

TESTICULAR ASYMMETRY AND SECONDARY SEXUAL CHARACTERS IN RED JUNGLEFOWL

REBECCA T. KIMBALL,¹ J. DAVID LIGON, AND MICHELE MEROLA-ZWARTJES

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

ABSTRACT.—The left testis tends to be larger than the right in most avian species. Møller (1994) hypothesized that the degree of directional asymmetry in the testes should be greater in high-quality males and hence should be positively correlated with secondary sexual traits. We examined both directional and absolute testicular asymmetry in Red Junglefowl (*Gallus gallus*), as well as the size of the left and of the larger testis, to determine whether these measures correlated with any of several potential phenotypic indicators of male quality. Such indicators included comb size; body size and condition; and fluctuating asymmetry in skeletal, plumage, and ornamental head traits (because fluctuating asymmetry may reflect an individual's ability to overcome developmental stresses). We found no evidence to support Møller's (1994) hypothesis of a relationship between directional testicular asymmetry and our measures of male quality. Moreover, there was little evidence to suggest a relationship between absolute testicular asymmetry, size of the left testis, or size of the largest testis and any measure of male quality. Finally, unlike some other studies, we did not find a tendency for the left testis to be larger than the right. Only 4 of 16 sexually mature males had a larger left testis at 10 months of age, whereas 10 of 19 males had a larger left testis at 12 months of age. Received 22 March 1996, accepted 4 November 1996.

MANY AVIAN SPECIES exhibit testicular asymmetry, with the left testis generally being larger than the right (Burke 1973, Lake 1981, Hocking 1992, Møller 1994), with some exceptions (Riddle 1918, Friedmann 1927, Law and Kosin 1958). Studies of domestic chickens have indicated that patterns of testicular asymmetry may be age-related, with larger left testes being found primarily in younger birds (Latimer 1924, Mimura 1928; but see Hocking 1992). The developmental processes leading to testicular asymmetry are not well understood. At the end of embryonic growth, the left gonad has more primordial germ cells than the right (Witschi 1935, Venzke 1954), although whether this leads to gonadal asymmetries in adults is not known.

If directional testicular asymmetry is adaptive, then the degree of testicular asymmetry may correlate with measures of male quality. Recently, Møller (1994) suggested that the degree of directional asymmetry in the testes is positively related to the size of male secondary sexual traits, because secondary sexual traits often are indicators of male quality. This hypothesis makes two assumptions. First, there is a cost to developing two equally large testes. Such costs may be the greater immuno-suppressive

effects of testosterone produced by two (vs. one) large testes (Folstad and Karter 1992), or the greater mass relative to one small and one large testis, which could affect flight performance. If mass reduction is the selective force favoring directional testicular asymmetry, then species that are primarily terrestrial may exhibit different patterns of testicular asymmetry than species that are more aerial. Second, Møller (1994) assumes that the right testis is primarily compensatory, i.e. it functions as a "back-up." In this view, a low degree of testicular asymmetry reflects a situation where the right testis has become fully developed to compensate for an inadequate left testis. This would indicate that high-quality males in good health, i.e. those males that are capable of developing large secondary sexual traits, will have left testes that function adequately, and hence will not develop large right testes. Only low-quality males, or those in poor health, will have right testes that are as large, or larger, than the left.

Møller (1994) found directional testicular asymmetry, with larger left testes, in Barn Swallows (*Hirundo rustica*) and House Sparrows (*Passer domesticus*). The degree of asymmetry was positively related to tail length in Barn Swallows and to badge size in House Sparrows. Both traits are reported to be indicators of male quality, lending support to Møller's (1994) hypothesis.

