Female mate choice and male behaviour in domestic fowl

MARTY L. LEONARD & LIANA ZANETTE

Centre for Food and Animal Research, Central Experimental Farm, Ottawa

ABSTRACT

The purpose of this study was to use paired choice tests to examine mate selection by female domestic chickens, *Gallus gallus domesticus*. We examined five behavioural and six morphological traits of 34 pairs of males to determine which male features influenced female mate choice. The frequency of a behavioural display known as wingflapping was the only variable that differed significantly between males that were chosen and males that were not. Within trials, females selected males with the highest wingflapping rate. Across trials, the wingflapping rate of chosen males ranged widely (3–82 wingflaps/h) suggesting that females used a relative choice mechanism when selecting a mate. These results differ from earlier work on the closely related red junglefowl, *G. g. murghi*, in which females use morphological traits and a threshold choice mechanism when selecting mates.

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Females are expected to choose mates with characteristics that will enhance their fitness. For example, males may provide high-quality resources and/or parental care, both of which should directly increase female reproductive success (e.g. Pleszczynska 1978; Muldal et al. 1986). Alternatively, males may provide good genes to their offspring, which also should enhance the fitness of the female. If females are to make adaptive mate choices, they must assess male traits before mating. The vigour of a male's display or the development of certain morphological traits may provide the female with information on his parental ability (e.g. Greig-Smith 1982), genetic quality (e.g. Zahavi 1975; Hamilton & Zuk 1982) or general attractiveness (e.g. Fisher 1958).

Male galliforms typically have fleshy head ornaments such as combs and wattles and perform elaborate courtship displays. Female galliforms of many species prefer males with well developed ornaments or weapons, presumably because they are reliable indicators of viability (e.g. von Schantz et al. 1989; Zuk et al. 1990b; Buchholz 1995; Ligon & Zwartjes 1995a; Mateos & Carranza 1995) and/or male dominance status (Graves et al. 1985; Brodsky 1988; Holder & Montgomerie 1993). Male courtship displays also appear to play a role in mate selection (e.g. Hillgarth 1990a; Gibson et al. 1991; Beani & Dessi-Fulgheri 1995). Although features associated with mating

preferences have been well studied in these species, relatively little is known of the mechanisms of mate choice. Female red junglefowl, *Gallus gallus murghi*, prefer males with combs above a threshold size (Zuk et al. 1990a), suggesting that they use an absolute rather than relative choice mechanism (Zuk et al. 1990a).

Although mate choice in domestic chickens, *G. g. domesticus*, is poorly understood, earlier work suggests that females may mate nonrandomly, showing preferences for socially dominant males (e.g. Guhl 1951; Graves et al. 1985). In a study of the effect of selection for increased comb size on morphological traits in chickens, females preferred males with large combs (von Schantz et al. 1995). The combs of the selected males in this study, however, were nearly double the size of the control males, making the results difficult to apply to unmanipulated situations. Furthermore, many behavioural features that may have correlated with comb size were not examined.

The purpose of the present study was to use paired mate choice tests to directly examine mate selection in domestic chickens. We evaluated (1) the morphological and behavioural traits associated with selection and (2) the mechanisms involved in making this selection. Feral chickens and red junglefowl form small social groups usually composed of a dominant male, several females and a subordinate male(s) (Collias & Collias 1967, 1996; McBride et al. 1969). Females mate most often with the dominant male, although they will also mate with subordinate flock members (e.g. Collias & Collias 1967, 1996). Thus a test situation that gives females a choice between two males is reasonable, given their natural mating system.

Correspondence and present address: M. L. Leonard, Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada (email: mleonard@is.dal.ca). L. Zanette is now at the Department of Ecosystem Management, University of New England, Armidale, New South Wales 2351, Australia.

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The subjects were layer parent stocks, which are the breeding stocks used to produce laying hens. In general, these females are not artificially inseminated, but rather are placed in large breeding pens with a selection of males. Thus, both males and females are free to mate without interference from humans. Although these stocks have been subject to artificial selection, traits typically associated with mate selection in galliforms, such as male ornaments and courtship behaviour have not been the focus of selection programmes. Indeed, the mating behaviour of chickens has remained indistinguishable from that of the undomesticated red junglefowl (Kruijt 1964; Zuk et al. 1990b, 1995). Thus, domestic chickens should provide a reasonable model in which to examine mate choice. They also add an applied aspect to the study of mate choice. For example, if male traits associated with female preference could be identified, breeders might increase productivity by providing females with more attractive males.

