
Multiple aspects of condition influence a heritable sexual trait: a synthesis of the evidence for capture of genetic variance in red junglefowl

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A long-standing question in the study of sexual selection is: if an attractive male trait signals heritable aspects of quality, how does genetic variation associated with that trait persist in the face of directional selection? It has been proposed that sensitivity to condition in general could allow a sexual signal to show heritable variation even under persistent directional selection. The multitude of genes underlying components of condition present a large target for mutation, and so genetic variance in condition may not be readily exhausted by selection. Insights gained in studies of the red junglefowl are relevant to this hypothesis, and provide a model for research in other systems. The fleshy comb of male red junglefowl is among the best-studied sexual signals. Multiple components of condition, such as health, immune function, testosterone, and social status, influence comb growth, and, in the present study, we provide the first comprehensive integration of this large body of evidence to lay out the compelling case for condition-dependence of the junglefowl comb. Variation in comb size is heritable and, most important to this issue, is genetically correlated with heritable variation in a body condition index. Although understanding of the red junglefowl's comb is far from complete, it exceeds our understanding of many other sexual signals and provides an empirical model for the study of condition-dependent signals in general. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **92**, 651–660.

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INTRODUCTION

The paradox of the lek was one of the first major theoretical problems in the study of sexual selection (Borgia, 1979; Kirkpatrick & Ryan, 1991; Andersson, 1994; Tomkins *et al.*, 2004). In lekking and many other polygynous species, a male's parental investment is limited to copulation (Ligon, 1999). Under these circumstances, what selection pressures favour choosy females? An early idea was that if males varied in genetic quality, and females could identify males with superior genotypes, then those males' genes would be passed to the offspring of selective females (Trivers, 1972). Females that choose high-quality males would be favoured because of increased

success (through natural and/or sexual selection) of their offspring as a result of their mate choice decisions (Andersson, 1994).

However, basic quantitative genetic theory predicts that if a trait experiences consistent directional selection, genetic variance associated with that trait will be rapidly eliminated (Fisher, 1930; Falconer & Mackay, 1996; Tomkins *et al.*, 2004). Thus, any genetic variance behind the expression of a male sexual signal should soon disappear if increased expression of that signal increased male mating success. Likewise, a sexual signal that conveyed information about some component of male fitness would not be expected to represent genetic variance in fitness because, by definition, fitness is under directional selection. Thus, if selection rapidly eliminates genetic variance underpinning fitness, why would selection favour female choosiness in cases where the hypothesized benefit to

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choosy females was acquisition of superior fitness-related genes for their offspring (Borgia, 1979)?

In 1996, Rowe and Houle proposed that condition-dependent traits retain heritability because their expression 'captures' the genetic variance in condition as a whole. Condition is a somewhat nebulous concept. It has often been used to refer to an individual's overall phenotypic quality, although it may be most useful to measure condition as the reserves available for investment in fitness-related traits (Blanckenhorn & Hosken, 2003; Tomkins *et al.*, 2004), keeping in mind that this is probably a function of factors such as the individual's health, nutritional status, and competitive ability, as determined by some combination of environmental and genetic effects. Rowe & Houle (1996) asserted that condition was likely to be dependent on the action of many genes, and thus susceptible to degradation from mutation at many loci. Thus, genetic variance in condition should rarely or never be driven to fixation. Indeed, genetic variance relevant to fitness is often present (Houle, 1992). Thus, if development of a sexual signal is dependent on condition, it should, at least partly, reflect genetic variance in condition (Rowe & Houle, 1996). Expression of sexual traits by males could be heritable, while also reflecting genetic variance relevant to fitness, thus favouring females who choose mates on the basis of such traits (Rowe & Houle, 1996).

