

MATE CHOICE AND AEROBIC CAPACITY IN RED JUNGLEFOWL

by

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Summary

In 'good genes' models of sexual selection, females choose mates whose genes confer increased survival value to offspring. One possible index of male quality is aerobic capacity (the metabolic basis of sustainable exercise), which is likely to be important for fitness. If it is both heritable and ecologically valuable, high aerobic capacity would be a direct signal of male genetic quality. If aerobic capacity is phenotypically plastic but dependent on health, it may provide an indirect index of male quality in other heritable traits (*e.g.* pathogen resistance). We examined the relationship between courtship behaviour, aerobic capacity (measured as maximum rates of oxygen consumption), and mating success in red junglefowl (*Gallus gallus*). We also tested the effects of intestinal parasites (the nematode *Ascaridia galli*) and plasma testosterone levels on aerobic capacity and behaviour. We found no relationship between testosterone and behaviour, mating success, or aerobic capacity. *A. galli* infection changed the relationship between mass and aerobic capacity; infected males had lower aerobic capacity than uninfected males, but only for small males. Discriminant function analysis suggested that aerobic capacity and display behaviour, together with male ornaments (comb size and colour), were the most important factors determining the mating success of males. However, aerobic capacity and display rate were not strongly correlated, and the manner by which females can discriminate among males with differing aerobic capacity is unclear.

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Introduction

Several models of sexual selection suggest that males with elaborate or prolonged courtship displays could be indicating their quality to females (Kirkpatrick & Ryan, 1991; Andersson, 1994). Under such 'good genes' models, females benefit from choosing mates whose genes confer increased survival value to the females' offspring, and male sexual ornaments and display behaviour allow females to evaluate male genetic quality. This concept is particularly germane in strongly polygynous species in which males contribute only sperm to their offspring.

Although the 'good genes' concept has received considerable theoretical attention, there have been few examinations of how the proximate cues used by females reflect the genetic quality of potential mates. One of the best-known 'good genes' models proposed that sexual ornaments in male birds (colourful plumage and elaborate soft tissue structures) are honest signals of a male's genetic resistance to parasites (Hamilton & Zuk, 1982). Tests with red junglefowl (*Gallus gallus*) support this hypothesis. Males infected with the nematode *Ascaridia galli* are less successful than uninfected males in mate choice trials (Zuk *et al.*, 1990c), and female preferences are based in part on male characters that depend on health (comb length, eye and comb colour; Zuk *et al.*, 1990d).

Of course, females might use other cues to identify high-quality mates, and many traits other than parasite resistance are important for fitness. From the perspective of overall physiological vigour, one reasonable candidate for a signal of male quality is aerobic capacity (*i.e.* the maximal rate of oxygen consumption). Aerobic respiration is the metabolic foundation of sustainable power production, and hence aerobic capacity presumably influences Darwinian fitness through effects on fighting ability, locomotor performance, predator avoidance, and other behaviours requiring intense and sustained exercise. In the context of female choice, energetically demanding courtship displays might allow females to assess male aerobic capacity (as well as other male traits). Vigorous courtship behaviours occur in many animals, and in some species (notably insects and frogs) metabolic power output during courtship signaling can be many-fold greater than resting metabolism (*e.g.* Prestwich & Walker, 1981; Taigen & Wells, 1985; Prestwich *et al.*, 1989; Vehrencamp *et al.*, 1989). Mating success is often correlated with the intensity of courtship displays (Gibson & Bradbury,

1985; Höglund & Robertson, 1990; Fiske *et al.*, 1994). These observations are consistent with the hypothesis that male aerobic capacity may be a factor in female choice. We examined this possibility as part of an ongoing study of female choice, parasite resistance, sex hormones, and male behaviour and ornamentation in red junglefowl, *Gallus gallus*. Previous work has shown that aerobic capacity is highly repeatable in adult junglefowl (Chappell *et al.*, 1996). In this paper we describe the relationship between aerobic capacity and mating success in both parasitized and unparasitized males. We also investigated the influence of plasma testosterone level, since androgens affect both male secondary sex characters and mating behaviour (Ligon *et al.*, 1990, Zuk *et al.*, 1990a, d), and may also influence aerobic capacity during maturation.