METHODS

Rearing Conditions

At hatch, we divided 840 female and 200 male white leghorn chickens equally by sex and randomly assigned them to either a single-sex rearing condition (i.e. males and females reared separately) or a mixed-sex rearing condition (i.e. males and females reared together; Leonard et al. 1996). The birds were reared under these conditions as part of another study on the effect of early experience on mating behaviour (Leonard et al. 1996).

When the birds were 24 weeks of age, we placed six males and 25 females in each of 16 pens. Eight groups of six males were chosen at random from each rearing condition and then randomly assigned to one of the 16 pens. Males in each group were from the same home pen. We also placed 16 groups of 25 females in the pens of males from the same rearing condition as themselves. Females from the same home pens were placed together with unfamiliar males.

Morphometrics

We measured comb and tarsus length (cm) and the length of the longest sickle feathers (curved tail feathers, cm) for each male when he was 24 weeks of age. We also took colour photographs of the head of each male under identical lighting conditions and then used a Macbeth TR527 transmission densitometer to determine the density of red pigments in the comb and right iris. Results from an earlier study indicated that morphological traits, such as comb size, would not have decreased in size in the 3 to 5-week interval between measuring the birds and conducting the experiment (Leonard et al. 1993).

Experimental Conditions

Experimental pens consisted of two compartments, separated by a solid metal partition, in the rear half and a
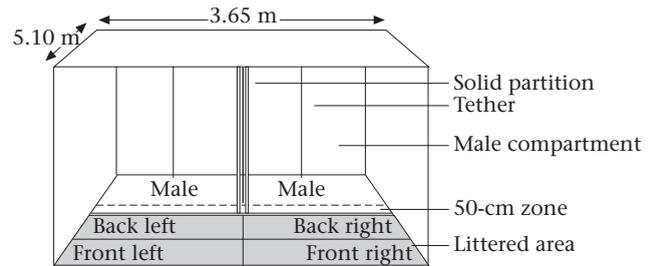

Figure 1. Experimental pen used in mate choice trials.

littered area in the front half (Fig. 1). The compartments were separated from the littered area by a chicken-wire gate which could be raised and lowered by the experimenter from outside the pen. Males were tethered in each compartment by a 2.27-m long cotton lead that was attached to a ring installed in the ceiling above the centre of the pen. The tether also was hooked to an elastic loop that was attached to a small piece of cotton cloth glued to the feathers of the lower back of each male. Observations from an earlier study (Leonard et al. 1996) indicated that once accustomed to the tether, males moved normally and displayed typical courtship behaviour.

Males could move freely throughout the entire compartment except in a 50-cm-wide zone at the front edge (Fig. 1). In this section, females could enter the compartment but remain outside the reach of the male. Males in separate compartments could hear but not see each other. This design was similar to that used by Zuk et al. (1990a, b, 1992) and Ligon & Zwartjes (1995a, b) for red junglefowl, and it allowed us to examine female choice independently of interactions between males.

Choice Trials

We conducted mate choice trials between 0800 and 1400 hours for 14 days beginning when males and females were 27 weeks old. At this age, males were showing the full repertoire of courting and mating behaviour and females were laying fertile eggs.

Twenty-four hours before a trial, we randomly chose up to five pairs of males from their home pens and tethered them in each of five holding pens (i.e. one pair of males per holding pen). Each pen was identical to the experimental pens, except that males had access to food and water and compartments did not have gates. This procedure allowed the males to become accustomed to the experimental set-up and to moving on the tether.

The next day, we tethered two randomly chosen males from the same rearing condition, but different home pens, in an experimental compartment with the gates closed. We selected females at random from their pens immediately before each trial. Females were from the same rearing condition as the two males but were not familiar with them. We ran trials using birds from single-sex rearing groups simultaneously with trials using birds

from mixed-sex rearing groups. We used each pair of males twice and their position alternated between trials, so if male A appeared in the left compartment in the first trial, he appeared in the right compartment in the second trial. Trials using the same pair of males were separated by a week. Each female was used in only one trial. We conducted 32 opposite trials (i.e. 32 pairs each presented twice) and four single trials (whose paired trials were discarded because of broken tethers) (N=68 trials).