¹ E-mail: rkimball@unm.edu

In the study reported here, we determined: (1) whether Red Junglefowl (*Gallus gallus*) exhibited directional testicular asymmetry, as has been reported in a majority of avian species; and (2) whether the degree of testicular asymmetry was correlated with possible indicators of individual quality or condition, as suggested by Møller (1994). The potential quality indicators include male secondary sexual traits, body size, spleen size, and fluctuating asymmetry (FA) in a variety of bilateral traits. Spleen size is predicted to be small in males whose immune systems function well, because these males can overcome infections rapidly, whereas low-quality males whose immune systems function poorly are predicted to have large spleens, because the spleen is enlarged when many types of infections are present (Møller et al. 1997). FA, the deviation from pure bilateral symmetry, may reflect the inability of an individual to overcome developmental stresses and can reflect individual quality (Palmer and Strobeck 1986, Parsons 1990).

METHODS

Study species.—The Red Junglefowl is the conspecific ancestor of the domestic fowl (Hutt 1949, Stevens 1991). Males are elaborately ornamented, with colorful orange, red, and black plumage and a fleshy red comb, ear lappets, and wattles on the head. In contrast, the plumage of females is drab and cryptic, and the fleshy traits are smaller. Red Junglefowl are polygynous, with males typically providing no parental care.

Previous studies indicate that mate choice by female Red Junglefowl primarily is correlated with the color and size of the male's comb (Zuk et al. 1990, 1995; Ligon and Zwartjes 1995a, b). These studies have not found a clear or strong preference by females for aspects of male plumage, particularly when the effect of comb size was controlled (Ligon and Zwartjes 1995b). Comb and wattle size are known to directly reflect current testosterone levels (Domm 1939, Collias 1943, Zuk et al. 1995) and thus are condition-dependent traits (Folstad and Karter 1992). In contrast, because normal male-type plumage develops in the complete absence of testosterone (Domm 1939), plumage traits probably cannot provide precise, current information about a male's condition (Ligon et al. 1990, see also Folstad and Karter 1992). Plumage traits may reflect other, as of yet unknown, aspects of male quality, hence we have included them in this study.

The Red Junglefowl used in this study were descendants of 150 birds obtained from the San Diego Zoo in 1985 and 1986. The zoo population formed a large, free-ranging flock descended from about 30 individu-

als of two subspecies that were released on the zoo grounds in 1942 (Collias et al. 1966, Collias and Collias 1985). All Red Junglefowl used in this study were hatched during a one-month period between mid-May and mid-June 1994. Chicks were fed *ad libitum* and, at about six weeks of age, were removed from the brooders and allowed to range freely. In December and January, when males were six to seven months old, they were placed into individual pens and provided with fresh water and food *ad libitum*.

Measurements.—Males were weighed and measured in March 1995 when they were about 10 months old and sexually mature (Zuk et al. 1990). Comb length was measured to the nearest 0.1 mm using dial calipers. We also measured wing chord (unflattened), spur length (spur length plus the width of the tarsus; see Grahn and von Schantz 1994), and tail length. The latter measure was taken only for males whose longest tail feathers were intact (in an undamaged tail, two feathers, one on each side, are longer than the rest, and these were measured to obtain tail length).

To measure FA in the fleshy bilateral traits of the head, color photographs were taken of each male. A frontal view, and both a right and left profile, were photographed to provide information on the size of the fleshy traits on the head. Any photograph in which the bird was not properly aligned, as determined by visual inspection of head position and by looking for shadows that should not have been there, was retaken. To provide scale, a ruler was placed above the head in each photograph: (1) perpendicular to the comb and approximately in the same plane as the front of the wattles for frontal photographs, and (2) in the plane of the comb for profile photographs. The photographs were digitized at 150 dpi. Measurements were then collected using NIH Image (developed at the U. S. National Institutes of Health and available on the Internet by anonymous FTP from zippy.nimh.nih.gov). Wattle and ear-lappet areas were measured by outlining the trait on the digitized profile photographs. Wattle length on each side was obtained from the frontal photograph, measuring from the posterior corner of the mouth to the tip of the wattle. Measurements were collected in pixels and converted into mm or mm² using the ruler in each photograph.