Methods

Animals and treatment groups

Red junglefowl were reared from eggs obtained from a captive flock. They were kept indoors in brooders for six weeks, after which they were maintained under semi-natural conditions (outdoor pens exposed to ambient weather conditions and photoperiod in Riverside, California; Zuk *et al.*, 1990c, 1995). Birds were obtained from the feral flock at the San Diego Zoo in southern California in the late 1980s and have been reared in captivity using a minimum of approximately 50 breeding males and 50 breeding females since that time (the San Diego Zoo flock was descended from 30 birds imported from Southeast Asia in 1942). The population has not experienced artificial selection for activity patterns, physiology, or reproductive biology.

Newly-hatched chicks were divided into four treatment groups housed in separate brooders. One group was inoculated with the intestinal nematode *Ascaridia galli* (~ 100 embryonated eggs administered orally in saline every week between the ages of 1-5 weeks; Zuk *et al.*, 1990c). *A. galli* occurs naturally in both domestic chickens and junglefowl. It has a direct life cycle and causes juvenile mortality and stunted growth in domestic chickens (Ruff, 1978; Chappell *et al.*, 1996), but has low infectivity and few obvious effects on non-ornamental characters in adult birds (Zuk *et al.*, 1990c). A second group of chicks was given subcutaneous testosterone implants (three 4 cm long, 0.32 cm diameter sealed silastic tubes packed with testosterone). A third group received both parasites and testosterone, and a final group served as controls. Parasite-treated and untreated birds were housed separately throughout the experimental period (*A. galli* infection is normally acquired from pecking at ground contaminated with faeces). At about 4 months, the birds were separated into male-female pairs; subsequently the males were kept separate from each other for the duration of the experiment. One month before mate choice trials, males were housed individually and females were kept in all-female groups for the course of the trials; male cages were out of view of the females. After the completion of experiments, males were euthanized and dissected to determine the presence and number of *A. galli* in the digestive tract.

Mate choice

Mate choice trials began when birds were 9-10 months old and had attained adult plumage and morphology. Each male participated in 5-9 trials. During each trial a female was offered the choice of two males (the males were visible and accessible to the female but not to each other; Zuk *et al.*, 1990d). Hidden observers recorded behaviour during trials, which lasted a maximum of 20 min. Each male's mating success was scored as the fraction of trials in which he was chosen (*i.e.* he actually mated or was solicited by the female). Trials in which females did not choose one of the two test males were excluded from analysis; this occurred in less than 10% of all trials. Pre-mating behaviour was recorded as the number of courtship displays per minute (crowing, wing-flapping, 'waltzing', crouch-scratching, and 'tidbitting'; Zuk *et al.*, 1990d). A score for overall display rate was obtained by averaging a male's displays over the cumulative time of all the trials in which he was used.

Morphological measurements and plasma testosterone

Within 14 days of mate choice trials, secondary sexual characters known to be important in mate choice (comb length and colour; Zuk *et al.*, 1990d) were measured, as described in Zuk *et al.* (1995). Birds were weighed (± 1 g) before and after trials.

Blood samples obtained from each male before and after his set of mate choice trials were analyzed for plasma testosterone level (radioimmunoassay; Diagnostic Products; Morton *et al.*, 1990) and haematocrit (post-trial only). Hormone samples were assayed in comparison to a standard curve of plasma testosterone concentration (T; ng/ml) ranging from 0.2 to 16.0 ng/ml. A standard tube containing 4.0 ng/ml of testosterone was included in each assay and yielded a mean of 3.95 ng/ml with 9.0% coefficient of variation. We used the mean of pre- and post-trial T in our analyses.

Aerobic capacity measurements

Within 4 days after the completion of mate choice trials, we measured the males' aerobic capacities as maximum rates of oxygen consumption. The system and protocol were as described previously for studies of performance consistency over time (Chappell *et al.*, 1996). In brief, we used open-circuit respirometry to measure oxygen consumption ($\dot{V}O_2$; ml O_2 /min) during intense exercise in an enclosed motorized running wheel. The wheel (76 cm diameter by 42 cm wide) was supplied with dry air at rates of 39-43 L/min STP. Excurrent air was dried, scrubbed of CO_2 , and analyzed for oxygen content (Applied Electrochemistry S-3A). Oxygen concentrations ($\pm 0.0015\%$) were displayed and recorded on a Macintosh computer. We ran birds at gradually increasing speeds until they could no longer maintain position and $\dot{V}O_2$ did not increase with increasing speed. The birds invariably showed signs of exhaustion by this time, but none suffered any injury. Complete measurements lasted from 8 to 15 min (3 to 11 min of actual exercise). This method reliably elicits maximal $\dot{V}O_2$, and measurements of maximal $\dot{V}O_2$ are highly repeatable in adult junglefowl over periods of up to 6 months (repeatabilities of 0.5-0.9; Chappell *et al.*, 1996). A blind trial arrangement ensured that the running wheel operator did not know the treatment group or mating success of birds being tested for aerobic capacity.