During a trial, an observer sat outside the experimental pen to videotape the trial for later analyses. A trial consisted of 5 min before videotaping, during which the males became accustomed to the presence of the observer, followed by 5 min during which the behaviour of each male was recorded in the absence of the female (stage 1), 5 min during which the female was placed in a wire enclosure in the centre of the littered area, equidistant from each male compartment (stage 2), 10 min in which this enclosure was lifted from outside the pen and the female had access to the littered area (stage 3), and 40 min during which the gates to the male compartments were opened and the female had access to each male (stage 4).

When females were released from the enclosure, we recorded the amount of time they spent in the: (1) back left quarter of the littered area; (2) back right quarter; (3) front left quarter; and (4) front right quarter (Fig. 1). Once the gates were opened, we also recorded the time females spent in each male compartment and the number of successful copulations (i.e. complete cloacal contact) with each male.

We also recorded the frequency of the following male behaviours (Wood-Gush 1956): crowing, wingflapping (the wings are raised above the back and flapped), tidbitting (the male pecks the ground while giving food calls), waltzes (the male drops his wing and circles the female with short steps), and bodyshakes (the feathers are raised and the entire body shaken). Male behaviour was recorded before the females were placed in the wire enclosure (stage 1), after the females were placed in the wire enclosure (stage 2), when the females had access to the males, but remained in the littered area outside the male compartments (stage 4), and when the females were in male compartments (stage 4). Waltzes and tidbits were included in the analyses of behaviour only when the female was in the male compartments because they rarely occurred in the other situations. When comparing the behaviour of the males during stage 4, we divided the frequency of each behaviour by the total time that females spent in the back and front litter on each side and in each male compartment to get a rate controlling for the differences in exposure time to the females. It is possible that in some positions males could see females when they were in the litter on the opposite side of the pen (e.g. a male in the right corner of the right compartment could potentially see a female in the front left side of the pen). However, we recorded only the time the female spent in the right or left half of the pen, because otherwise it was difficult to determine when females were visible to males.

Table 1. Mean±SE morphological measurements for chosen and unchosen males during trials in which only one male was selected

Measurement	Chosen	Unchosen
Comb length (cm)	7.3±0.10	7.1±0.20
Tarsus length (cm)	11.5±0.10	11.4±0.30
Sickle length (cm)	21.8±0.90	23.1±0.60
Comb pigment (red)	1.1±0.04	1.0±0.02
Iris pigment (red)	1.9±0.04	1.9±0.03

A MANOVA was used to determine whether these variables differed significantly between chosen and unchosen males (N=27 pairs).

Measures of Preference and Analyses

We considered a female to have made a choice if she copulated with one of the males. In 28 trials, females did not copulate with either male, and in eight trials they copulated with both males. We excluded these trials from the analyses examining the relationship between male traits and female choice. In the remaining 32 trials, only one male was chosen. Five pairs of males were represented twice in these 32 trials (i.e. one member of the pair was chosen in both parts 1 and 2). To avoid pseudoreplication, we randomly chose one trial to include in the analyses for each pair (N=27 trials in which one male was chosen). We used a MANOVA to determine whether the morphological and behavioural variables varied significantly between chosen and unchosen males. We applied a log transformation to the behavioural rates to correct for non-normality. Results, however, are reported in the original scale.

When examining mechanisms of choice, we restricted our analyses of male behaviour to the period in stage 4 when females were outside male compartments. We chose this period because behavioural traits recorded during this time were important determinates of mating success, and because this allowed a longer period in which to record male behaviour. Using behaviour measured during stage 2 for this particular analysis did not alter the reported results.

Preliminary analyses showed that the results from trials using birds reared under single-sex conditions did not differ from those using birds reared under mixed-sex conditions. Therefore we pooled data from different rearing conditions in further analyses. Means are reported ±1 SE.

RESULTS

Morphological traits

The morphological variables did not vary with male mating success (MANOVA: $F_{5,22}$=0.99, P=0.44; Table 1).

