. Each male could reach all portions of its compartment, but a 1-m wide strip between the males' compartments and the female observation pen was beyond the reach of the tethered males. This strip provided a neutral area for the female that allowed her to move freely from one male to the other without interference or to remain away from both males.

We left the hen in the observation pen for 20 min and then released her into the enclosure. The behaviour of the males and the female was recorded by an observer in a blind outfitted with one-way glass and located outside the enclosure. Upon release from the observation pen, females usually solicited copulation by approaching one of the males and crouching near it with the wings locked in a semi-extended position (Kruijt 1964; Wood-Gush 1971). In a few cases, the female approached a male and copulation ensued without a preliminary crouch. Our criterion of mate choice by females was approach to a male and mating within 10 min; most matings occurred within 2 min (Ligon & Zwartjes 1995).

Experimental Manipulations of Male Ornaments

Before conducting manipulations of morphological traits we carefully matched pairs of males for comb size, as well as for other traits, such as body size and tarsus length (Ligon & Zwartjes 1995). Controlling these traits permitted us to test for the effects of specific manipulated characters on the females' mating preferences.

Comb and wattle size

To certify that the female subjects were capable of assessing and discriminating between males, we investigated their responses to pairs of males; one male had a large comb, while the other had an artificially reduced small comb. Pairs were matched from a pool of five males; three had large combs, and two had small combs. Thus, more than one female saw the same pair of males.

Like the comb, the paired red wattles of male red junglefowl are conspicuous facial ornaments. Because the comb and wattles are influenced by testosterone (e.g. Hardesty 1931), and because the comb is used by females in mate choice, we surmised that the wattles might also be important in mate assessment by female junglefowl. To test for their possible importance, we surgically removed them from one member of each of two pairs of males with combs of almost equal size. To ensure that female choices were not affected by the males' combs, we also removed the combs from two additional matched pairs of males and the wattles from one member of each of these two pairs.

Following instructions provided by the university veterinarian, combs and wattles were surgically reduced in size after they had been anaesthetized with Lidocaine (Zuk et al. 1992; Ligon & Zwartjes 1995).

Ear lappet colour

Paired fleshy ear lappets are beneath the ear openings of both male and female junglefowl. Like the comb and wattles, they are much more colourful and highly developed in males. In our population of junglefowl, these lappets are usually red, although white ear lappets occur in some individuals. Ear lappet colour varies geographically as well as within populations. In two of the five subspecies of red junglefowl they are usually white, and whitish lappets also occasionally

occur in the others (Delacour 1977). The inter-population variation in ear lappet colour suggested the possibility that female red junglefowl are attracted to the white ears (as, for example, by some sort of sensory exploitation process, e.g. Ryan et al. 1990).

To the human eye, white lappets contrast with the surrounding red-coloured area. We conducted a series of mate choice trials using four matched pairs of roosters that originally had red ear lappets. Both lappets of one male of each pair was then painted white. The paint was readily removable, so we could use each individual male as both the experimental and control bird.

Plumage

In an earlier study (Ligon & Zwartjes 1995), female junglefowl did not discriminate between normal-plumaged and mutant males with female-like ('henly') plumage, with both males bearing large combs. This result suggests that the ornamental feathers of male red junglefowl are not important to female mate choice decisions. An alternative interpretation is that, since both members of the pairs of test males had large combs, the females may have relied on comb size, which may have 'overridden' other signals. That is, since both males had large combs of equal size, females may have judged the two males as equally acceptable, made no additional assessment, and simply mated randomly.

This interpretation leaves open the possibility that, under some conditions, females do assess male plumage. If female red jungle fowl use a hierarchy of cues (Zuk et al. 1992), such as comb size first, and plumage characters or behavioural displays second, then when combs of both males are large, females might be equally likely to mate with either male (Ligon & Zwartjes 1995). A hierarchy of cues could come into play only when the primary cue is deficient, such as when combs of both males are small or absent. The female's attention might then switch to other, 'secondary' characters, such as plumage.