We used the 'instantaneous' calculation (Bartholomew *et al.*, 1981) to compensate for the mixing characteristics of the large-volume wheel and accurately resolve short-term

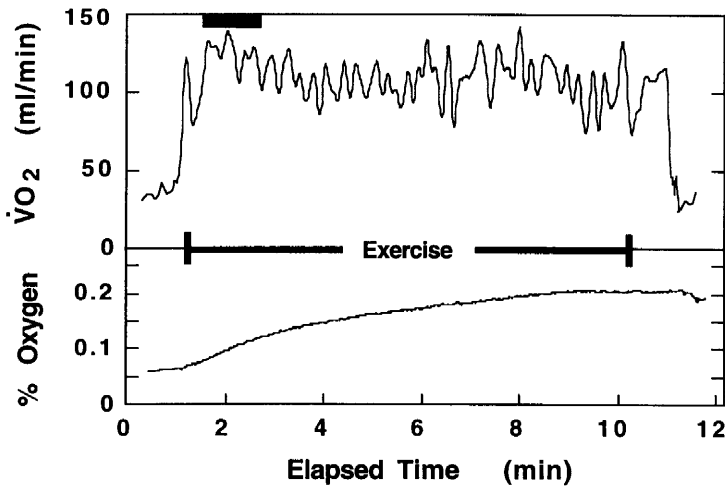


Fig. 1. Measurement of aerobic capacity during treadmill exercise in red junglefowl. The bottom trace is the change in O_2 concentration in excurrent air (offset to equal zero % for incurrent air). The top trace is oxygen consumption ($\dot{V}O_2$) computed with the 'instantaneous' conversion (Bartholomew *et al.*, 1981) to compensate for chamber mixing characteristics. We calculated aerobic capacity as the highest continuous average over a 1-minute interval (black bar at top). This male weighed 1488 g and was exercised for about 9 minutes at gradually increasing speeds.

changes in metabolic rates. We computed aerobic capacity as the highest instantaneous $\dot{V}O_2$ averaged over a continuous 1-min interval (Fig. 1).

Statistics

Because metabolism is a power function of mass, we \log_{10} -transformed mass and aerobic capacity to linearize these variables prior to analyses. Percentage data (mating success and haematocrit) that were not normally distributed were arcsine square-root transformed. All transformed variables were normally distributed (Chi-square and Kolmogorov-Smirnov tests). We used 2-tailed *t*-tests, ANOVA and ANCOVA for comparisons between treatment groups, and product moment correlations (Pearson's *r*) for analyses of continuous variables. To compare successful and unsuccessful males on the basis of several traits simultaneously, we used discriminant function analysis, which assigns each individual a score that is the multivariate expression of univariate traits. A significant discrimination suggests that the treatment groups can be separated on the basis of these traits. We applied a sequential Bonferroni procedure to correct for Type I errors in multiple simultaneous tests (Rice, 1989). The significance level was $p = 0.05$; results are expressed as mean \pm SD. Analyses were performed with Statistica/Mac software (StatSoft, Inc.). Statistical power (the probability of a Type II error) was computed according to Rotenberry & Wiens (1985) and Cohen (1977).

Results

Variance

We obtained data from 62 male junglefowl ranging in mass from 761 to 1664 g. There was substantial variance in all physiological and behavioural variables (Fig. 2; variance in aerobic capacity was computed from mass residuals expressed as percentage of predicted values; see 'Treatment groups', below). Coefficients of variation ranged from 9% (haematocrit) to 75% (T). Counts of *A. galli* were highly skewed, with most birds (46;