Sixteen males were sacrificed after measurements were completed in March 1995 (when males were about 10 months old). An additional 19 males were sacrificed in early June 1995 (at about 12 months old). Because males become sexually mature at eight months of age and remain in reproductive condition until the late summer (Zuk et al. 1990), males in both age classes should have had mature, functional testes. Right and left testes were removed (a second observer insured that the side of the body a testis was removed from was identified correctly) and individually weighed to the nearest 0.1 g on a digital scale. Maximum length and width of the spleen were measured using dial calipers. Following the methods of Møller

TABLE 1. Testes measurements (\bar{x} with SD in parentheses; all measurements in g) of 10- versus 12-month-old Red Junglefowl. *P*-values have not been corrected with a sequential Bonferroni; no results were significant after performing sequential Bonferroni adjustment.

Trait	10 months (<i>n</i> = 16)	12 months (<i>n</i> = 19)	<i>t</i> (<i>P</i>)
Avg. testis mass	6.39 (1.16)	6.48 (1.07)	0.23 (0.821)
Left testis mass	6.16 (1.12)	6.50 (1.24)	0.84 (0.409)
Right testis mass	6.62 (1.29)	6.45 (1.00)	-0.43 (0.671)
Larger testis mass	6.73 (1.13)	6.78 (1.11)	0.16 (0.877)
Absolute testis asymmetry	0.67 (0.48)	0.62 (0.40)	-0.36 (0.725)
Directional testis asymmetry	-0.46 (0.70)	0.05 (0.75)	2.05 (0.049)

et al. (1997), spleen measurements were used to compute the volume of the spleen, assuming the spleen was an ellipsoid:

$$\text{spleen volume} = \frac{4}{3} \cdot \pi (\text{width}^2) \cdot \text{length}. \quad (1)$$

We feel that this provided a good approximation of spleen size. The tarsus, tibia, femur, and humerus were carefully removed so as not to damage the ends of the bones. After removing the meat, the length of each bone was measured using dial calipers. All bilateral traits (bones, wing chord, tail length, wattles, and ear lappets) were measured three times on each side of the body to allow determination of measurement error (Palmer and Strobeck 1986, Swaddle et al. 1994).

Data analysis.—We defined directional testicular asymmetry as the mass of the left testis minus the mass of the right testis. Absolute testicular asymmetry is the absolute value of testicular asymmetry, ignoring direction. Average testis size is the average mass of the right and left testis, and maximum testis size is the size of the larger testis, regardless of whether it is the left or the right testis.

To determine the FA of bilateral traits, the three measurements of each trait were averaged for each side. The absolute value of the left minus the right side was then calculated. A body size index was calculated by adding together the standardized lengths (length of trait/average length of trait) of the tarsus, tibia, femur, and humerus. Body condition was calculated by dividing body mass by tarsus length, which is a better predictor of fat reserves than is mass alone (Johnson et al. 1985).

We analyzed FA data with nonparametric tests because absolute values of FA have half-normal distributions. All other analyses involved parametric tests. To prevent Type I error, without greatly increasing the chances of Type II error, we performed a sequential Bonferroni adjustment (Rice 1989) on each set of analyses within a table (e.g. correlates of directional asymmetry). We have also indicated which results were significant at $P \leq 0.05$ before a sequential Bonferroni adjustment was performed. Analyses were performed on SAS for the PC (SAS Institute 1988).

Statistically, traits exhibiting FA have a normal distribution and a mean of zero (Palmer and Strobeck 1986). All of the FA values reported here have a nor-

mal distribution (measured by a Shapiro-Wilks test). With the exception of wattle area, all traits also had a mean of zero. Because differences between the right and left side generally are small, measurement error can account for much of the variation in FA. We followed the procedure of Swaddle et al. (1994) and used a mixed-models ANOVA to determine whether measurement error was low, relative to FA. All traits included in our analyses had low measurement error relative to the degree of asymmetry (Kimball et al. 1997).

RESULTS

Average testis size did not differ between 10- and 12-month-old males (Table 1), indicating that the testes were fully developed at 10 months. Testicular asymmetry differed between 10- and 12-month-old males, although the difference was not significant after Bonferroni adjustment. At 10 months, the right testes were significantly larger than the left testes (paired *t*-test: $t = -2.61$, $df = 15$, $P = 0.017$); however, by 12 months, the difference was not significant ($t = 0.28$, $df = 18$, $P = 0.945$). Therefore, testes data from 10- and 12-month-old males were analyzed separately.

