

Female mating preferences in red junglefowl: a meta-analysis

T.H. PARKER¹ and J.D. LIGON

Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA

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Numerous experiments have been conducted in an effort to understand the mating preferences of female red junglefowl (*Gallus gallus*). Males of this species have both colourful ornamental plumage and fleshy head ornaments, including the comb. Previous studies produced conflicting results regarding the responses of females to these different ornaments. Several studies indicated that the comb influences female choice, but others failed to support this finding. Similarly, feather ornamentation correlated with female choice in some studies, whereas in a number of others it did not. Our meta-analyses show that when all mate choice experiments involving combs are analysed together, female preference is significantly related to male comb morphology. Subsets of these data (non-manipulation experiments, comb length [not colour] experiments, or manipulation experiments that leave one comb unaltered) make this point more strongly. This evidence is consistent with current understanding of the signalling value of the comb of male red junglefowl. Interestingly, when the combs of both males in each choice trial were altered (by painting, tine removal, or covering with latex false comb), we detected no female preference for comb morphology, which suggests that females prefer larger, brighter combs only when these combs appear natural. Our meta-analysis of feather experiments indicated that feather ornamentation was not associated with female mate choice. There was only a weak, non-significant indication that feather ornaments influence female choice in our meta-analysis of non-manipulation studies. In contrast, studies in which male plumage was experimentally manipulated provided no evidence that females utilize feathers in mate choice.

KEY WORDS: *Gallus*, mate choice, multiple ornaments.

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¹ Current address: Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK (E-mail: timothy.parker@zoo.ox.ac.uk).

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INTRODUCTION

The red junglefowl (*Gallus gallus*) is a highly sexually dimorphic avian species. Males have showy plumage, including long iridescent tail feathers, long golden hackle feathers, and various other patches of red, orange, and black feathers. Possibly even more striking are the fleshy head ornaments. The large comb atop the head varies in size among males. Both the comb and the paired wattles dangling below are red due to their high vascularization. In contrast, females have cryptic plumage and limited growth of the comb and wattles. Female mass is about 2/3 that of males. Red junglefowl are polygynous and both male dominance and female choice influence male mating success.

More than a dozen studies containing over 30 experiments on the mate choice behaviour of female red junglefowl have been published. These have sought to understand the basis of female choice of males, and have compared the mating success of males based on (i) plumage (e.g., LIGON & ZWARTJES 1995a), (ii) fleshy ornaments (e.g., LIGON et al. 1998), (iii) courtship behaviour (e.g., ZUK et al. 1995b), (iv) health (ZUK et al. 1990c) and (v) aerobic capacity (CHAPPELL et al. 1997). Many of these data indicate that female preferences are affected by male comb morphology. However, even for combs, results vary among studies (e.g., ZUK et al. 1990a, 1998). To address the issue of female preference more comprehensively, we conducted a series of meta-analyses based on all the available data on mate choice by female red junglefowl.

METHODS

Study species

Red junglefowl, the wild ancestor of domestic chickens, are native to Southeast Asia. The San Diego Zoo acquired birds to found a free-ranging population on the zoo grounds in the 1940's. All published mate choice studies have been conducted with descendents of captive birds obtained from the San Diego Zoo.

Mate choice studies

All the studies reviewed here involved mate choice trials in which a female was allowed to choose between two males. In these trials, the males were on either side of a barrier and could not see each other, so did not influence each other's response to the female. Males were tethered to keep them in their portion of the choice arena. A female was placed in an observation cage at the front of the arena, from which she could see both males. After a habituation period ranging from 20 to 90 min, depending on the study, the female was released, which allowed her to associate with the males. A mate choice was scored for one male or the other when the female approached a male and copulated or solicited copulation by crouching

(ZUK et al. 1990d). If a study did not report data on the direction of female preference for feathers or combs, it is not described here.