Behavioural Traits

The behaviour of the males changed after females were introduced into the experimental pens. Males wingflapped significantly more after the females were placed in the enclosure (Table 2). The frequency of crowing and

Table 2. Mean±SE number of wingflaps, crows and bodyshakes/h before (i.e. stage 1) and after (i.e. stage 2) females were placed in the experimental pens

Behaviour	Before female	After female	Paired t	P
Wingflapping	12.0±2.4	28.8±4.8	−3.90	0.0006
Crows	45.6±7.2	56.4±7.2	−1.40	0.26
Bodyshakes	4.8±1.2	6.0±1.2	−0.80	0.42

Means were based on the mean value for each pair of males and were compared using a paired t test (N=27).

bodyshaking, however, did not change significantly (Table 2).

The behaviour of chosen and unchosen males differed significantly during the stage when females were confined but were equally visible to each male (stage 2; MANOVA: $F_{3,23}$=3.32, P=0.03). In particular, chosen males performed significantly more wingflaps than did unchosen males (chosen: 33.6 ± 4.8/h, unchosen: 20.4 ± 4.8/h; $F_{1,25}$=8.27, P=0.008). The number of crows and bodyshakes did not vary significantly.

Male behaviour during stage 4, when females had access to the males but remained outside their compartments, also differed significantly between the males (stage 4; MANOVA: $F_{3,23}$=7.35, P=0.001). Again, chosen males wingflapped significantly more when females were outside their compartments than did unchosen males (chosen: 25.2 ± 3.6/h, unchosen: 7.2 ± 1.5/h; $F_{1,25}$=22.9 P=0.0001). None of the behavioural measures differed significantly between chosen and unchosen males when the females were in their compartments (MANOVA: $F_{5,12}$=2.37, P=0.10).

Consistency of Female Choice

Females were consistent in their choice of male in three of the five pairs of trials in which a male was chosen in both trials. In the remaining two pairs, a reversal occurred (i.e. females chose different males). In all five trials, females chose the male with the highest wingflapping rate. Thus in the two cases where reversals occurred, the successful male wingflapped more often than the unsuccessful male.
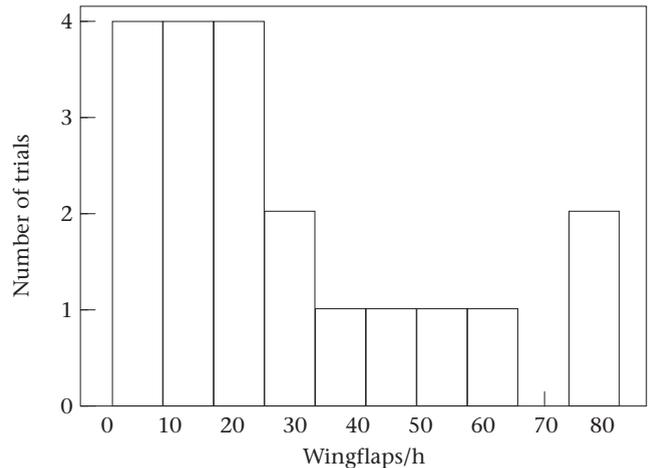
Figure 2. Distribution of wingflapping rates for chosen males during trials in which females copulated with one of the males. Wingflapping rates were for the period in which females had access to males but remained in the litter outside their compartments.

Correlations between Male Morphological and Behavioural Traits

The correlations between the males' behaviour when females were in the litter and morphological traits were low (Pearson product-moment correlations; Table 3), and when the Bonferroni correction was applied to correct for the high number of simultaneous tests, none of the correlations was significant (significance was set at P≤0.002 after the correction).

Mechanisms of Choice

In 24 of the 27 trials in which one male was chosen, there was a difference in the wingflapping rate of the two males. In 19 of these 24 trials, females selected the male that performed the most wingflaps (sign test: Z= − 3.5, P=0.0005). Across trials, females selected males that flapped at rates ranging from 3 to 82 wingflaps/h (Fig. 2).