At 10 months, directional testicular asymmetry was significantly different from zero ($t = -2.61$, $df = 15$, $P = 0.02$). However, by 12 months there was no directional testicular asymmetry ($t = 0.28$, $df = 18$, $P = 0.79$). Absolute testicular asymmetry was significantly different from zero in both age classes (10 months: $t = 5.54$, $df = 15$, $P < 0.001$; 12 months: $t = 6.70$, $df = 18$, $P < 0.001$), indicating that the testes always exhibited asymmetry, although the direction varied.

Average testis size was not correlated with the degree of either directional or absolute testicular asymmetry (Table 2). That is, those individuals with larger testes, on average, were neither more nor less likely to have asymmetric testes.

TABLE 2. Pearson correlation coefficients between testis asymmetry and male quality indicators in 10- and 12-month-old Red Junglefowl. Sample sizes are 16 and 19 for 10 months and 12 months, respectively, unless noted otherwise in parentheses.

	Directional asymmetry		Absolute asymmetry	
	10 months	12 months	10 months	12 months
Ornamental traits				
Comb length (mm)	-0.26	-0.15	0.24	-0.07
Tail length (cm)	0.48 (6)	-0.20 (6)	-0.57 (6)	-0.81 (6) ^a
Non-ornamental traits				
Body condition (g/mm)	0.25	0.04	-0.11	-0.18
Body size index	0.10	-0.30	-0.05	-0.24
Wing chord length (cm)	0.15	-0.07	-0.21	-0.27
Spleen volume (mm ³)	0.52 ^a	0.22 (18)	-0.36	0.06 (18)
Avg. testis mass (g)	-0.26	0.34	-0.20	0.11

^a Significant $P \leq 0.05$ before performing sequential Bonferroni adjustment.

There were no significant relationships between-directional testicular asymmetry and comb size, body size, or spleen size (Table 2). In addition, there also were no significant correlations between testicular asymmetry and any measure of FA (Table 3).

Møller (1994) hypothesized that directional testicular asymmetry with larger left testes is indicative of a healthy, high-quality individual. However, because the degree, but not the direction, of asymmetry may be important, we also examined absolute testicular asymmetry. We found no significant relationships between absolute asymmetry and comb size or other non-FA traits (Table 2). However, a significant relationship appeared between absolute testicu-

lar asymmetry and one measure of FA, ear-lappet area, in one age class (Table 3).

If the right testis fully develops only when the left testis is inadequate, as Møller's (1994) testicular-asymmetry hypothesis suggests, then there should be greater variability in the size of the right testis than in the left. Contrary to Møller's prediction, the right testis was not more variable in size in either 10-month ($F = 1.33$, $df = 15$ and 15 , $P = 0.295$) or 12-month-old males ($F = 0.64$, $df = 18$ and 18 , $P = 0.821$; F -test between coefficients of variation [Zar 1984]).

If we hypothesize that one large testis may function more effectively than two smaller ones, then the degree of asymmetry may not be as important as either the size of the left testis or the

TABLE 3. Spearman correlation coefficients between testis asymmetry and fluctuating asymmetry in 10- and 12-month-old Red Junglefowl. Sample sizes are 16 and 19 for 10 months and 12 months, respectively, unless noted otherwise in parentheses.

	Directional asymmetry		Absolute asymmetry	
	10 months	12 months	10 months	12 months
Ornamental traits				
Wattle length (mm)	0.03	0.22	-0.27	0.28
Wattle area (mm ²)	-0.05	-0.31	0.13	-0.04
Ear-lappet area (mm ²)	0.17	0.11	0.16	0.67 ^a
Tail length (cm)	0.41 (6)	-0.54 (6)	-0.70 (6)	-0.77 (6)
Spur length, 10-mos. (mm)	0.03	-0.12	0.00	-0.01
Spur length, 12-mos. (mm)	—	0.19	—	0.24
Non-ornamental traits				
Humerus length (mm)	0.03	0.00	-0.11	0.11
Tarsus length (mm)	-0.51 ^b	0.41	0.36	-0.30
Tibia length (mm)	0.00	-0.17	-0.18	-0.45
Femur length (mm)	-0.30	0.18	0.35	0.17
Wing chord length (cm)	0.41	0.01	-0.15	0.24

^a Significant at $P \leq 0.05$ after performing sequential Bonferroni adjustment.