STUDY SYSTEM

There is abundant empirical evidence for condition-dependence of many sexual signals. One of the most well studied vertebrate species from this standpoint is the red junglefowl (*Gallus gallus*), the wild ancestor of the domestic chicken. Based on studies of red junglefowl in the wild and free-ranging on the grounds of the San Diego Zoo, we know that they live in flocks composed of several females, a single dominant male, and several subordinate males relegated to the periphery of the flock (Collias & Collias, 1965, 1967, 1985, 1987, 1996; Collias *et al.*, 1966; Collias & Saichuae, 1967; Johnsen, Zuk & Fessler, 2001). The dominant male copulates most frequently with females, and actively interferes with copulation attempts by lower-ranking males. However, lower ranking males also attempt to copulate with females, and females choose to copulate with such males on occasion. Furthermore, female *Gallus* eject sperm after copulation with less desirable males (Pizzari & Birkhead, 2000). Thus, there is a role for female choice in determining male mating success. Females leave the flock to nest, and incubate their eggs and rear their chicks with little or no help from their male consort. The most striking sexual ornaments in male junglefowl are the bright red fleshy comb atop the head and the paired fleshy red

wattles dangling below the bill. Comb size varies dramatically among males, and thus appeared likely to act as a social signal. The results of over 30 sets of mate-choice trials strongly support the hypothesis that female junglefowl are attracted to males with large combs (Parker & Ligon, 2003).

Other research has clearly demonstrated that the red junglefowl comb is a condition-dependent sexual signal. Age, health, immune function, testosterone, and social status are known to influence comb size, and other likely factors, such as nutrition, have not yet been investigated. Recently, a rigorous set of standards was proposed for determining whether sexual signals are particularly condition-dependent. These standards include manipulating condition within a realistic range, comparing condition effects on sexual and nonsexual traits, and controlling for body size variation (Cotton, Fowler & Pomiankowski, 2004). The results from studies of the red junglefowl comb meet these criteria, and provide some of the strongest support from a vertebrate for the model of genetically influenced condition determining the expression of a sexual trait. In the following section, we review some of the evidence for condition-dependence of the male's comb (see Supplementary Material, Appendix S1).

CONDITION-DEPENDENCE OF THE JUNGLEFOWL COMB

TESTOSTERONE INFLUENCES COMB GROWTH

Testosterone is important to the development of a variety of male sexual characters across many taxa (Andersson, 1994; Ligon, 1999). It has long been recognized that testosterone is essential for comb growth in chickens (Parkes & Emmens, 1944). Testosterone must be present within the comb for fibroblasts to produce the viscous intercellular solution that promotes the comb's turgidity (Hardesty, 1939). Experimental administration of testosterone has a strong positive effect on comb size in young or castrated birds (Deyhim, Moreng & Kienholz, 1992; Fennell & Scanes, 1992b; Fennell *et al.*, 1996). Furthermore, when the primary source of testosterone (the testes) is removed, the combs of adult males shrink dramatically (Parkes & Emmens, 1944). However, in mature domestic roosters, testosterone implants or injections do not always trigger additional comb growth (Parkes & Emmens, 1944), and testosterone levels do not always correlate with comb size or colour (Furr & Thomas, 1970). When 4-month old, sexually immature red junglefowl males were administered testosterone, their combs grew more than control males (Zuk, Johnsen & Maclarty, 1995) and, among sexually mature junglefowl males, individuals with higher testosterone levels tend to have larger combs (Zuk *et al.*,

1995; Johnsen & Zuk, 1998; Parker, Knapp & Rosenfield, 2002), although this relationship does not hold in all circumstances (Parker *et al.*, 2002). Thus, although testosterone is necessary for normal comb expression in adult roosters, individual differences in comb size are not due solely to differences in testosterone levels.

By contrast to comb growth, which is enhanced by testosterone, administration of testosterone to immature male junglefowl (Chappell *et al.*, 1997) or chickens (Ma, 1954; Deyhim *et al.*, 1992; Fennell & Scanes, 1992a, 1992b; Fennell *et al.*, 1996) inhibits body growth (mass gain), a trait presumably important in male competition. Thus, testosterone appears to mediate a trade-off between two important sexually-selected traits. Although this trade-off is evident in testosterone-treated birds (Fennell *et al.*, 1996), in unmanipulated birds, lighter males do not have larger combs. In fact, the pattern is just the opposite. Heavier males, whether or not body size is statistically controlled, have larger combs (Parker, 2003; Parker & Garant, 2004; T. H. Parker, unpubl. data). This suggests that large-combed males are generally of higher quality and are able to avoid this physiological trade-off.