Meta-analyses

In meta-analysis, statistical results from multiple studies are compiled and analysed in a single statistical test of a hypothesis. Methods of data analysis differed among the various mate choice studies on red junglefowl. Some used regressions to compare ornament expression with the proportions of a male's trials in which he was chosen, while manipulative studies tested the proportion of trials won by males of alternative phenotypes. Therefore, we could not use correlation coefficients as the basis of the meta-analyses. Rather, using "Meta-Analysis Software", version 5.3 (SCHWARZER 1989), we conducted calculations developed by ROSENTHAL (1984) in which one-tailed probabilities are converted to z scores (test statistics). Meta-Analysis Software (SCHWARZER 1989) then uses the z scores and the corresponding sample size (results based on larger sample sizes are given more weight) for each experiment to generate an overall P -value and effect size (correlation coefficient: r) for the hypothesis being tested, as well as a "fail-safe" n and a test for heterogeneity. The fail-safe n is an estimate of the number of studies finding an absence of the predicted relationship that would have to be added to the analysis to eliminate statistical significance at the $P = 0.05$ level. A significant heterogeneity test indicates variation in trends among studies. The r -value provides a description of the direction and strength of the pattern. Conducting meta-analysis based on P -values can sometimes lead to biased results (SCHWARZER 1989), thus we conducted a second set of analyses using r -values estimated for each experiment. Because transformations to r -values can also be biased (SCHWARZER 1989), and because effect sizes were nearly identical with the alternative methods, we report results only from our initial calculations.

We were interested in testing two basic hypotheses: (a) female mating decisions correlate with male comb morphology, and (b) female mating decisions correlate with male feather morphology. Most experiments testing either hypothesis report one P -value. However, several experiments reported P -values for multiple measures of comb morphology or feather morphology. If we simply choose the lowest P -value related to our hypothesis for one of these experiments, we would risk a type I error. This potential problem was particularly strong in one study reporting on three experiments (ZUK et al. 1990d). In each of these experiments, P -values were presented for any significant relationship (positive or negative) between female preference and four comb and six feather variables. Thus we used Bonferroni corrected P -values when an experiment contained multiple tests of one of our hypotheses.

Most two-tailed P -values were converted to one-tailed values for the analyses (see one-tailed values in Appendices). If the observed pattern was opposite to that expected (i.e., if females preferred less ornamented males), then the one-tailed P -value was entered as a negative value in the calculation (SCHWARZER 1989). This presented a problem for some studies using feather colour scores because we did not have an a priori expectation concerning the direction of female response to unmanipulated feather colour. In fact, one study found a significant positive correlation between hackle feather hue and mating success in 1 year, and a significant negative relationship in the other year (ZUK et al. 1990d).

To avoid introducing a bias against a role for feather ornaments in female choice, we made the liberal assumption that a relationship, either positive or negative, between feather colour and female choice indicated female preference. Therefore, in cases of unmanipulated feather colour, we used the reported (or Bonferroni corrected) two-tailed P -value. Similarly, in the one case where a P -value for only comb colour was reported (ZUK et al. 1990d: table 1, 1988 data), we also used a two-tailed P -value, although the direction of female preference was toward brighter combs.

Two studies provided incomplete information concerning statistical tests. In one experiment, 19 females chose between 1-year old and 2-year old or older males (ZUK et al. 1990d). Although several feather measures correlated significantly with male success, neither comb length nor comb colour did so. Unfortunately, P -values for combs were not reported. It is

important to include this study, however, because its failure to find a relationship between comb morphology and mate choice contradicts some other studies. There was a non-significant trend for the younger males to be chosen, along with trends for younger males to have brighter (significant) and larger (non-significant) combs. Thus it probably would be reasonable to assume larger- and brighter-combed males were chosen more often than smaller-, duller-combed males. However, we made the neutral assumption that comb colour and size were unrelated to female choice, assigning a one-tailed P -value of 0.5 (r -value of 0) to the experiment.

In the other study with incomplete information, 173 trials were run with no more than 56 females and 36 males (when experimentally infected females are included, there were 256 trials involving 84 females) (ZUK et al. 1998). Although the authors reported the number of trials in which the large-combed male was chosen, they did not report either a per-female mean preference or a per-male proportion of trials won based on comb size. We conducted a chi-square analysis, but felt that using the sample size of 173 (or 256) in the meta-analysis would inappropriately inflate (due to non-independence) the effect of the study. The only experiments to use the number of trials as a sample size were those in which different females were used for each trial (all other studies used number of males as the sample size and the proportion of trials won by each male as the dependent variable). Thus, to avoid giving this study undue weight in the meta-analysis, we used the maximum number of females that could have been used in the study (56 for the uninfected female trials, 84 for all trials combined) as the sample size. We conducted several meta-analyses based on different subsets of the various studies.