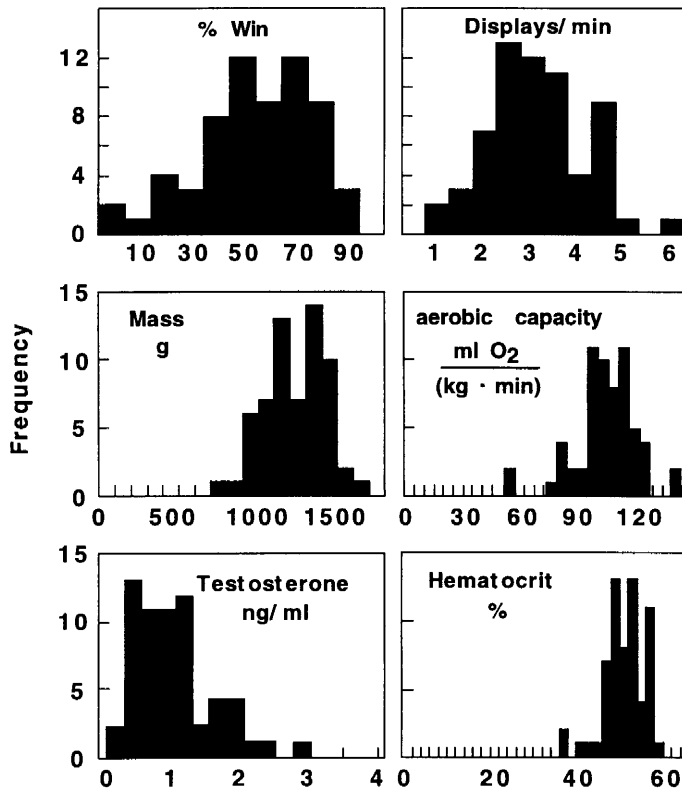


Fig. 2. Variance in behavioural and physiological parameters in 62 male red junglefowl. Symbols: % Win: percentage of mate choice trials in which a male was selected; displays/min: the number of courtship displays per minute during mate choice trials. Variance in aerobic capacity was computed as the difference between observed values and values predicted (both expressed as ml O₂/[kg·min]) by regressions of aerobic capacity on mass; separate regressions were used for infected and uninfected birds.

74%) carrying no worms. Worm counts of 16 infected birds ranged from 1 to 111 (mean = 11.2 ± 28.0), which are typical for free-living junglefowl populations (Zuk *et al.*, 1990b).

Treatment groups

Two aspects of the results influenced our interpretation of the experimental design and hence our analyses. First, the experimental treatments with testosterone increased T during maturation compared to controls (at 5 months of age, $T = 0.40 \pm 0.05$ ng/ml vs 0.16 ± 0.04 ng/ml, $N = 47$ and 43, respectively; $p = 0.0004$; T.S. Johnsen, unpubl. data). However, at the time of this study testosterone titers were highly variable and pre-trial T did not differ significantly among birds with implants and controls (1.04 ± 0.68 vs 0.88 ± 0.45 ng/ml, respectively; $N = 31$ each; $p = 0.27$; *t*-test). Therefore we analyzed the effects of testosterone both as a categorical variable (with respect to possible effects resulting from different T during maturation) and as a continuous variable (with respect to individual variation in circulating testosterone at the time of aerobic capacity and mate choice tests).

Second, many of the birds inoculated with *A. galli* contained no parasites at the end of the experiment, while a few birds in other groups became infected from unknown sources (most likely wind-blown soil particles contaminated with *A. galli* eggs). It is unclear whether the inoculated but parasite-free birds were (1) never infected (*i.e.* the parasite eggs were inviable or the inoculation failed for other reasons) or (2) initially became infected but subsequently rid themselves of the parasites prior to testing. Similarly, we are not certain of the extent to which the non-inoculated birds were exposed to *A. galli* from other sources. Because of this uncertainty, we classified birds as 'infected' or 'uninfected' on the basis of presence or absence of worms in the digestive tract at the conclusion of measurements, rather than by initial treatment group.

Treatment effects

Both testosterone treatments and infection status influenced body mass (ANOVA; $p = 0.016$ and $p < 0.001$, respectively). There was no interaction between testosterone treatments and infection status, and neither

treatment had a significant effect on comb colour, haematocrit, display rate, or mating success.

Among uninfected males, birds that had received testosterone treatments averaged about 10% smaller than control birds (1237 ± 174 g and 1357 ± 140 g, respectively; $N = 46$, $p = 0.012$; t -test). We found a similar mass ratio in infected males (1025 ± 172 g in testosterone-treated birds and 1145 ± 148 g in control birds; $N = 16$; t -test), but due to smaller sample size the difference was not significant. Infected males had significantly smaller combs than uninfected males ($p = 0.0008$; t -test), but this difference disappeared when comb size was corrected for body mass (ANCOVA with mass as a covariate).

