Aerobic Performance Does not Affect Social Rank in Female Red Jungle Fowl

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Summary

1. Exercise capacity ultimately constrains behaviour, and therefore may influence social interactions. The hypothesis was tested that individual differences in maximal rates of oxygen consumption ($\dot{V}_{O_2max}$) – a primary determinant of sustainable exercise capacity – affect dominance hierarchies in experimental all-female flocks of the highly social Red Jungle Fowl (*Gallus gallus*). It was also examined whether social rank could in turn influence $\dot{V}_{O_2max}$ (which is quite plastic in most vertebrates), and whether these relationships were influenced by a common and relatively benign parasite, the intestinal nematode *Ascaridia galli*.

2. Substantial between-individual variation was found in $\dot{V}_{O_2max}$ that was significantly repeatable over time, but there was no indication that $\dot{V}_{O_2max}$ was affected by *A. galli* infection. Stable social hierarchies were quickly established in 26 of 28 experimental flocks (each contained three females previously isolated from each other). Infection status affected social rank, but there was no consistent pattern between rank and infection.

3. No indication was found that individual differences in $\dot{V}_{O_2max}$ either predicted the social rank in newly formed flocks, or were affected by social status in established flocks.

Key-words: Dominance, energy metabolism, parasites, repeatability, social behaviour

Functional Ecology (1999) **13**, 163–168

Introduction

Social hierarchies exist in most group-living animals, and social status (e.g. rank in a dominance hierarchy) is often critically important in determining an individual's access to resources such as food, mates or shelter. The factors affecting social rank have been extensively studied, particularly in domestic fowl (the first vertebrate species for which dominance relations were systematically examined; e.g. Schjelderup-Ebbe 1922; Guhl & Fischer 1969). Sex, body size and age are the attributes most commonly cited as affecting social rank, but other factors – hormonal status, moult stage, social experience, etc. – may also be important (Collias 1943).

In this paper we examine the relationship between social rank and individual variance in a major whole-animal physiological trait: aerobic exercise capacity. Aerobic respiration is the metabolic basis of sustainable power production. Hence, aerobic capacity sets an upper limit to an animal's ability to engage in sustained vigorous activity. Potentially, this includes fighting, displaying and other behaviours important in establishing social rank (e.g. Brackenbury & El-Sayed 1985; Chappell *et al.* 1997). Recent work shows that substantial and repeatable individual variation in aerobic capacity is typical of endothermic vertebrates (Hayes & Chappell 1990; Chappell & Bachman 1995;

Chappell, Zuk & Johnsen 1996). Accordingly, individual differences in aerobic performance might influence the ability to compete in a social hierarchy. Conversely, aerobic capacity is often quite plastic under various conditioning and acclimatization regimes (e.g. Dawson & Smith 1986; Hayes & Chappell 1986; Hayes 1989), and because it depends on the integrated functioning of a suite of organ systems (pulmonary, cardiovascular, skeletal musculature; Weibel 1984) it is dependent on overall physical condition. Therefore one might expect that physiological repercussions of social status (access to food, stress levels, etc.) might affect aerobic capacity.

These hypotheses were tested in female flocks in the highly social Red Jungle Fowl *Gallus gallus*. Jungle fowl are ancestral to domestic fowl, and in natural conditions most aspects of their social behaviour are similar to those of small groups of domestic chickens (Collias & Collias 1967). A bird's dominance status may have an important impact on fitness; for example, Collias, Collias & Jennrich (1994) found that dominant hens in an unconfined population had higher reproductive success than subordinate individuals.

The influence of an intestinal nematode *(Ascaridia galli)* on the relationship between social rank and aerobic physiology was also examined. This parasite is endemic and common in a variety of galliform birds. Infection with *A. galli* affects juvenile growth,

secondary sexual characters, aerobic performance and mating success in male Red Jungle Fowl (Ruff 1978; Zuk *et al.* 1990a, b; Zuk, Popma & Johnsen 1995; Chappell *et al.* 1996, 1997), so it is reasonable to expect it to influence any interaction between aerobic physiology and social status in females.

Materials and methods

ANIMALS AND TREATMENT GROUPS

Red Jungle Fowl were obtained from a captive colony at the University of California, Riverside. The ancestral stock was obtained in the late 1980s from a feral flock at the San Diego Zoo in southern California; subsequently they were reared using a minimum of 50 breeding males and 50 breeding females per generation (the zoo flock was descended from 27 birds imported from India and Burma in 1942). The population has not experienced artificial selection for activity patterns, physiology or reproductive biology.