^b Significant at $P \leq 0.05$ before performing sequential Bonferroni adjustment.

TABLE 4. Pearson correlation coefficients between testis size and male quality indicators in 10- and 12-month-old Red Junglefowl. Sample sizes are 16 and 19 for 10 months and 12 months, respectively, unless noted otherwise in parentheses.

	Left testis size		Maximum testis size	
	10 months	12 months	10 months	12 months
Ornamental traits				
Comb length (mm)	-0.04	0.25	0.08	0.32
Tail length (cm)	0.25 (6)	-0.42 (6)	-0.03 (6)	-0.56 (6)
Non-ornamental traits				
Body condition (g/mm)	0.43	0.05	0.32	0.02
Body size (mm)	0.52 ^a	0.21	0.47	0.30
Wing chord length (cm)	0.32	0.19	0.23	0.19
Spleen volume (mm ³)	0.26	0.51 (18) ^a	0.02	0.50 (18) ^a

^a Significant at $P \leq 0.05$ before performing sequential Bonferroni adjustment.

size of the larger testis. There were no significant relationships between size of either the left or the larger testis and comb size, body size, or spleen size (Table 4). However, a significant relationship existed between the size of the left testis and FA of the femur in 10-month-old males, but not in 12-month-old males (Table 5).

DISCUSSION

Patterns of testicular asymmetry.—Our data are not consistent with previously described patterns of testicular asymmetry. In the majority of species studied, the left testes are larger (Burke 1973, Lake 1981, Hocking 1992, Møller 1994), although a few studies have found the right testes to be larger (Riddle 1918, Law and Kosin 1958). Two studies of domestic fowl observed

age-related differences in testicular asymmetry. Mimura (1928) observed that 91% of chicks, but only 57% of males more than one year old, had larger left testes, and Latimer (1924) observed that 88% of males less than six months old, but only 43% of males more than six months old, had larger left testes. In our study, most 10-month-old males had larger right testes, whereas there was no consistency in which testis was larger among one-year-old males.

Interestingly, we observed directional testicular asymmetry in only one of two sample periods, and even then it was in a direction (right testis larger) opposite that observed by Møller (1994). If directional testicular asymmetry exists, then we would have expected to observe it in both samples. That we did not indicates that there may not be strong selection for directional

TABLE 5. Spearman correlation coefficients between testis size and fluctuating asymmetry in 10- and 12-month-old Red Junglefowl. Sample sizes are 16 and 19 for 10 months and 12 months, respectively, unless noted otherwise in parentheses.

	Left testis size		Maximum testis size	
	10 months	12 months	10 months	12 months
Ornamental traits				
Wattle length (mm)	-0.38	-0.01	-0.43	-0.11
Wattle area (mm ²)	-0.19	-0.08	-0.15	0.03
Ear-lappet area (mm ²)	-0.53 ^a	0.04	-0.59 ^a	-0.24
Tail length (cm)	0.61 (6)	-0.31 (6)	0.52 (6)	-0.23
Spur length, 10-mos. (mm)	0.08	-0.20	-0.01	-0.14
Spur length, 12-mos. (mm)	—	0.26	—	0.24
Non-ornamental traits				
Humerus length (mm)	0.05	-0.08	-0.03	-0.04
Tarsus length (mm)	-0.05	0.31	0.22	0.07
Tibia length (mm)	0.13	0.29	-0.10	0.40
Femur length (mm)	-0.71 ^b	0.10	-0.53 ^a	0.17
Wing chord length (cm)	0.20	0.14	0.01	0.21

^a Significant at $P \leq 0.05$ before performing sequential Bonferroni adjustment.