It has been hypothesized that an ornament influenced by testosterone (such as the comb) might be an honest signal of male immune function, because testosterone may compromise immune function. According to the hypothesis of Folstad & Karter (1992), only males with low pathogen burdens, presumably because of inherited immunocompetence, will be able to maximally elevate testosterone levels without risking dangerous infection. We discuss this possibility in more detail in the immune function section.

UNHEALTHY BIRDS GROW SMALL COMBS

Pathogen infection inhibits ornament expression in a wide variety of species, from birds (McGraw & Hill, 2000) to fish (Houde & Torio, 1992). Among male junglefowl culled at the San Diego Zoo, those with more intestinal nematode parasites had smaller combs (Zuk *et al.*, 1990a). When captive junglefowl chicks were experimentally administered intestinal nematodes and developed natural levels of infection, comb growth was significantly reduced (Zuk *et al.*, 1990b). By contrast to combs, nonsexual traits were generally not strongly effected by nematode infection (Zuk *et al.*, 1990b), thus supporting the hypothesis that the junglefowl comb is more strongly influenced by condition than nonsignal traits (Cotton *et al.*, 2004). Other research in which junglefowl chicks were infected by intestinal nematodes also found that this infection hindered comb growth (Chappell *et al.*, 1997; Johnsen & Zuk, 1998). The evidence from these

studies does not allow us to partition the direct effects of disease from the potential costs of mounting an immune response, but whether the effects are from one, the other, or most likely both, comb size is still an effective signal of health status. We do not have experimental evidence regarding the effects of other pathogens on comb growth. However, we have no reason to expect a unique role for intestinal nematodes, and we have anecdotally observed that the combs of birds naturally infected with other diseases tend to become paler and less turgid.

COMB SIZE REFLECTS IMMUNE FUNCTION

Several links between signal expression and immune function have been proposed. It is possible that testosterone, a hormone necessary for comb growth, limits immune function (Folstad & Karter, 1992), although, alternatively, it may be that aspects of immune function mediate testosterone production and thus comb growth (Zuk, 1996; Gallagher, 1999), limit comb growth more directly (through production of free radicals; von Schantz *et al.*, 1999), or divert resources and thus promote trade-offs (Sheldon & Verhulst, 1996). None of these hypotheses have yet emerged as the most likely sole contender. For example, there is evidence for an immunosuppressive role for testosterone in some bird studies (Peters, 2000; Casto, Nolan & Ketterson, 2001), but not in others (Ros, Groothuis & Apanius, 1997; Hasselquist *et al.*, 1999; Lindstrom *et al.*, 2001). Similarly, the trade-off hypothesis assumes that immune function is costly (Sheldon & Verhulst, 1996) and evidence from a variety of birds is consistent with this hypothesis (Nordling *et al.*, 1998; Ardia, Schat & Winkler, 2003; Bonneaud *et al.*, 2003; Faivre *et al.*, 2003; Martin, Scheuerlein & Wikelski, 2003). However, when considered in greater detail, it appears that certain aspects of immune function, such as acquired immunity, may have trivial direct costs, whereas the acute phase response (including fever and reduced mass and bone growth), stimulated by components of the innate immune system, can be very expensive (Klasing & Johnstone, 1991; Lochmiller & Deerenberg, 2000; Hangalapura *et al.*, 2004). Regardless of which mechanisms are at work, if comb expression is correlated with measures of immunocompetence or is influenced by stimulation of the immune system, we can conclude that the comb is a signal of these aspects of condition.