To address this possibility, we matched three pairs of test males for comb and body size. In each pair, one male had normal plumage and the other had hen-feathered plumage. The combs and wattles were then surgically removed from all six males, as described above, prior to conducting a series of mate choice trials. This procedure

allowed us to determine whether, in the absence of possible cues to male quality based on combs and perhaps wattles, mate choice by females would be affected by the males' plumage.

Symmetry Manipulations of Males

To obtain evidence concerning the possible role of ornament symmetry in mate choice, we manipulated two bilaterally paired sets of morphological structures that appear to be ornamental: the wattles and ear lappets. We also altered the symmetry of the specialized neck, or hackle, feathers. Finally, we used an abnormal male that was asymmetrical in body shape in mate choice tests to ascertain whether females would avoid such a male.

Wattle size asymmetry

We used five matched pairs of males. Individuals comprising four of the pairs showed little natural asymmetry. We trimmed wattles of two control males with slight natural asymmetry to make them symmetrical. In two other cases, to control for a manipulation effect, we also barely trimmed both wattles of the symmetrical rooster of each matched pair. For these four pairs of males, we manipulated the wattles so that a 10-mm difference existed between the left and right side. Wattle lengths of each pair of roosters were adjusted so that the total wattle lengths (left plus right) of both individuals were equal. For example, if the asymmetric male had a left wattle 25 mm long and a right wattle 35 mm long, each wattle of the symmetrical member of the pair was 30 mm.

To test for a relationship between natural asymmetry of males and female choice, the fifth pair consisted of a symmetrical male and a male that was naturally conspicuously asymmetric in wattle development (8-mm difference in length of the left and right wattles).

Ear lappet colour asymmetry

As mentioned above, white lappets are characteristic of some subspecies of red junglefowl. We therefore tested for a response of females to conspicuous colour asymmetry of the lappets, as follows. For one male in each of four matched pairs of males, one ear lappet was painted white

and the other retained the normal red colour. Because the white paint was easily removed, we were able to use both members of each matched pair as both the experimental and the control individual in different trials. Both ear lappets are visible from a frontal view of the bird; thus this asymmetry probably was not difficult for females to see.

Hackle asymmetry

Some correlational evidence suggests that the neck hackles of males may be weakly involved in female mate choice (Zuk et al. 1990, 1992), although more recent studies indicate that male plumage is not important in female mate choice decisions (Ligon & Zwartjes 1995; Zuk et al. 1995). Thus, as another test for the possible sensitivity of females to ornament asymmetry, we clipped off the feathers from either the left or right side of the hackle of one male in each of three matched pairs.

Body shape asymmetry

We also opportunistically conducted mate choice trials to test for an effect of body asymmetry. Early in its development, we had noticed that one young male was conspicuously abnormal morphologically, with a bowed back. We do not know whether this deformity was genetic in origin or due to an accident early in the bird's life. This individual appeared healthy in other respects (e.g. the bird's ornaments and courtship vigour appeared to be normal), and it provided us with the opportunity to ascertain whether females were sensitive to asymmetrical body shape or to atypical or abnormal courtship movements. The abnormal male was matched with two other roosters, and we obtained mate choice tests for each male pair.

RESULTS

Experimental Manipulations of Male Ornaments

Comb size

Most females (13 of 15) chose the large-combed male ($\chi^2_1=8.07$, $P=0.005$). This result demonstrates that (1) if females are responsive to a particular trait, many trials are not required to obtain statistical significance, (2) the hens used

here, like those of a previous study (Ligon & Zwartjes 1995), responded to comb-manipulated males, and (3) female junglefowl are consistently sensitive to certain male traits. These points indicate that the negative results reported in the following sections are not due to an absence of discrimination by females.

When presented with two males with different-sized combs, females made a mate choice decision in about 83% of the trials (N trials=18). In contrast, when comb size was controlled, either by matching males with very similar comb sizes or by removing the combs, females made a mate choice decision in only about 45–65% of the trials (N trials=481, $\chi^2_1=9.519$, $P=0.002$). Females were significantly more likely to make a mating choice when comb sizes were conspicuously unequal than when any other trait was similarly manipulated.