For this study, chicks were hatched in incubators and kept indoors in brooders for 6 weeks, after which they were maintained in outdoor pens exposed to ambient weather and photoperiod (Zuk *et al.* 1990a, 1995). Food (commercial poultry feed, 18–21% protein) and water were available *ad libitum*. Newly hatched chicks were divided into two treatment groups that were kept separate until adulthood. One group served as controls. A second group was inoculated with *Ascaridia galli* ($\approx$ 100 embryonated eggs administered orally in 0·5 ml saline every week between the ages of 1–5 weeks; Zuk *et al.* 1990a). *Ascaridia galli* has a direct life cycle and causes juvenile mortality and stunted growth (Ruff 1978; Chappell *et al.* 1996), but has few obvious effects on non-ornamental characters in adults (Zuk *et al.* 1990a). At about 4 months of age, the birds in each group were separated into male–female pairs. At about 9 months, small blood samples (< 0·1 ml) were obtained from the alar vein for measurements of haematocrit (previously shown to be correlated with aerobic capacity in males; Chappell *et al.* 1997). Three-bird all-female groups were then assembled (test flocks) for the social rank study. *Ascaridia galli* is weakly infective in jungle fowl of this age; after the completion of experiments, birds were killed and dissected to determine the presence and number of *A. galli* in the digestive tract. The dissections confirmed that no control females were contaminated during the tests.

SOCIAL RANK

Twenty-eight test flocks were formed and housed in wood and chicken wire cages 2·5 m long by 1·1 m wide and 1·25 m high. Flocks consisted of one parasitized and two control birds, all of which had been visually isolated from each other for one month. Each bird was marked with a unique combination (within flocks) of a coloured leg band and a metal identification band.

Test flocks were observed from a distance of 4–6 m and three behaviours were recorded: *fighting, pecking* and *displacement* (Zuk *et al.* 1997). All interactions observed were between pairs of females. In *fighting,* both hens attacked, and the one retreating was scored as subordinate in that interaction. *Pecks* were usually aimed at or near the opponent's head; again, the hen being pecked was considered the subordinate when she retreated. In *displacement,* one hen threatened another, as evidenced by chasing, sometimes accompanied by raised hackle feathers. In these situations, the object of the chase would retreat and was deemed subordinate. Based on at least 10 interactions per pair the females were ranked from 1 to 3, 1 being the dominant and 3 the most subordinate.

On the day it was formed, each test flock was observed for 30 min. The next day it was observed for 15-min intervals until each pair had interacted at least 10 times and the ratio of dominant to subordinate interactions was statistically significant. When necessary, food was provided during observations to instigate dominance interactions. On the third day, and again after three weeks, the flocks were observed for an additional 30 min to confirm that the recorded hierarchy was stable. No changes in social rank were observed, so it was assumed the rank systems of the test flocks were stable throughout the experimental period. All observations took place between 07·00 hours and 12·00 hours on fair-weather days. Stable social hierarchies were determined within all but 2 of the 28 flocks.

AEROBIC CAPACITY

The birds' aerobic capacities were measured as described previously (Chappell *et al.* 1996, 1997). Briefly, open-circuit respirometry was used to measure rates of oxygen consumption ($\dot{V}_{O_2}$; ml O_2 min^{-1}) during intense exercise in an enclosed motorized running wheel. The wheel (76 cm diameter by 42 cm wide; internal volume 190 l) was supplied with dry air at rates of 40–44 l min^{-1} STP, metered $\pm$ 1% with mass flow controllers (Tylan, CA, USA) calibrated against a precision dry volume meter. A portion (about 100 ml min^{-1}) of the excurrent air stream was dried, scrubbed of CO_2 and analysed for oxygen content (%O_2; Applied Electrochemistry S-3 A; PA, USA). Reference baselines (ambient incurrent air) were obtained immediately before and after each test. Oxygen concentrations ($\pm$ 0·0015% relative to atmospheric pressure) were recorded on a Macintosh computer. Birds were run at gradually increasing speeds until they no longer maintained position and $\dot{V}_{O_2}$ did not increase with increasing speed. The birds always showed behavioural signs of exhaustion by this time, but none was injured. Complete measurements lasted 6–12 min (2·5–8 min of actual exercise). Data from tests in which birds could not run for at least

2 min were not used. A blind trial arrangement ensured that the running wheel operator did not know the treatment group or social rank of birds being tested.