There is substantial evidence for correlation between various measures of immune function and comb size in red junglefowl. Both cell-mediated (T-lymphocyte) immunity, as measured by a cutaneous hypersensitivity (wing-web swelling) response to antigen injection, and concentrations of lymphocytes in general were greater in larger-combed males (Zuk

& Johnsen, 1998). During the breeding season, however, lymphocyte concentrations were lower in large-combed males with high testosterone levels (Zuk *et al.*, 1995; Zuk & Johnsen, 1998), although these males did not consistently exhibit lesser immune function. For example, cell-mediated immune response remained positively related to comb length. Also, the increase in heterophil (a phagocytotic white blood cell responsible for attacking antigens, particularly bacteria, after they are bound by antibodies) number in response to antigen injection was greater in larger-combed males (Zuk *et al.*, 1998). Other research by Zuk's group indicates that dominance interactions may further complicate these patterns (Zuk & Johnsen, 2000). Comb size was a positive predictor of cell-mediated immunity among dominant males, but comb size in subordinate males did not predict this component of immune function (Zuk & Johnsen, 2000). Although this research did not identify a mechanistic link between these aspects of immune function and comb expression, the frequent correlations suggest that comb expression can act as a signal of certain immune capabilities.

Verhulst, Dieleman & Parmentier (1999) found evidence in *Gallus* for a trade-off between aspects of immune function and comb growth, possibly mediated through testosterone. In divergent lines of chickens selected for either high or low antibody response to a nonpathogenic antigen, the line selected for high antibody production showed reduced testosterone levels, comb growth, and body size, whereas the opposite responses were found in the line selected for low antibody production. Furthermore, immune function in general appears to have responded to selection, with the high antibody line being more resistant to a number of natural avian diseases. Thus, a strong immune response conflicts with testosterone production, comb growth, and mass gain. This result is consistent with the mechanism of testosterone limiting immune function described by Folstad & Karter (1992), but also with other mechanisms, including a trade-off in which lines selected for increased antibody production suffer declines in mass gain and comb growth because of correlated increases in activity of other components of immune system that lead to acute phase responses and increased corticosterone production (Parmentier *et al.*, 1996; Verhulst *et al.*, 1999).

When, during the period of peak comb growth, yearling male red junglefowl had their immune system stimulated with injection of a nonpathogenic antigen (sheep red blood cells), comb growth tended to cease during the 2-week period of expected peak immune response (mean \pm SE increase in comb length = 1.5 ± 8.4 mm, adjusted for initial comb size), whereas combs of males receiving a control injection continued to grow (increase in comb length =

19.4 ± 8.4 mm, adjusted for initial comb size; T. H. Parker and P. Campbell, unpubl. data). Differences in comb growth between the treatments were marginally nonsignificant and this effect was not strong enough to explain a large proportion of the variation in comb size. However, studies of other taxa suggest this may be a real effect. In a variety of species, including chickens and wild birds, immune stimulation diverts resources away from growth (Klasing *et al.*, 1987; Ilmonen, Taarna & Hasselquist, 2000; Lochmiller & Deerenberg, 2000), possibly because the acute phase response is triggered (Parmentier *et al.*, 1996; Verhulst *et al.*, 1999).

Because the immune system is composed of diverse components, it may be difficult to draw general conclusions about the strength of immune functions within an individual (Matson *et al.*, 2006). However, the available evidence allows us to draw certain important conclusions regarding the relationships between the junglefowl comb and aspects of immunity. First, many measured features of immune function (cell-mediated immunity, heterophil number, concentrations of lymphocytes) correlate positively with comb size at least part of the time, and thus large-combed males may often be able to respond to certain types of immune challenges more quickly or effectively than small-combed males (Zuk *et al.*, 1995; Zuk & Johnsen, 1998, 2000). However, as mentioned above, the metabolic costs of producing these immune cells may be small (Klasing, 1998), and so it is not clear what mechanism may be linking these immune cell numbers to comb expression. Manipulative studies that have presumably triggered the costly acute phase of the immune response demonstrated negative effects of immune stimulation on comb size (Verhulst *et al.*, 1999; T. H. Parker and P. Campbell, unpubl. data). Thus, our interpretation of the comb-immune function interaction in red junglefowl is that unmanipulated large-combed males either have experienced fewer acute immune responses or, due to abundant reserves, have suffered less from these acute responses than have small-combed males. Regardless, the information available strongly suggests that, in many circumstances, comb size reflects condition: (1) as expressed by numbers of certain types of immune system cells and (2) as influenced by the costly aspects of immune function.