Testosterone treatments did not influence aerobic capacity. Although infected birds had lower aerobic capacities ($p = 0.036$), this finding was probably an artifact of effects of *A. galli* on body mass, as ANCOVA revealed a significant difference between infected and uninfected males in the slope of mass vs aerobic capacity relationships (Fig. 3; $p < 0.001$). Absolute differences in aerobic capacity between infected and uninfected

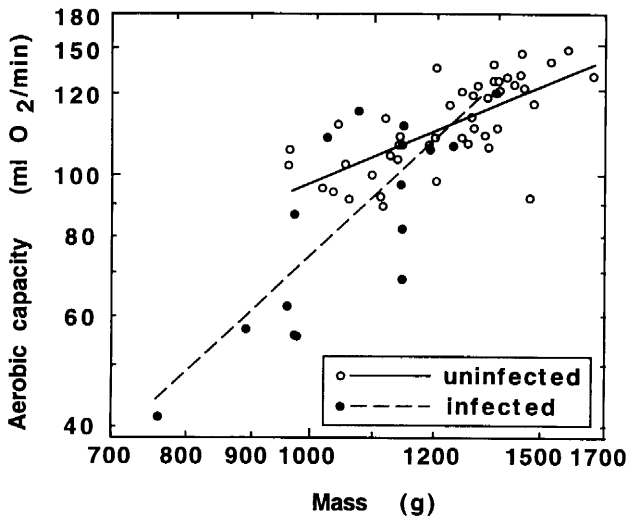


Fig. 3. Body mass and aerobic capacity (maximum rates of oxygen consumption) in 62 male red junglefowl. Both axes have \log_{10} scales. The relationship differed significantly ($p < 0.001$) between males infected with the intestinal parasite *Ascaridia galli* and uninfected males (infected: aerobic capacity = $0.00017 \times \text{mass}^{1.811}$; $r^2 = 0.58$; uninfected: aerobic capacity = $0.281 \times \text{mass}^{0.847}$; $r^2 = 0.51$).

birds were substantial at low body mass but there was little difference at masses above 1100 g. In subsequent analyses, we used residuals from these regressions to test for effects of aerobic capacity without the confounding influence of body mass.

Mating success, behaviour, morphology, and physiology

Mating success was not significantly correlated with any individual variable (Table 1). After Bonferroni correction, the only significant correlations in our data set were between body mass and comb length, and between aerobic capacity and haematocrit.

To examine interactions between display behaviour, physiology, morphology, and mating success, we used *t*-tests to compare data from 'successful' males (chosen in >50% of their trials) with that of 'unsuccessful' birds (chosen in <50% of their trials). Males with 50% success rates ($N = 5$) were excluded from these tests. After Bonferroni correction, the only significant difference between successful and unsuccessful males was in aerobic capacity in uninfected birds (Table 2). The difference in aerobic capacity was roughly 11% (after accounting for body mass).

We used a stepwise discriminant function analysis (DFA) to determine which combination of measured male characters that females could use as cues (body mass, comb size and colour, haematocrit, display rate, and aerobic capacity) best discriminated between successful and unsuccessful males. This test sequentially incorporates variables in descending order of predictive importance until addition of the next variable does not increase discriminant power (by $r \geq 0.01$). For all males combined, a combination of display rate and aerobic capacity (in descending importance) separated successful and unsuccessful birds (Wilks' Lambda = 0.85, canonical $r = 0.38$, $p < 0.016$); the remaining variables were not included. For uninfected males, a combination of aerobic capacity, display rate, comb size, comb colour, and haematocrit (in descending importance) separated successful from unsuccessful birds (Wilks' Lambda = 0.66, canonical $r = 0.59$, $p < 0.0093$); body mass was not included. In the small sample of infected males, DFA could not differentiate successful from unsuccessful individuals.

TABLE 1. *Correlations (Pearson product moments) among variables for male red junglefowl*

| Variable | Mass | Comb _L | Comb _C | T | HCT | AC | Display | %Win |
|---------------------------------------|--------------------------------------|-------------------------------------|-------------------|--------------------------------------|------------------|-------|--------------------------------------|------|
| <i>A. All males combined (N = 62)</i> | | | | | | | | |
| Comb _L | 0.647 (<i><0.001</i>) | | | | | | | |
| Comb _C | 0.073 | 0.223 (0.086; $\beta = 0.5$) | | | | | | |
| T | 0.006 | 0.353 (0.0056) | 0.103 | | | | | |
| HCT | 0.152 | 0.294 (0.023) | 0.095 | 0.236 (0.069; $\beta = 0.49$) | | | | |
| AC | 0.008 | 0.053 | 0.144 | 0.039 | 0.422 (0.001) | | | |
| Display | 0.231 (0.075; $\beta = 0.49$) | 0.360 (0.005) | -0.001 | 0.235 | 0.060 | 0.158 | | |
| %Win | 0.179 (0.17; $\beta = 0.63$) | 0.312 (0.015) | 0.047 | 0.126 | 0.034 | 0.136 | 0.246 (0.058; $\beta = 0.36$) | |