Comb morphology analyses:

- (1) All experiments reporting a relationship between comb morphology and female preference: $n = 14$;
- (2) Experiments that did not manipulate comb morphology or female health status: $n = 6$;
- (3) Experiments reporting healthy females' preference for non-manipulated comb length (not comb colour): $n = 3$;
- (4) Experiments comparing males with intact combs to those with manipulated (trimmed) combs: $n = 3$;
- (5) Experiments that manipulated combs of both males in a trial (through painting, tine removal, or placements of latex false combs): $n = 5$.

Feather morphology analyses:

- (6) All experiments reporting a relationship between feather morphology and female preference: $n = 12$;
- (7) Experiments that did not manipulate feather morphology: $n = 4$;
- (8) Experiments comparing males with normal ornamental plumage (or, in one case, lengthened tail feathers) to males with experimentally dull, shortened, or asymmetrical feathers: $n = 8$.

RESULTS

In four of five meta-analyses, female red junglefowl preferred to mate with the larger, brighter-combed male. This result was not found in the subset of experiments in which *both* males had altered combs (painted, trimmed tines, false latex combs). For non-manipulation and comb length experiments, effect sizes were moderate. Not surprisingly, effect size was smaller when all experiments were considered, because all cases in which combs of both choice males were altered were included in this analysis. Altering the comb appears to have a strong negative influence on females. When females chose between a normal-combed and altered-

Table 1.

Results of meta-analyses testing the hypotheses (a) female mating decisions correlate with male comb morphology and (b) female mating decisions correlate with male feather morphology. See text for further details on the data used in the different analyses.

Experiments used (analysis number)	n experiments	z	P -value (one-tailed)	Effect size (r)	Fail-safe n ($P = 0.05$)	Test of homogeneity P -value
Comb						
1. All	14	3.3	0.000510	0.13	90	0.0074
2. Non-manipul.	6	4.1	0.000014	0.24	28	0.3496
3. Length only	3	3.3	0.000532	0.24	8	0.3682
4. Manipulation (large intact)	3	5.0	0.000001	0.71	25	0.9676
5. Manipulation (both altered)	5	- 0.05	0.714196	- 0.03	—	0.7166
Feathers						
6. All	12	0.3	0.393979	0.01	—	0.3258
7. Non-manipul.	4	1.4	0.082847	0.10	—	0.8886
8. Manipulation	8	- 0.9	0.813368	- 0.05	—	0.4269

combed male, they strongly preferred the unmanipulated male, and the effect size was large (Table 1).

In contrast, there is no clear trend for females to make mating decisions based on male plumage. In no meta-analysis was there a significant indication that females responded to feather ornamentation (Table 1).

DISCUSSION

Comb

All studies. The meta-analyses provide strong confirmation for the proposition that when choosing to mate, female red junglefowl respond to male comb morphology. There was a highly significant trend for female choice to be positively related to comb brightness or length (Table 1). This result is robust: the fail-safe n for the all-inclusive analysis indicates that to eliminate the observed pattern, there would need to be 90 additional studies finding no relationship between mate choice and comb morphology.

Manipulative studies. However, within comb manipulation studies there was an interesting pattern (Table 1). When females were given a choice between a male with an intact comb and a male with an altered (trimmed, tines removed) comb, the overwhelming preference was for the male with an intact comb. In contrast, when comb manipulations involved altering both males (by trimming tines, painting, or covering with latex comb), females showed no preference for either treatment. This suggests that for a comb to be attractive to females, it must have tines, natural colour, and possibly natural texture (the texture of the latex combs was

unlike that of a natural comb). These results indicate that design and interpretation of experimental manipulations of ornament appearance must account for the biological plausibility of the manipulations.

Signalling value. The comb of a male red junglefowl is a classic condition-dependent ornament. Factors related to condition or vigour, including health, immune response, dominance, and testosterone, influence comb size (reviewed in LIGON 1999; see also ZUK et al. 1990b, 1990c, 1995a; ZUK & JOHNSEN 1998, 2000; PARKER et al. 2002, PARKER & LIGON 2002). Presumably because it is condition-dependent, the red-junglefowl comb appears to signal paternal genetic quality. Mass of offspring at 11 weeks is significantly predicted by paternal comb size (sons: $r = 0.47$; daughters: $r = 0.53$; JOHNSON et al. 1993). In a study that controlled for the possibility of differential maternal investment in response to male attractiveness, the sons of large-combed males were in significantly better condition and grew significantly larger combs than the sons of small-combed males (PARKER in press). Therefore, the condition dependence of the comb appears to make it a signal of male genetic quality.