^b Significant at $P \leq 0.05$ after performing sequential Bonferroni adjustment.

asymmetry in Red Junglefowl, contrary to what Møller (1994) has suggested for other species.

Because we did not measure the gonads of the same birds at 10 and 12 months of age, we could not determine if testicular asymmetry changed within individuals. Average testis mass did not differ between the 10- and 12-month-old males, so it is possible that the right testis regresses while the left testis increases in size. However, although the right testes weigh less at 12 months than at 10 months, the difference is small and not significant. Other researchers (Latimer 1924, Mimura 1928) who reported age-related differences in testicular asymmetry provided no information that could be used to determine what might occur during an age-related shift in testicular asymmetry.

If testicular size is dependent upon the number of primordial germ cells, then it is unlikely that patterns of asymmetry would change with age. The age-related pattern of testicular asymmetry found in this study and others (Latimer 1924, Mimura 1928) indicates that, at least in some species, factors other than (or in addition to) the number of primordial germ cells may be responsible for testicular asymmetry in the adult. The identity of these factors remains to be determined.

Testicular asymmetry and male quality.—Møller (1994) hypothesized that directional asymmetry in avian testes is adaptive, and that the degree of asymmetry is positively correlated with male quality or condition. However, we found no significant relationships between directional testicular asymmetry and any male morphological trait, even in 10-month-old males, when significant directional asymmetry was observed. In addition, comb size (which is a condition-dependent trait known to be involved in sexual selection; Zuk et al. 1990, 1995; Ligon and Zwartjes 1995a, b) was negatively related with directional testicular asymmetry, whereas spleen volume (which may reflect male immune function; Møller et al. 1997) was positively related to testicular asymmetry. Both of these results are contrary to what is expected if Møller's (1994) testicular-asymmetry hypothesis is correct.

An alternative hypothesis is that possessing asymmetric testes may be important, but the direction of the asymmetry may be irrelevant. Absolute testicular asymmetry was positively correlated with ear-lappet area, but only in one age class, and hence it was not a general and con-

sistent result. There was no other evidence to support this hypothesis.

Factors affecting testicular asymmetry and male quality.—The ancestors of the Red Junglefowl we studied originated from a small population released at the San Diego Zoo in 1942. Therefore, these birds have undergone a genetic bottleneck in their recent evolutionary history, which may have affected the results we obtained.

Rearing conditions, particularly the availability of *ad libitum* food, also may have affected our results by reducing the condition-dependent expression of secondary sexual traits and confounding the relationship between such traits and testicular asymmetry. However, this scenario cannot explain the difference in testicular asymmetry between our study and Møller's (1994). Møller's hypothesis predicts that males in good condition should exhibit the greatest directional testicular asymmetry, with the left testes larger than the right. Because our males should have been in good nutritional condition, we should have seen a high degree of testicular asymmetry (with the left testes larger than the right) in both age classes if the testicular-asymmetry hypothesis applied to Red Junglefowl. However, we did not observe this result, indicating that male condition may not affect directional testicular asymmetry in Red Junglefowl.

Testis size and male quality.—If one large testis functions better than two smaller ones, then the size of either the left or the larger testis may be a better measure of male quality than the degree of testicular asymmetry. Primordial germ cells give rise to the spermatogonia (Lake 1981), which in turn produce sperm in the mature adult. Because the left testis contains the majority of germ cells (Witschi 1935, Venzke 1954), it may be advantageous to produce a large left testis that will be capable of supporting high sperm production. The size of the left testis was negatively correlated with the degree of FA in the femur. However, this occurred in only one age class, and hence was not indicative of a general and consistent pattern. We obtained no other evidence that the size of the left testis reflected male condition or quality. Size of the larger testis, whether left or right, showed no relationship with any of our measures of male condition or quality.