TABLE 1. (Continued)

| <i>B. Upper right: uninfected males (N = 46); lower left: infected males (N = 16)</i> | | | | | | | |
|---|-------------------------|------------------|--------------------------------------|--------------------------------------|--------------------------------------|--------|--------------------------------------|
| Mass | <i>0.564</i> (0.001) | 0.135 | -0.204 (0.18; $\beta = 0.39$) | -0.057 | -0.025 | 0.110 | 0.241 (0.15; $\beta = 0.6$) |
| Comb _L | 0.555 (0.025) | 0.144 | 0.345 (0.021) | 0.199 (0.19; $\beta = 0.62$) | 0.022 | 0.080 | 0.278 (0.069; $\beta = 0.49$) |
| Comb _C | -0.219 | 0.294 | 0.195 | 0.025 | 0.292 (0.054; $\beta = 0.35$) | -0.087 | 0.113 |
| T | 0.110 | 0.222 | -0.334 | 0.353 (0.019) | 0.053 | 0.139 | 0.194 |
| HCT | 0.308 | 0.289 | 0.176 | -0.249 | 0.324 (0.031) | -0.005 | 0.072 |
| AC | -0.001 | 0.048 | 0.170 | -0.027 | 0.545 (0.029) | 0.182 | 0.170 |
| Display | 0.235 | 0.617 (0.011) | 0.157 | 0.363 (0.167; $\beta = 0.61$) | 0.078 | 0.130 | 0.230 (0.18; $\beta = 0.53$) |
| %Win | 0.217 | 0.583 (0.018) | 0.168 | 0.235 | 0.330 | 0.110 | 0.477 (0.062; $\beta = 0.51$) |

Symbols: AC: aerobic capacity; %Win: success in mate choice trials; Display: courtship display rate; Comb_L: comb length; Comb_C: comb colour index; T: mean plasma testosterone; HCT: haematocrit. %Win and HCT data were arcsine square-root transformed to produce a normal distribution. Probabilities are shown for all $p < 0.2$; the likelihood of making a Type II error (β) is shown for all cells where $0.05 < p < 0.2$. Significant correlations ($p < 0.05$) after a sequential Bonferroni test to correct for Type I errors are printed *in italics*.

TABLE 2. Comparison between successful and unsuccessful males

| | All males | | | Uninfected | | | Infected | | |
|-------------------|---------------|---------------|-----------------|---------------|---------------|----------------|---------------|---------------|----------------|
| | successful | unsuccessful | <i>p</i> | successful | unsuccessful | <i>p</i> | successful | unsuccessful | <i>p</i> |
| | <i>N</i> = 32 | <i>N</i> = 25 | (β) | <i>N</i> = 24 | <i>N</i> = 19 | (β) | <i>N</i> = 8 | <i>N</i> = 6 | (β) |
| Display | 3.10 ± 1.88 | 2.46 ± 1.00 | 0.012 | 3.22 ± 0.96 | 2.61 ± 0.86 | 0.036 | 3.73 ± 0.47 | 1.96 ± 1.32 | 0.15 (0.17) |
| AC | 119 ± 27.7 | 109 ± 23.2 | 0.072 (0.45) | 130 ± 18 | 114 ± 17 | <i>0.0059</i> | 87.7 ± 28.7 | 94.0 ± 33.8 | 0.86 |
| Comb _L | 92.4 ± 8.2 | 87.5 ± 14.4 | 0.11 (0.34) | 91.3 ± 9.7 | 94.8 ± 6.8 | 0.17 (0.65) | 85.3 ± 8.0 | 76.0 ± 20.4 | 0.26 |
| HCT | 52.1 ± 3.5 | 51.2 ± 4.9 | 0.47 | 52.7 ± 3.8 | 51.6 ± 0.86 | 0.51 | 50.9 ± 2.4 | 50.0 ± 67 | 0.73 |
| Mass | 1263 ± 189 | 1228 ± 190 | 0.49 | 1323 ± 155 | 1266 ± 180 | 0.28 | 1084 ± 177 | 1108 ± 182 | 0.81 |
| Comb _C | 305 ± 68 | 313 ± 72 | 0.71 | 321 ± 83 | 307 ± 59 | 0.53 | 304 ± 93 | 292 ± 81 | 0.81 |
| Mean T | 0.934 ± 0.526 | 0.968 ± 0.648 | 0.83 | 1.01 ± 0.62 | 1.07 ± 0.68 | 0.75 | 0.716 ± 0.354 | 0.653 ± 0.445 | 0.77 |