Heterogeneity. In the broadest meta-analyses of combs (1. All comb experiments) we detected significant heterogeneity among experiments (Table 1). Our analyses of sub-sets of the data give some insight into the causes of this heterogeneity. When only non-manipulation experiments were analysed (Analysis 2), heterogeneity was eliminated. Further, the two types of manipulative experiments (Analyses 4 and 5) clearly differed from each other. Thus the observed significant heterogeneity in the first analysis may have been due either to differences among manipulative studies or between manipulative and non-manipulative studies. Other factors that cannot be assessed without additional experiments might also have contributed to the observed heterogeneity. There may have been variation among experiments in the tendency of female red junglefowl to assess male comb morphology during mate choice. For instance, variation in the strength of female preference has been noted previously. In the one study where this was examined, females that mated more quickly were much more likely to choose the larger-combed male (ZUK et al. 1990a). This might have been because the females were at different stages of the reproductive cycle. Females in laying condition probably actively seek a male to avoid infertility, but females that are not laying may not show directed mate choice, or any mate choice (LIGON & ZWARTJES 1995a). In studies involving many females, the laying condition of all individuals is not always known, and different proportions of laying females were used in different experiments.

Feathers

Manipulative studies. Feather manipulation studies strongly suggest that female junglefowl do not respond to male ornamental plumage (Table 1). In most experiments involving feather manipulation, the plumage of one male was unmanipulated, while the other was often conspicuously manipulated (e.g., a female-like plumage; LIGON & ZWARTJES 1995a). If feather ornaments influence female choice, we would expect males with normal feather ornamentation to be preferred over males lacking such ornaments or those with dramatically shorted or asymmetrical feather ornaments. However, females consistently failed to show a preference when one male had normal plumage and the other did not. Thus plumage of males appears to be unimportant to females.

Non-manipulative studies. In contrast, experiments that did not manipulate feathers (i.e., both males exhibited normal ornamental plumage) lend some support to the hypothesis that females respond to male feather ornaments (a non-significant, $P = 0.08$, relationship between feather ornamentation and female choice). Because of the small number of non-manipulation experiments, low statistical power may have limited detection of a subtle or variable female preference. However, this was a liberal test of a female preference based on feathers. Although in the feather manipulation experiments we had a priori expectations that males with duller feathers would be avoided if females made choices based on feather ornaments, we made no such assumption for non-manipulation experiments. In other words, we did not assume that females should prefer a higher or lower colour score. In fact in one non-manipulation study, significant female choice for feather hue was in opposite directions in the two different years (ZUK et al. 1990d), though for purposes of analyses we considered both to be female choice based on feather ornamentation.

All studies. In a meta-analysis which combined manipulation and non-manipulation data, we found no support for the hypothesis that feather ornaments influence female choice (Table 1). Thus the consistency of the negative results with manipulated plumage appear to negate the weak indication in non-manipulation studies that females might be influenced by male plumage ornamentation.

Signalling value? The weak or absent relationship between female choice and feather ornaments is consistent with what we know about the signalling value of junglefowl feathers. There is growing support for the importance of testosterone mediated male traits to female choice in birds in the order Galliformes, but ornate plumage in red junglefowl and other Galliformes is not dependent on testosterone (LIGON et al. 1990, BEANI & DESSI-FULGHERI 1995, BUCHHOLZ 1995, OWENS & SHORT 1995, FUSANI et al. 1997, KIMBALL & LIGON 1999, HAGELIN & LIGON 2001). Furthermore, ornamental feathers are moulted annually, thus, unlike the comb, they cannot respond dynamically to the onset of illness or to a change in dominance status. Although many of the ornamental feathers of junglefowl are red or yellow, the pigments responsible for these colours are melanins rather than carotenoids (LIGON 1999). Unlike carotenoid pigmented feathers, intensity or extent of melanin-based coloration may not be sensitive to illness (MCGRAW & HILL 2000), though in one pair of studies of junglefowl, some feather colour measures were correlated with parasite infection (ZUK et al. 1990b, 1990c). Finally, in red junglefowl feather ornaments do not seem to signal genetic quality; e.g., neither paternal feather length nor colour is related to offspring growth (JOHNSON et al. 1993).