Other ornaments: plumage, ear lappet colour, and wattles

The presence or absence of wattles had no detectable effect on mate choice decisions by the female junglefowl. When presented with two males bearing normal combs of equal size, one with wattles and the other without wattles, the 20 females showed no significant preference for either type of male ($\chi^2_1=0$, $P=1.00$). The results were similar when the males possessed combs that had been surgically reduced. Ten of 20 females chose the male with wattles; 10 others chose the male without wattles ($\chi^2_1=0$, $P=1.00$).

Painting the red ear lappets of males white likewise had no significant effect on the mate choice decisions of females. Fifteen females chose the altered male and 15 others chose the control male.

Using normal and hen-feathered males without combs or wattles, females chose both phenotypes with equal frequency (23 of 45 females chose the normal male; 22 chose the hen-feathered male, $\chi^2_1=0.02$, $P=0.882$; also see Ligon & Zwartjes 1995). These results indicate that, when confronted with comb-less males, the females did not shift their attention to plumage characteristics.

Tests for a Role for Symmetry of Bilateral Paired Ornaments

None of our results indicated that asymmetry of bilateral ornaments affected female mate choice.

Seventeen of 30 females chose the male with asymmetrical wattles ($\chi^2_1=0.533$, $P=0.465$). In the tests in which a male with naturally asymmetric wattles was used, five of eight females mated with that individual (i.e. the naturally asymmetrical male was not avoided). Similarly, females were unaffected by experimentally-produced asymmetry either in ear lappet colour or in hackle plumage (ear lappet colour: 14 of 30 females chose the asymmetrical male, $\chi^2_1=0.133$, $P=0.715$; hackle: 16 of 30 females chose the asymmetrical male, $\chi^2_1=0.133$, $P=0.715$). The same was true for the tests dealing with body shape asymmetry: females chose the deformed male in 16 of 30 trials ($\chi^2_1=0.133$, $P=0.715$), indicating that any abnormal postures or movements that may have been associated with this male's courtship did not affect female mate choice.

DISCUSSION

The Issue of Multiple Ornaments

Why many species bear more than a single ornament is an important issue with regard to theories about the evolution and maintenance of male ornamentation and behavioural display, and it provokes several questions. (1) Why are some ornaments of males used by females in their mate choice decision, while other, apparently equally complex ornaments appear not to be important to females? (2) Why do ornamental signals become increasingly elaborated? (3) Why might certain ornaments lose the ability over time to convey accurate information to females; that is, why does a single, simple ornamental trait not suffice indefinitely?

Møller & Pomiankowski (1993a) concluded that the evidence supports the unreliable signal hypothesis, and that it does not support either the multiple message (which posits that each ornamental trait reflects a single aspect of the male's overall quality), or the redundant signal (each ornament gives a partial signal of condition) hypotheses. This conclusion led them to place male ornaments into two categories. If a particular ornament is unrelated to male condition, and is not currently used by females as they assess prospective mates, these authors consider it to be a non-functional 'Fisher trait'. (Use of the term Fisher trait is misleading, in that it implies that the trait in question evolved via Fisherian runaway

selection (Fisher 1958), which has not been documented (Kirkpatrick & Ryan 1991). In contrast to 'Fisher traits', if the ornament is related to its bearer's condition, and is thus more costly for low-quality than for high-quality males to produce and maintain, the ornament will reliably reflect good genes. Such ornaments may become ever larger, more colourful, or more intricately designed, until further elaboration is stopped by the counteracting forces of natural selection (Møller & Pomiankowski 1993a).

Because we obtained no evidence that females rely on two or more male ornaments, our results appear to support the conclusions of Møller & Pomiankowski (1993a), rather than those of Zuk et al. (1992). Our results argue against both the multiple message hypothesis and the redundant signal hypothesis, but they are consistent with the unreliable signal hypothesis, in that (1) the one ornament, the comb, that females use is a condition-dependent trait (e.g. Ligon et al. 1990; Zuk et al. 1995), and (2) females appear not to be influenced by other male ornaments.