Symbols are the same as for Table 1. Units are as follows: display (displays/min); AC (ml O₂/min); comb_L (mm); HCT (%); mass (g); comb_C (colour score); mean T (ng/ml). Values are shown as ± SD; probabilities (*p*) were determined by *t*-tests. Significant probabilities after a Bonferroni correction for Type I errors are printed *in italics*. Probabilities of Type II errors (β) are given in parentheses when $0.05 < p < 0.2$.

Discussion

In the context of sexual selection our most interesting finding is the association between aerobic capacity and male mating success. Results from DFA indicate that aerobic capacity, along with display rate and (to a lesser extent) comb morphology and haematocrit, are major factors that distinguish successful males from unsuccessful males. If, as our results indicate, female red junglefowl tend to mate with males with high aerobic capacity, several questions arise. First, do females actually choose mates on the basis of aerobic capacity *per se* or is this apparent preference a response to other male characters that are correlated to aerobic performance? Second, how might females benefit from a preference for males with high aerobic capacity? Finally, how do androgens and parasites — both of which are important in other aspects of mate choice — affect aerobic capacity?

How do females detect male aerobic capacity?

Previous studies (and our own results) suggest that female junglefowl select mates on the basis of courtship display rate and male ornaments such as comb length and comb colour (Zuk *et al.*, 1990d, 1995). Could the apparent preference for high aerobic capacity be an artifact of preference for these other traits? We found no significant correlations between aerobic capacity and comb morphology in our test males (Table 1), so it seems unlikely that these ornaments could have served as indirect cues of aerobic performance. However, aerobic capacity may be correlated with some aspect of male morphology we did not measure.

A priori, a relationship might be expected between aerobic capacity and courtship display, which requires substantial muscular activity. If courtship is sufficiently vigorous and prolonged it may be constrained by aerobic capacity (as may be the case in some frogs; *e.g.* Prestwich *et al.*, 1989 and possibly the sage grouse *Centrocercus urophasianus*; Vehrencamp *et al.*, 1989), and hence would provide an honest signal of a male's aerobic capabilities. Whether this concept is applicable to red junglefowl is uncertain. Although summed courtship display rates and aerobic capacity were both higher in successful than in unsuccessful males, the correlation between these two variables — although positive — was not statistically significant. Moreover, it is unclear if male courtship behaviour requires high aerobic capacity. When a female junglefowl interacts with a prospective

mate, the male normally crows and wing-flaps initially. When the female begins to approach the male he usually shifts to one of two displays: 'tidbitting', in which food items or objects such as twigs and rocks are picked up and dropped repeatedly, and 'waltzing', in which the male lowers one wing and circles rapidly behind the female (Zuk *et al.*, 1990a, 1995). A third display, 'crouch-scratching', occurs less commonly. Only one of the courtship displays used by male junglefowl — wing-flapping — appears subjectively to be as energy-demanding as the level of exercise we used to elicit aerobic capacity (crowing appears to require considerable effort but the energy cost is minimal; Chappell *et al.*, 1995). The displays used most frequently during the final stages of courtship (tidbitting and waltzing) probably do not require maximal metabolic effort (although actual energy costs have not been measured). As a caveat, it should be pointed out that our courtship display index includes the occurrence of various behaviours but does not quantify the intensity with which they were performed. Females may be able to use display intensity to obtain better information on male aerobic capacity from courtship behaviour than our data provided.

Aerobic capacity and 'good genes'

Assuming that females can discriminate among males of differing aerobic capacities, how might this ability increase female fitness? High aerobic capacity provides increased performance and stamina at high power outputs during exercise (predator escape, locomotion, aggressive behaviour, *etc.*), thermogenesis, reproduction, and other functions important for fitness. For example, in domestic chickens male aerobic capacity is almost twice that of females on a mass-specific basis, and as a result males have a maximum sustainable running speed of about 9 km/h, compared with about 5 km/h for females (Brackenbury & El-Sayed, 1985). If aerobic performance is heritable, mating with males of high aerobic capacity should provide females with evolutionary benefits through the survival advantage conferred to offspring. Unfortunately there are no data on heritability of aerobic capacity in birds and the very few quantitative genetic studies of aerobic performance in other vertebrates are inconclusive: aerobic capacity is significantly heritable in garter snakes (Garland & Bennett, 1990) and possibly humans (Bouchard *et al.*, 1989) but not in laboratory mice (M. Dohm, J. Hayes, and T. Garland, pers. comm.).