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APPENDIX A

Each experiment used in the comb meta-analyses, including the paper in which it was described, the trait(s) examined, manipulations conducted, the sample size, the *P*-value, and the list of meta-analyses (see Methods or Table 1 for explanations of analysis numbers) in which it was included.

Citation	Trait	Manipulation/ Experiment	<i>n</i>	<i>P</i> -value ¹	Analysis
ZUK et al. 1990d	length	none – 1987	33	0.02	1, 2
ZUK et al. 1990d	colour	none – 1988	60	0.04	1, 2
ZUK et al. 1990d	none	none – 1 year vs 2 year old	19	0.5	1, 2
ZUK et al. 1992	length and colour	latex painted	45	– 0.228 ²	1, 5
ZUK et al. 1992	length	latex	59	0.35 ²	1, 5
ZUK et al. 1992	colour	latex painted	77	– 0.45 ²	1, 5
ZUK et al. 1992	length	natural, both trimmed	47	– 0.099 ²	1, 5
ZUK et al. 1992	colour	natural, both painted	34	0.36 ²	1, 5
ZUK et al. 1995a	length, colour, etc.	none	66	0.002	1, 2
ZUK et al. 1995a	length	none (subset)	66	0.008	3
LIGON & ZWARTJES 1995a	length	natural, 1 trimmed	20	0.0018	1, 4
LIGON & ZWARTJES 1995b	length	natural, 1 trimmed	15 ³	0.005	1, 4
CHAPPELL et al. 1997	length	none	62	0.015/ 0.0075 ⁴	1, 2, 3
ZUK et al. 1998	length	some females experimentally infected	84	0.285	1
ZUK et al. 1998	length	none (subset – only females not experimentally infected)	56	0.245	2, 3
LIGON et al. 1998	length	natural, 1 trimmed	15	0.005	1, 4

¹ *P*-values differ from those reported in the original papers in cases where one-tailed values or Bonferroni corrections are used. See Methods for explanation.

² *P*-values are based on Chi-square analyses we conducted based on data in Table 1 of citation.

³ In this study, a female chose between the same two males in five successive trials. Only results from the first set of trials for each of the 15 females in each trial type are reported here.

⁴ Smaller *P*-value is for comb length only (Analysis 3), larger *P*-value is Bonferroni corrected because *P*-values for both comb length and colour were reported.

APPENDIX B

Each experiment used in the feather meta-analyses, including the paper in which it was described, the trait(s) examined, manipulations conducted, the sample size, the *P*-value, and the list of meta-analyses (see Methods or Table 1 for explanations of analysis numbers) in which it was included.

Citation	Trait	Manipulation/ Experiment	<i>n</i>	<i>P</i> -value ¹	Analysis
ZUK et al. 1990d	colour	None – 1987	33	0.18	6, 7
ZUK et al. 1990d	colour	None – 1988	60	0.24	6, 7
ZUK et al. 1990d	colour	None – 1 year vs 2 year old	19	0.06	6, 7
ZUK et al. 1992	length	Tails shortened, Lengthened	40	– 0.10 ²	6, 8
ZUK et al. 1992	presence	Tails removed	48	0.05 ²	6, 8
ZUK et al. 1995a	several colour	None	66	0.312	6, 7
LIGON & ZWARTJES 1995a	colour	Mutant ‘silver’ Plumage	47	– 0.095	6, 8
LIGON & ZWARTJES 1995a	colour	Mutant ‘hen’ Plumage	45	– 0.225	6, 8
LIGON & ZWARTJES 1995b	colour	Mutant ‘silver’ plumage	15 ³	– 0.0985	6, 8
LIGON & ZWARTJES 1995b	colour	Mutant ‘hen’ Plumage	15 ³	– 0.395	6, 8
LIGON et al. 1998	colour	Mutant ‘hen’ plumage, both males with trimmed comb	45	0.441	6, 8
LIGON et al. 1998	symmetry	Hackles trimmed	30	– 0.357	6, 8

¹ *P*-values differ from those reported in the original papers in cases where one-tailed values or Bonferroni corrections are used. See Methods for explanation.

² *P*-values are based on Chi-square analyses we conducted based on data in Table 1 of citation.

³ In this study, a female chose between the same two males in five successive trials. Only results from the first set of trials for each of the 15 females in each trial type are reported here.