Other evolutionary hypotheses also address the question of multiple ornaments. For example, females may shift their attention from one trait to another because of a fundamental conflict of interest between the sexes. Females may seek accurate indicators of male quality or condition, but the majority of males (the average and below-average individuals), on the other hand, may attempt to 'cheat' by attempting to produce signals that falsely indicate that they are of above-average quality (Hill 1994). This model provides an explicit mechanism for the continued elaboration of a male ornamental trait, and it also relates to the question of multiple ornaments by accounting for a shift by females from one ornamental trait to another.

Because males compete for females via ornaments, it pays a high-quality male to produce signals honestly indicating cost, either by continued elaboration of a single trait or by producing a new ornamental trait attractive to females. Both evolutionary responses are driven by the importance to females of honest signals of male quality, together with the attempts of low-quality males to express those signals dishonestly. Hill (1994) argued that extreme development of ornamental traits will occur only if average and below-average males can somehow match the ornaments of high-quality males. That is, if males of both low

and high quality can produce traits of equal development, females will strongly favour further elaboration of the same trait. Alternatively, females may change their focus to a new trait that more reliably signals quality. If average and low-quality males cannot match the signals produced by high-quality males, simple traits of high-quality males can function indefinitely as reliable indicators. Thus the females' demand for accurate indicators of male quality can either drive continued elaboration of traits, or lead to a shift from reliance on one male ornamental trait to another (Hill 1994).

With regard to male red junglefowl, if all males can produce equivalent ornamental plumage, then plumage should not be important to females. The plumage of red junglefowl is coloured by melanins produced within the male's body (Witschi 1961), and normal male plumage develops fully in the absence of testosterone (Domm 1939; Ligon et al. 1990). Male junglefowl are able to produce normal plumage on a low-quality diet (M. Zuk, K. Johnson, R. Thornhill & J. D. Ligon, unpublished data); thus, plumage ornamentation in this species does not appear to be costly. These points are consistent with both Hill's (1994) model and with the unreliable signal hypothesis (Møller & Pomiankowski 1993a), and they may explain why female junglefowl apparently do not rely on male plumage when making mate choice decisions. In contrast, in the house finch, *Carpodacus mexicanus*, colourful male plumage is used by females in mate choice decisions (Hill 1990, 1991). The red plumage colour of males of this species is produced by carotenoid pigments that must be obtained from the environment, and the colourful plumage is thought to be costly to produce (Hill 1990, 1991).

The comb of male red junglefowl appears to have evolved its present characteristics specifically to serve as an indicator of the individual's condition, via its reflection of testosterone level, as follows. (1) The size and turgidity of the cock's comb is due to a highly viscous intercellular mucoid produced by fibroblasts of the connective tissue, in direct response to the presence of testosterone. The pressure exerted by the mucoid affects the arterioles and capillaries and produces dilation of the capillaries. The haemoglobin from the blood showing through the epidermis gives the colour to the comb (Hardesty 1931). (2) In accordance with a handicap hypothesis, a negative

relationship exists between testosterone and the immune system (Folstad & Karter 1992). Male junglefowl with larger combs and higher levels of circulating testosterone also have fewer circulating lymphocytes (Zuk et al. 1995). Thus, in agreement with the arguments of both Møller & Pomiankowski (1993a) and Hill (1994), male red jungle fowl appear to possess both low cost-low information traits (plumage ornaments) and a high cost-high information trait (the comb). The most direct evidence that large-combed males may also be genetically superior is seen in the positive relationship between sire's comb size and growth rates of offspring (Johnson et al. 1993).

In view of the importance of the male's comb to females, the negative results of the mate choice tests focusing on the wattles was surprising to us on two counts. First, wattle size is highly correlated with comb size (R. Kimball, J. D. Ligon, & M. Merola-Zwartjes, unpublished data), and the wattles, like the comb, develop under the influence of testosterone (e.g. Hardesty 1931). Thus both structures might be expected to reflect male condition. Second, from an ethological perspective, the red wattles might be expected to enhance the visual stimulus provided by the comb and thus possibly elicit a stronger response than the comb alone. For these reasons, we had predicted that (1) males with both a comb and wattles would be more attractive to females than males without wattles, and (2) in pairs of roosters without combs, males with wattles would be more attractive than those without wattles. Neither prediction was supported.