Alternately, if male aerobic capacity itself is not heritable, it may still provide useful information to a female if it serves as an indicator of other heritable traits that affect fitness. High aerobic capacity depends on the proper function of a broad range of physiological systems, including the pulmonary, cardiovascular, and muscular systems, and is sensitive to overall health. In this context, and from the perspective of Hamilton & Zuk's (1982) hypothesis of the influence of parasites on sexual ornaments and mate choice, it is interesting to ask if junglefowl aerobic capacity is influenced by *A. galli* infection. If so, aerobic capacity could provide females with an honest signal of parasite burdens (similar to the way sexual ornaments may serve as indirect indices of infection; Zuk *et al.*, 1990a; Johnson *et al.*, 1993). Data from lizards (*Sceloporus occidentalis*; Schall *et al.*, 1982; Schall & Dearing, 1987) and canaries (*Serinus canarius*; Hayworth *et al.*, 1987) reveal strong effects of malarial parasites (*Plasmodium*) on aspects of metabolic performance and behaviour — unsurprising given that *Plasmodium* is highly destructive to erythrocytes. In contrast, blood-borne filarial parasites have no apparent effect on aerobic performance in Australian frillneck lizards (*Chlamydosaurus kingii*; Christian & Bedford, 1995).

Initially, we did not expect to find an effect of *A. galli* on the aerobic capacity of adult males. This nematode causes significant mortality and retards weight gain in galliform chicks (Ruff, 1978; Chappell *et al.*, 1996), but causes few obvious effects on non-ornamental characters in adult junglefowl (Zuk *et al.*, 1990d). A previous study with a smaller sample size of males (Chappell *et al.*, 1996) detected no differences in the aerobic capacity of infected and uninfected adults. In the present study we did find significant differences between infected and uninfected males in the slope of the relationship between mass and aerobic capacity, but absolute differences in aerobic capacity were only apparent for small males (Fig. 1). The aerobic capacity of male junglefowl increases very rapidly during growth from small chicks to adulthood (scaling to mass^{1.106}; Chappell *et al.*, 1996). Since *A. galli* infection stunts the growth of chicks, the reduced aerobic capacity observed in our cohort of infected males may simply be a result of small size due to reduced growth rates (the infected birds averaged significantly smaller than uninfected males at the time of testing), rather than a direct pathological consequence of infection. In any event, female jun-

glegfowl probably cannot use aerobic capacity to obtain useful information on the *A. galli* infection status of large males — which are the males most likely to be socially dominant and to have the easiest access to females.

Factors affecting aerobic capacity

Given the apparent role of aerobic capacity in mate choice, it is useful to consider additional physiological factors that might influence aerobic capacity. The best predictor of aerobic capacity (after mass correction) was haematocrit, and there was little or no effect of plasma testosterone, either in terms of treatment group or in plasma testosterone levels at the time of measurement. The former is not surprising because of the critical role of erythrocytes in oxygen transport. The second finding is more interesting. Testosterone and other androgens are necessary for the development and expression of male mating behaviour and secondary sex characters (Hardesty, 1931; Allee *et al.*, 1939; Sossinka *et al.*, 1980; Harding, 1983; Wingfield & Farner, 1993), and are also known to increase exercise endurance in lizards (John-Alder, 1994) and body and muscle mass in birds and mammals (Wade, 1976; Dark *et al.*, 1987; Mooradian *et al.*, 1987). Male red junglefowl have substantially higher mass-specific aerobic capacity than females (Chappell *et al.*, 1996), presumably due in part to differences in androgen levels between the sexes. Nevertheless, in our sample of adult males we found no correlation between testosterone titers or testosterone treatment group and aerobic capacity. To our knowledge the present study is the first report of the relationship between testosterone and aerobic capacity in birds. Our results are consistent with findings for humans (*e.g.* Lombardo, 1993) which show few consistent effects of testosterone on aerobic capacity. However, an understanding of the effects of long-term differences in testosterone levels on avian aerobic capacity — particularly during maturation and growth to adulthood — requires additional study.

In conclusion, our data indicate that female red junglefowl tend to mate with males of high aerobic capacity. We speculate that this apparent preference could benefit females through a 'good genes' mechanism. The mechanism by which females discriminate between males of differing aerobic capacity is unclear, but the most likely cue is courtship display behaviour.

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