SUBORDINATE MALES HAVE SUPPRESSED COMB GROWTH

The role of direct dominance interactions in determining morphological sexual signal expression in birds has not been widely investigated, but it has been convincingly demonstrated in junglefowl. In male red junglefowl, dominance rank not only correlates with

comb size (Ligon *et al.*, 1990; Sullivan, 1991; Zuk & Johnsen, 2000; Parker *et al.*, 2002), but also it either promotes or suppresses comb growth. In experimentally formed groups each composed of two yearling males and three females, the male that became dominant continued to experience comb growth, whereas the combs of males which became subordinate decreased in size (Zuk & Johnsen, 2000). In another study, when yearling males were removed from contact with other males, and thus removed from dominance interactions, smaller-combed individuals showed rapid comb growth (Parker *et al.*, 2002). Small-combed individuals that remained in flocks did not show rapid comb growth, indicating that some aspect of social interaction limits comb expression. Although neither testosterone, nor corticosterone variation explained these patterns of comb growth and the hormonal mechanisms underpinning this pattern remain unclear (Parker *et al.*, 2002), a likely social mechanism is evident. When we allowed dominant males to choose between two potential fighting opponents, these males typically attacked larger-combed, dominant-acting males instead of smaller-combed, subordinate-acting males (Parker & Ligon, 2002). Thus, any males displaying a large comb and behaviours associated with dominance, such as crowing, are likely to elicit attack from a dominant male, and presumably will suffer physical harm or exile from the flock if they lose the confrontation. Surprisingly, this sort of behavioural mechanism tying dominance interactions with signal expression is known from only one other bird species (Møller, 1988), and it may not apply in other bird species with correlations between morphological signal expression and dominance rank (Slotow, Alcock & Rothstein, 1993).

INTEGRATION OF THE FACTORS INFLUENCING COMB SIZE

We attempted to determine the relative importance of the different components of condition that influence comb size by considering standard effect sizes from different correlations and experiments. We generated standard effect sizes (r) from all published relationships between measures of condition and junglefowl comb size (Appendix S1). Positive effect sizes (indicating a positive relationship between condition and comb size) for relationships between comb size and health or immune function measures ranged from $r = 0.20$ – 0.48 across 12 comparisons, although negative effects (counter to prediction) were observed in two cases, one as low as $r = -0.47$. Effect sizes were all positive for testosterone, but ranged from the negligible $r = 0.07$ up to $r = 0.53$. Most dominance rank effects were approximately $r = 0.35$, although, in one case, essentially no relationship was detected ($r =$

-0.05), and, in another case, the effect of dominance was very strong ($r = 0.62$). Some other hypothesized indices of condition, such as fluctuating asymmetry, explained no variance in comb size, although the body condition index (mass statistically controlling for skeletal size) was strongly correlated with comb size ($r = 0.53$). The ranges of effect sizes largely overlap for most condition determinants or indicators studied, including testosterone, health, immune function, and size-corrected body mass. Thus, determining which aspects of condition are most important to comb expression is not possible with current data.