Nonadaptive testicular asymmetry.—The previous hypotheses have assumed that having either a high degree of testicular asymmetry or one

very large testis is advantageous. Two large testes may be disadvantageous in birds, but there is no evidence to support the idea that having asymmetric testes is more advantageous than, for example, having two moderately sized symmetric testes. Testicular asymmetry may instead arise from selection for ovarian asymmetry in females, rather than from selection for asymmetry in males. The left ovary in most avian species is functional, whereas the right remains undeveloped, probably as an adaptation to morphological constraints related to flight and the production of large eggs (Jones et al. 1993). Movement of the primordial germ cells to the left gonad occurs prior to gonadal differentiation; hence, testicular asymmetry could be driven by selection on females for ovarian asymmetry. Although power analysis (Cohen 1969) indicates that we cannot conclusively reject a weak relationship between testicular asymmetry and measures of male quality in Red Junglefowl, we feel that nonadaptive explanations of testicular asymmetry should also be considered.

Differences between our results and those of Møller (1994) also may be due to differences in the species studied. Species that are primarily terrestrial, as are most galliforms (including the Red Junglefowl), may be under less selection in both males and females to reduce body mass compared with more aerial species. Thus, selection for testicular and ovarian asymmetry may be weak or absent in more terrestrial species. Although a positive relationship between male condition and testicular asymmetry may exist in aerial avian species, as Møller's (1994) hypothesis predicts, the pattern may or may not exist in terrestrial species. Although there are too few data to test this idea, Møller's (1994) data reveals that relative testicular asymmetry (testicular asymmetry/combined testis size) in the Barn Swallow (a highly aerial species) is about twice that (0.18 vs. 0.09) in the House Sparrow (a less aerial species), and both of these species have greater relative testicular asymmetry than does the highly terrestrial Red Junglefowl (0.05).

General conclusions.—Our study does not support Møller's (1994) testicular-asymmetry hypothesis that directional asymmetry in testes is adaptive and positively correlated with male quality or condition. We examined several alternative hypotheses and searched for a relationship between male quality and absolute testicular asymmetry, size of the left testis, and size of the larger testis. Again, we found no consistent

relationship among these characters and any measure of male quality. That we observed directional testicular asymmetry in only one sample suggests that there is little or no selection for directional testicular asymmetry in Red Junglefowl.

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LITERATURE CITED

- BURKE, W. H. 1973. Testicular asymmetry in the turkey. *Poultry Science* 52:1652-1654.
- COHEN, J. 1969. *Statistical power analysis for the behavioral sciences*. Academic Press, New York.
- COLLIAS, N. E. 1943. Statistical analysis of factors which make for success in initial encounters between hens. *American Naturalist* 77:519-538.
- COLLIAS, N. E., AND E. C. COLLIAS. 1985. Social behavior of unconfined Red Jungle Fowl. *Zoonooz* 58:4-11.
- COLLIAS, N. E., E. C. COLLIAS, D. HUNSAKER, AND L. MINNING. 1966. Locality fixation, mobility and social organization within an unconfined population of Red Jungle Fowl. *Animal Behaviour* 14:550-559.
- DOMM, L. V. 1939. Modifications in sex and secondary sexual characters in birds. Pages 227-327 in *Sex and internal secretions: A survey of recent research* (E. Allen, Ed.). Williams and Wilkins, Baltimore, Maryland.
- FOLSTAD, L., AND A. J. KARTER. 1992. Parasites, bright males, and the immunocompetence handicap. *American Naturalist* 139:603-622.
- FRIEDMANN, H. 1927. Testicular asymmetry and sex ratio in birds. *Biological Bulletin* (Woods Hole) 52:197-207.
- GRAHN, M., AND T. VON SCHANTZ. 1994. Fashion and age in pheasants: Age differences in mate choice. *Proceedings of the Royal Society of London Series B* 255:237-241.
- HOCKING, P. M. 1992. Bilateral testicular asymmetry and supernumerary testes in the domestic fowl (*Gallus domesticus*). *British Poultry Science* 33:455-460.
- HUTT, F. B. 1949. *Genetics of the fowl*. McGraw-Hill, New York.
- JOHNSON, D. H., G. L. KRAPU, K. J. REINECKE, AND D. G. JORDE. 1985. An evaluation of condition indices for birds. *Journal of Wildlife Management* 49:569-575.