We also used the 28 trials in which neither male was chosen to further examine whether females used relative or threshold choice mechanisms. For example, matings may not have occurred in these trials because males

Table 3. Pearson product-moment correlation coefficients among male morphological traits and behaviour when females had access to males, but remained in the litter outside their compartments (stage 4)

	Comb length	Tarsus length	Sickle length	Comb pigment	Iris pigment	Crows	Wingflaps
Comb length	1.00						
Tarsus length	0.30	1.00					
Sickle length	−0.10	−0.20	1.00				
Comb pigment	−0.10	−0.003	0.20	1.00			
Iris pigment	0.10	0.10	−0.04	0.10	1.00		
Crows	0.10	−0.20	−0.10	−0.10	−0.04	1.00	
Wingflaps	0.30	−0.10	0.20	0.03	0.20	−0.10	1.00
Bodyshakes	−0.04	−0.04	0.30	0.30	−0.10	0.10	0.30

Waltzes and tidbits were rare during this stage and were omitted from this analysis (N=54 roosters).

wingflapped at rates below a threshold rate. The male flapping at the highest rate in trials in which neither male was preferred, however, did not flap at a significantly lower rate than chosen males in trials in which one male was selected (highest: 18.7 ± 3.6 wingflaps/h, chosen: 27.1 ± 5.1 wingflaps/h; unpaired t test: $t_{48} = -1.4$, $P = 0.18$). This result suggests that the wingflapping rate in trials in which neither male was selected was not below a threshold rate. However, the difference in wingflapping rate between males in these trials was significantly lower than the difference between males in trials in which one male was chosen (neither chosen: 12.1 ± 2.3 wingflaps/h, one chosen: 24.3 ± 4.5 wingflaps/h; unpaired t test: $t_{51} = -2.4$, $P = 0.02$). This result provides support for a relative choice mechanism and suggests that matings may not have taken place in these trials because females did not have adequate time to assess males.

Males in trials in which both males mated may have flapped at rates above a potential threshold. (i.e. at rates similar to those of chosen males in trials in which one male was chosen). The males flapping at the lowest rate in trials in which both males were chosen flapped at significantly lower rates than preferred males in trials in which one male was selected (lowest: 7.1 ± 2.4 wingflaps/h; $t_{31} = 2.2$, $P = 0.04$). This result suggests that both males were not above a threshold rate. The difference in wingflapping rate between males in trials in which both males were chosen, although lower, did not significantly differ from the difference in rate between males in trials in which one male was selected (both chosen: 13.6 ± 4.2 wingflaps/h; $t_{32} = -1.2$, $P = 0.24$).

DISCUSSION

Female chickens in this study based their choice of mate on the frequency of a behavioural display known as wingflapping. This behaviour is typically performed by males during aggressive interactions with other males and when courting females (Wood-Gush 1956; M. Leonard, unpublished data). The mean frequency of wingflaps for both males increased when females were introduced into the experimental pens, suggesting that the display was directed towards females. Because wingflapping is audible, however, it is also possible that males were responding to the wingflapping of the other male rather than to the female. However, crowing, a vocal signal used in competitive interactions between males (Leonard & Horn 1995), did not increase in the presence of the female, which would be expected if males were interacting with one another.

It is not clear what information this display conveys to females. Sexually active males wingflap at higher rates than do sexually inactive males (Leonard et al. 1996). Similarly, males that are frustrated sexually also tend to increase their wingflapping rate (Duncan 1970). Both results suggest that wingflapping may reflect the readiness of the male to mate. If wingflapping is energetically costly to perform, it also may be a reliable indicator of the male's condition, although the energetic cost of this display has not been measured directly. Finally, wingflapping also might convey information about the social rank of the male. In an earlier study dominant males wingflapped significantly more often than did subordinate males in the presence of a model female (M. Leonard, unpublished data). Thus wingflapping rate may also provide females with information on the social status of the male.

Contrary to the results of this study, Zuk et al. (1990b, 1995) and Ligon & Zwartjes (1995a) found that female red junglefowl base their choice of mate on morphological traits such as comb size and colour. Although the frequency of wingflapping was measured, it was not an important determinant of mating success. Features of the comb such as size and colour are positively correlated with dominance status in both domestic roosters and junglefowl (e.g. Collias 1943; Marks et al. 1960; Graves et al. 1985; Ligon et al. 1990), again suggesting a link between female preference and male status. Fleshy head ornaments such as the comb also may indicate something about the bearer's physical condition and/or resistance to parasites (Zuk et al. 1990b, c). Thus females could use the size and colour of a male's comb to assess his social status and condition.