Particularly because both combs and wattles of males develop in response to testosterone, why might female junglefowl ignore the latter structures? One possibility is that, although their development is controlled by testosterone, the wattles may provide less accurate information about male condition than is signalled by the comb. Over evolutionary time, the signal function of the wattles and ear lappets (as well as the plumage) may have been superseded by the comb. In contrast to the turgidity of the comb, the wattles and ear lappets are very thin and soft, and they probably differ histologically from the comb in not having the specialized testosterone-sensitive fibroblasts that produce the mucoid responsible for comb size and turgidity. Thus, although the wattles and ear lappets, like the comb, attain their full development in response to testosterone, they

probably do not provide either the kind or the precision of information about male condition that is signalled by the comb. This hypothesis suggests that the single, medially-located comb may have evolved more recently than the wattles and ear lappets.

The Issue of Ornament Asymmetry

None of the four sets of tests using asymmetrical wattles, ear lappets, neck hackles and body shape, had a detectable effect on mate choice in our population of female red junglefowl. These results suggest two points. First, overall the pairs of test males were well matched, that is, our attempt to pair males of equal 'quality' were successful. Second, and more importantly, it appears that female red junglefowl are not sensitive to asymmetry of the bilaterally paired ornaments of males.

Although negative results, such as those reported here, are always liable to the suspicion that something in the study design may have been overlooked, we believe that these findings provide important information about male ornaments and the mate choice strategies of female red junglefowl. The results reported here lead to two questions, at both proximate and ultimate levels.

First, why do female red junglefowl making mate choice decisions apparently ignore asymmetry in two paired morphological ornaments (wattles, ear lappets), as well as hackle feather and body asymmetry? The evidence suggests that females mostly or entirely rely on the males' comb. If females typically pay no attention to plumage, wattles or ear lappets of males, it should not be surprising that asymmetry in these traits does not elicit a response. This suggestion is supported by the fact that in their courtship displays, male red junglefowl typically do not present their bilaterally symmetrical ornaments so that both can be assessed simultaneously by the female. Although males sometimes approach prospective mating partners head-on, the waltz, which is the major copulation-encouraging display of males (Zuk et al. 1990), is a lateral display.

Second, those bilateral traits used in female choice show a negative relationship between fluctuating asymmetry and trait size (Møller 1993); that is, larger traits are also more symmetrical. In contrast, in ornaments not important to females, the relationship between fluctuating asymmetry

and trait size is either flat or U-shaped. No evidence suggests that fluctuating asymmetry in the ornamental wattles or ears of male red junglefowl reflects condition. Kimball et al. (1997) found no relationship between size and asymmetry of either the ear lappets or the wattles, nor did the symmetry of these traits correlate with other probable indicators of male condition (e.g. comb size, testis size, body condition). Møller's (1993) predictions about the relationship between fluctuating asymmetry and ornament size, together with the results reported by Kimball et al. (1997), suggest that female junglefowl ignore all of the bilateral ornaments of males.

The evidence is growing that female birds do consistently rely on condition-dependent traits when choosing a mate, and surveys of avian ornamental characters indicate that male condition can be signalled in many different ways (e.g. Ryan & Keddy-Hector 1992; Andersson 1994; Johnstone 1995). Thus, in some species, the degree of symmetry of paired ornaments may convey information about male quality that is used by females, but in others such symmetry may not be important in this regard (Møller 1993; Oakes & Barnard 1994; the present study). To illustrate, even within a single group, such as the pheasants, the kinds of indicators used by females in mate choice vary between species. In the red junglefowl, the male's single, medially-located comb seems to be important to females, but ornamental plumage appears to be unimportant. In contrast, in the peafowl, male plumage is important; both the size and the symmetry of the male's train are correlated with female preference and male quality (Manning & Hartley 1991; Petrie 1994). The evidence suggests that fluctuating asymmetry of male ornaments may be important for female choice in some cases, but not in others (Watson & Thornhill 1994).

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