The 'instantaneous' calculation (Bartholomew, Vleck & Vleck 1981) was used to compensate for the mixing characteristics of the large-volume wheel and accurately resolve short-term $\dot{V}_{O_2}$ changes. The wheel rotation, dispersal baffles on the incurrent and excurrent air ports, and the activity of the birds insured that chamber air was well mixed. The raw data were smoothed to minimize artefacts due to electrical noise or position changes, and maximal $\dot{V}_{O_2}$ ($\dot{V}_{O_2max}$) was computed as the highest instantaneous $\dot{V}_{O_2}$ averaged over a continuous 1-min interval (Chappell *et al.* 1997; Fig. 1). Although an individual's exercise $\dot{V}_{O_2}$ typically varied by 15–25% during a given test, there was no tendency for $\dot{V}_{O_2max}$ to occur at any particular stage (start, middle or end) of exercise bouts.

Each female's $\dot{V}_{O_2max}$ was tested twice: immediately prior to the formation of the experimental flocks, and again after the conclusion of the social hierarchy measurements ≈ 10 weeks later (the interval differed slightly for each individual). Birds were weighed ± 1 g at the time of each test.

STATISTICS

Because avian metabolism is a power function of mass, we $\log_{10}$-transformed mass and $\dot{V}_{O_2max}$ to linearize these variables prior to analyses. To correct for the possible influence of body size, ANCOVA with mass as covariate was used for comparisons between treatments (parasitized and control) and social ranks. For comparisons where mass was not a factor, 2-tailed *t*-tests and ANOVA were used. The significance level was $P = 0.05$; a sequential Bonferroni procedure was applied to correct for Type I errors in multiple simultaneous tests (Rice 1989). Analyses were performed with Statistica/Mac software (StatSoft, Inc., Tulsa, OK).

Results

VARIANCE

Complete data were obtained on $\dot{V}_{O_2max}$ and social rank from 68 female jungle fowl (26 parasitized, 42 control) ranging in mass from 624 to 1145 g at the initial test and 653–1232 g at the final test. Incomplete results (physiological variables but not rank) were obtained from two additional 'control' birds. There was substantial variance in the physiological variables (Fig. 1).

Coefficients of variation were 13% (initial and final mass) and 10% (haematocrit). The mean differences between observed and predicted values for $\dot{V}_{O_2max}$ (mass residuals expressed as percentage of predicted values) were 11% (initial test) and 22·5% (final test). After correction for body mass, $\dot{V}_{O_2max}$ was not correlated with haematocrit ($P > 0.65$; ANCOVA).

Individual differences in $\dot{V}_{O_2max}$ were significantly consistent between initial and final tests, as has previously been shown for male jungle fowl (Chappell *et al.* 1997). Repeatability was estimated from mass residuals (computed using $\log_{10}$ values of mass and $\dot{V}_{O_2max}$; Fig. 2). The regression of initial *vs* final residuals was positive and significant ($F_{1,66} = 6.9$; $P = 0.0107$), with a repeatability (r) of 0·31. Body mass was highly repeatable across this interval ($r = 0.73$, $F_{1,66} = 75.1$; $P < 0.0001$).
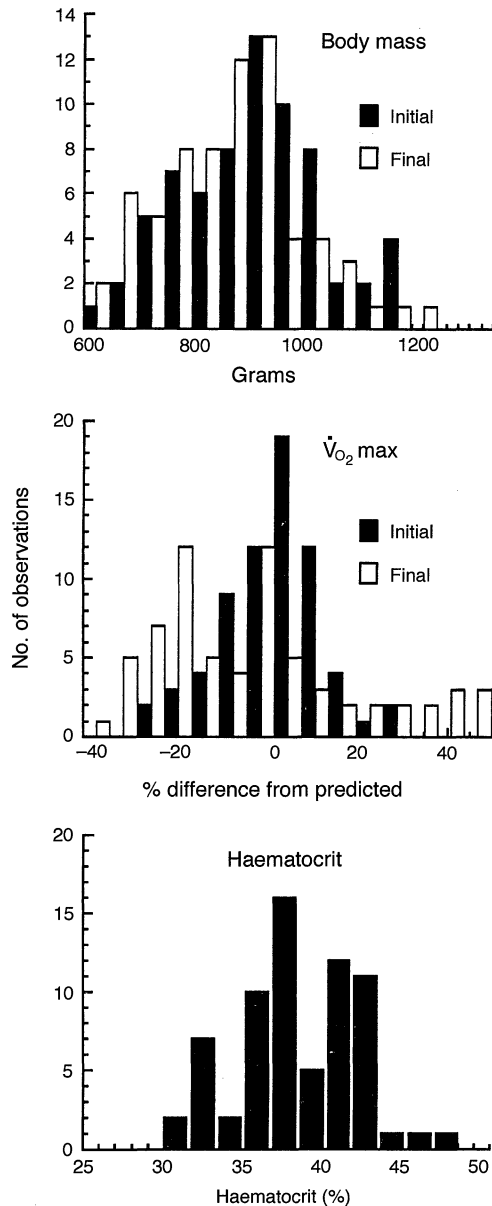