Indirect evidence suggests that male status may influence female choice in both junglefowl and domestic fowl. Female red junglefowl spend more time near high-ranking males (Graves et al. 1985; Collias & Collias 1996) and solicit more copulations from dominants than subordinates (Thornhill 1988), suggesting a preference based on male status. Dominant domestic roosters also copulate more often than do subordinates (e.g. Guhl & Warren 1946; Graves et al. 1985) and fertilize a larger number of eggs (e.g. Guhl & Warren 1946). This pattern appears to be at least partly explained by female preferences for high-ranking males (Guhl 1951).

The earlier studies on red junglefowl (e.g. Zuk et al. 1990b; Ligon & Zwarjtes 1995a) and the present study on domestic chickens both suggest that female fowl may prefer high-ranking males. It is not clear, however, why morphological cues were important in the former but not the latter study. Although there has not been direct selection on comb size, one possibility is that artificial selection on domestic fowl has incidentally reduced variation in this trait, making it difficult for females to separate males. The coefficient of variation for comb length, however, was larger for domestic chickens in this study than it was for the red junglefowl in Zuk et al.'s (1990b) study (9.70 and 8.35%, respectively) suggesting that females should have had a basis for choice. Another explanation is that, by chance, the difference in comb size between pairs of males used in this study was relatively small, thus preventing females from distinguishing between males based on that feature. The mean difference in comb length between pairs of males in our study was, however, comparable to the difference found for pairs of male junglefowl by Zuk et al. 1990a (0.88 and 0.98–1.02 cm, respectively). Thus, it is not obvious why the traits varied between the two studies.

Both behavioural and morphological traits have been associated with female preferences in other gallinaceous birds. For example, male displays are determinants of mating success in sage grouse, *Centrocercus urophasianus*

(Gibson et al. 1991), grey partridge, *Perdix perdix* (Beani & Dessi-Fulgheri 1995) and some populations of ring-necked pheasants, *Phasianus colchicus* (Hillgarth 1990a), but ornaments seem particularly important for mate selection in wild turkeys, *Meleagris gallopavo* (Buchholz 1995), ring-necked pheasants (Mateos & Carranza 1995) and rock ptarmigan, *Lagopus mutus* (Brodsky 1988; Holder & Montgomerie 1993). Behavioural displays could, like ornament size, convey information about male condition. If displays are energetically costly to perform, as has been shown for sage grouse (Vehrencamp et al. 1989; but see Chappell et al. 1995; Horn et al. 1995), then only males in good physical condition could afford the full display. Thus, females could use the vigour or intensity of the display to assess males.

The results of our study suggest that females in this population use a relative choice mechanism, although a threshold may exist below three wingflaps/h. In contrast, red junglefowl females appear to use a threshold preference mechanism based on features of the comb (Zuk et al. 1990a). Again, it is not clear why this difference may exist, but it is difficult to compare the studies because Zuk et al. (1990a) used a method that we could not apply to our study population. Feral chickens and red junglefowl form small groups in the breeding season consisting of a dominant male, several females and subordinate male(s) (Collias & Collias 1967, 1996; McBride et al. 1969), and females encounter relatively few males during the breeding season. A relative choice mechanism would ensure that females always mated and with the highest-quality male.

To summarize, female chickens in this study based their choice of mate on the relative frequency of a behavioural display known as wingflapping. This result is in contrast to earlier work on the closely related red junglefowl (Zuk et al. 1990a, b, 1995; Ligon & Zwartjes 1995a). A similar difference in the use of behavioural and morphological cues also has also been found in populations of ring-necked pheasants. Female pheasants in some Swedish populations appear to use morphological traits such as spur length (von Schantz et al. 1989), and those in some British populations appear to use display rate (Hillgarth 1990a, b). Even within populations of red junglefowl, female preferences for particular traits vary from year to year (Zuk et al. 1990b) and from study to study (Zuk et al. 1992). Together, these results suggest that females potentially use a variety of male traits when selecting a mate (Zuk et al. 1992). Differences in results across studies may indicate a shift in female preference for particular traits under different experimental conditions or the failure to measure all features relevant to females in each study.

Acknowledgments

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