If we were to calculate and sum the coefficients of determination (R^2) for all these relationships, it would appear that more than 100% of the variation in comb size is explained by our incomplete list of condition measures in junglefowl, which is obviously an impossibility. Thus, the various aspects of condition that influence comb growth presumably interact. For example, a pathogen infection might directly damage the body and would stimulate multiple components of the immune system, which in turn might lead to decreased investment in growth or tissue maintenance and lowered testosterone production. All these factors might correlate with comb expression, but the correlations would not be independent. Although the interactions among factors have rarely been explicitly studied in red junglefowl, this is clearly a complex biological system. Just a subset of observed and hypothesized interactions includes many possible feedback loops, both positive and negative. All variables may influence comb growth through multiple pathways, and this means that some, like testosterone, may both promote and suppress comb growth, depending on the causal path. These various factors have not been studied simultaneously in the same individuals, and so quantifying their relative contributions through path analysis or some other formal means is not yet possible. However, the junglefowl comb appears to be condition-dependent when controlling for skeletal size and is influenced more strongly than nonsexual traits by manipulations of condition within the realm of natural variability. Thus, the comb appears to be condition-dependent according to the rigorous standards of Cotton *et al.* (2004). Furthermore, we conclude that the model of capture of genetic variance by condition-dependent traits is likely to apply in this system because so many components of phenotype influence signal expression.

GENETIC VARIABILITY IN A CONDITION-DEPENDENT TRAIT

ROWE AND HOULE'S MODEL

Comb size in red junglefowl is influenced by a number of aspects of condition and is much more complex

than earlier single-axis models that predicted signal expression dependent on a single aspect of condition, such as pathogen infection or testosterone. The rooster's comb thus appears to support Rowe & Houle's (1996) model of a condition-dependent signal dependent on overall condition, rather than particular aspects of condition. Rowe and Houle's model did not just predict broad-brush condition-dependence. In their scenario, expression of the condition-dependent signal is influenced by genetic variance in condition. Thus, heritable variability in condition will account for heritable variability in signal expression; in other words, they predicted a genetic correlation between condition and signal expression (Tomkins *et al.*, 2004). Powerful multivariate quantitative genetics methods known as animal models, which take into account all known pedigree information, are excellent tools for examining this. These models were developed by animal breeders, and have recently been adopted by evolutionary biologists because of their power and flexibility (Kruuk, 2004).

RELATIVE MASS AS AN INDEX OF CONDITION

To test for a genetic correlation between condition and a signal trait, we must first identify a plausible index of condition. Relative mass, mass controlled for body size (tarsus length), has often filled this role in red junglefowl (Parker & Garant, 2004). Typically, this has been measured as residual mass; the residuals from a regression of log body mass on log tarsus length (Parker & Garant, 2004). The role of relative mass has also been assessed by controlling for tarsus length in a general linear model (e.g. to demonstrate the relationship between relative mass and comb length; Parker, 2003). Relative mass is easy to measure and is likely to be sensitive to a number of underlying aspects of condition, such as nutrition and health. However, relative mass is not a universally accepted condition index and it has been shown that, in some species, mass is a poor index of condition (e.g. in birds that maintain low mass at certain times to increase flight capabilities; Gosler & Harper, 2000). Fortunately, relative mass seems to be a useful index of condition in certain species (Tomkins *et al.*, 2004), including in red junglefowl (Parker & Garant, 2004). For example, diseased red junglefowl are lighter than healthy individuals (Zuk *et al.*, 1990b; Chappell *et al.*, 1997), and aspects of immune function appear to trade off with mass gain in chickens (Parmentier *et al.*, 1996; Verhulst *et al.*, 1999; Hangalapura *et al.*, 2004). Furthermore, quantitative genetics analyses indicate that mass and residual mass are more strongly influenced by environmental variance, particularly maternal effects, than is tarsus length, indicating greater sensitivity to environmental influences

(Parker & Garant, 2004, 2005) as expected for a condition-dependent trait (Cotton *et al.*, 2004). Relative mass can also be a good predictor of dominance rank (Parker & Garant, 2004), and dominance interactions can lead to mass loss in males (Zuk & Johnsen, 2000), possibly because of stress (Parker *et al.*, 2002).