- JONES, R. E., H. M. SMITH, AND C. E. BOCK. 1993. Reptilian and avian ovarian cycles and the evolutionary origin of volant birds. *Journal of Theoretical Biology* 161:527–536.
- KIMBALL, R. T., J. D. LIGON, AND M. MEROLA-ZWARTJES. 1997. Fluctuating asymmetry in Red Junglefowl. *Journal of Evolutionary Biology* 10: in press.
- LAKE, P. E. 1981. Male genital organs. Pages 1–61 in *Form and function in birds* (A. S. King and J. McLelland, Eds.). Academic Press, London.
- LATIMER, H. B. 1924. Postnatal growth of the body, systems, and organs of the single-comb white leg-horn chicken. *Journal of Agricultural Research* 29:363–397.
- LAW, G. R. J., AND I. L. KOSIN. 1958. Seasonal reproductive ability of male domestic turkeys as observed under two ambient temperatures. *Poultry Science* 37:1034–1047.
- LIGON, J. D., R. THORNHILL, M. ZUK, AND K. JOHNSON. 1990. Male-male competition, ornamentation and the role of testosterone in sexual selection in Red Jungle Fowl. *Animal Behaviour* 40:367–373.
- LIGON, J. D., AND P. W. ZWARTJES. 1995a. Female Red Junglefowl choose to mate with multiple males. *Animal Behaviour* 49:127–135.
- LIGON, J. D., AND P. W. ZWARTJES. 1995b. Ornate plumage of male Red Junglefowl does not influence mate choice by females. *Animal Behaviour* 49:117–125.
- MIMURA, H. 1928. On the bilateral asymmetry of testes in the domestic fowl. *Japanese Journal of Zoology* 2:24.
- MØLLER, A. P. 1994. Directional selection on directional asymmetry: Testes size and secondary sexual characters in birds. *Proceedings of the Royal Society of London Series B* 258:147–151.
- MØLLER, A. P., R. DUFVA, AND J. ERRITZØE. 1997. Host immune defense and sexual selection in birds. *Evolution* 51: in press.
- PALMER, A. R., AND C. STROBECK. 1986. Fluctuating asymmetry: Measurement, analysis, patterns. *Annual Review of Ecology and Systematics* 17:391–421.
- PARSONS, P. A. 1990. Fluctuating asymmetry: An epigenetic measure of stress. *Biological Reviews of the Cambridge Philosophical Society* 65:131–145.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- RIDDLE, O. 1918. Further observations on the relative size and form of the right and left testes of pigeons in health and disease and as influenced by hybridity. *Anatomical Record* 14:283–334.
- SAS INSTITUTE. 1988. SAS/STAT user's guide, release 6.04. SAS Institute, Inc. Cary, North Carolina.
- STEVENS, L. 1991. Genetics and evolution of the domestic fowl. Cambridge University Press, Cambridge, United Kingdom.
- SWADDLE, J. P., M. S. WITTER, AND I. C. CUTHILL. 1994. The analysis of fluctuating asymmetry. *Animal Behaviour* 48:986–989.
- VENZKE, W. G. 1954. The morphogenesis of the indifferent gonad of chicken embryos. *American Journal of Veterinary Research* 15:300–308.
- WITSCHI, E. 1935. Origin of asymmetry in the reproductive system of birds. *American Journal of Anatomy* 56:119–141.
- ZAR, J. H. 1984. *Biostatistical analysis*, 2nd ed. Prentice Hall, Englewood Cliffs, New Jersey.
- ZUK, M., T. S. JOHNSON, AND T. MACLARTY. 1995. Endocrine-immune interactions, ornaments and mate choice in Red Jungle Fowl. *Proceedings of the Royal Society of London Series B* 260:205–210.
- ZUK, M., R. THORNHILL, J. D. LIGON, K. JOHNSON, S. AUSTAD, S. H. LIGON, N. W. THORNHILL, AND C. COSTIN. 1990. The role of male ornaments and courtship behavior in female mate choice of Red Jungle Fowl. *American Naturalist* 136:459–473.

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