QUANTITATIVE GENETIC TEST FOR CAPTURE OF GENETIC VARIANCE IN CONDITION BY A SIGNAL TRAIT

Demonstrating heritability of a sexually-selected trait is a necessary initial step in demonstrating capture of genetic variance in condition (Kotiaho, Simmons & Tomkins, 2001; Tomkins *et al.*, 2004; Bonduriansky & Rowe, 2005). Heritability of comb size in red junglefowl was first estimated based on regression analysis comparing the comb sizes of 18 sires and their sons (Johnson *et al.*, 1993). Comb size appeared to be moderately heritable ($h^2 = 0.24$), but the sample sizes were small and this estimate was not significantly greater than zero. Using morphological data from 221 male red junglefowl reared in three consecutive years, and a pedigree containing 498 individuals, Parker & Garant (2004) conducted a more thorough quantitative genetic assessment of several junglefowl traits. With multivariate animal models, they found a moderate to large heritable component of variance in residual mass ($h^2 = 0.68$). Parker and Garant also observed moderate and significant heritability of comb length ($h^2 = 0.39$), and most important, they detected a strong genetic correlation between comb length and residual mass ($r^G = 0.86$). In other words, the genetic variance underlying phenotypic variance in residual mass had a high degree of overlap with the genetic variance that explained variability in comb length (Parker & Garant, 2004). If, as we hypothesize, genetic variance in aspects of condition is responsible for variance in residual mass, then genetic variance in condition is also expressed in combs (Parker & Garant, 2004). Evidence for a genetic correlation between signal expression and a condition index is available from only a limited set of other species, primarily arthropods (Kotiaho *et al.*, 2001; Tomkins *et al.*, 2004; Bonduriansky & Rowe, 2005).

If relative mass is itself an index of condition, of what extra utility is the comb as a signal of condition? The simple answer is that the comb is readily visible and likely easier for conspecifics to assess (Zahavi, 1975). Furthermore, comb length has a higher coefficient of variation (SD/mean) than does mass (and especially the cube root of mass, a more appropriate scale for comparison with variation in length). In other words, comb length is much more variable relative to its mean than is mass, a pattern expected if

one trait (the comb) has been selected to convey information about another (mass or relative mass) (Parker & Garant, 2004). Thus, comb length provides more readily visible and amplified information about condition, as reflected by mass or relative mass (Parker & Garant, 2004).

CONCLUSIONS

In this review, we lay out the compelling case that: (1) the red junglefowl comb is condition dependent; (2) many aspects of condition influence comb growth; (3) comb growth shows substantial heritable variation; (4) this heritable variation is genetically correlated with a useful condition index; and thus (5) variation in comb size reflects and amplifies information about genetic variation in condition. There is a considerable amount that we do not know about red junglefowl signal expression. However, what we do know represents an important contribution to the understanding of condition-dependent signals in general, and provides compelling evidence for a role of the capture of genetic variance hypothesis proposed by Rowe & Houle (1996).

To our knowledge, this is the only vertebrate system in which a well-documented condition-dependent signal trait has been shown to be genetically correlated with a component of condition or a condition index, although such evidence is strong in at least two arthropods (Kotiaho *et al.*, 2001; Bonduriansky & Rowe, 2005) and suggestive in several other species (Tomkins *et al.*, 2004). However, the generality of condition-dependence of sexual traits is still uncertain (Bonduriansky & Rowe, 2005). We have shown that one potential solution to the lek paradox may be viable in one vertebrate. Other possibilities also exist, however, and further tests in a wide range of species will be needed to demonstrate that capture of genetic variance in condition is a general explanation for signal utility and the maintenance of heritable variation in sexual displays.

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SUPPLEMENTARY MATERIAL

The following material is available for this article online:

Appendix S1. Size of effects (r) of correlated or experimentally manipulated variables on comb size (typically length) of red junglefowl males. Results from domestic chickens are not shown, but also support the hypothesis of condition-dependence of comb expression. If a correlation coefficient or R^2 was not provided, one was estimated from the available statistical information using the statistical calculator in the meta-analysis program MetaWin 2.0. Negative values of r indicate that, counter to prediction, poorer-condition individuals (as measured by the variable in question) have larger combs. According to nearly every measure of condition except testis size at 10 months, average fluctuating asymmetry, breeding season lymphocytes, and breeding season lymphocytes in subordinate males, males in better condition have larger combs.

Appendix S2. References cited in the Supplementary Material.

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