Fig. 1. Variance in mass and physiological parameters in female Red Jungle Fowl. Results for mass and maximal rates of oxygen consumption ($\dot{V}_{O_2max}$) are shown for both initial and final measurements (before and after social dominance trials, respectively). Oxygen consumption is strongly dependent on body size, so individual variance in $\dot{V}_{O_2max}$ was computed as the difference between observed values and values predicted by regressions of log $\dot{V}_{O_2max}$ on log mass.
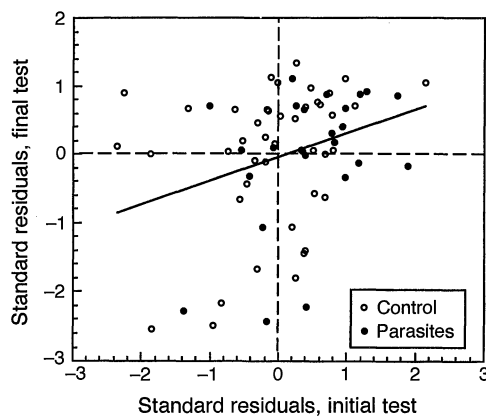
Fig. 2. Repeatability of $\dot{V}_{O_2max}$ in 68 female Red Jungle Fowl tested $\approx$ 10 weeks apart. The plot shows the residuals from regressions of log $\dot{V}_{O_2max}$ against log body mass from both initial and final measurements. The regression of initial and final residuals is significant ($P = 0\cdot0107$) with a repeatability of about $0\cdot31$.

EFFECTS OF PARASITES

A significant effect of *A. galli* infection was found on body mass during the initial measurements ($t = 2\cdot4$, $P = 0\cdot018$), but not for the final measurements made $\approx 2\cdot5$ months later ($t = 0\cdot65$, $P = 0\cdot51$). Infected birds gained significantly more mass than controls during the test period ($t = 2\cdot47$; $P = 0\cdot016$), but infection status did not influence either haematocrit or $\dot{V}_{O_2max}$ ($P = 0\cdot29$ and $P = 0\cdot64$, respectively; ANCOVA with mass as covariate).

SOCIAL RANK

In our sample of 68 females, social rank was associated with *A. galli* infection ($\chi^2 = 7\cdot9$, $P = 0\cdot018$), but not in a clearly interpretable rank order (Zuk *et al.* 1998). Social rank was not influenced by initial mass ($P = 0\cdot20$; ANOVA) and, in turn, rank did not influence final mass ($P = 0\cdot58$; ANOVA).

There was no relationship between rank and either absolute pretest $\dot{V}_{O_2max}$ ($P = 0\cdot85$; ANOVA) or mass-adjusted pretest $\dot{V}_{O_2max}$ ($P = 0\cdot74$; ANCOVA with mass as covariate), and the interaction terms between pretest $\dot{V}_{O_2max}$ and infection status were also not significant ($P > 0\cdot7$ for both absolute and mass-adjusted $\dot{V}_{O_2max}$). Thus individual variance in aerobic performance is not a factor in determining social dominance when females form new flocks.

The social rank birds attained during the experiment was not significantly correlated to $\dot{V}_{O_2max}$ after the social acclimation period ($P = 0\cdot88$; ANCOVA with mass as covariate). Similarly, changes in body mass and $\dot{V}_{O_2max}$ between initial and final tests were not correlated to social rank ($P = 0\cdot75$ and $0\cdot89$, respectively; ANOVA). These results show that a bird's social rank in a stable flock did not influence aerobic performance or growth.

Discussion

Physiological performance characters set upper limits on an animal's ability to engage in activity (e.g. Bennett & Ruben 1979) and therefore ultimately constrain the intensity or duration of behaviours that require vigorous movement. Given that the outcomes of many social interactions – courtship, aggressive displays, fighting, chasing, etc. – depend at least partially on strength and endurance, it is reasonable to assume that individual differences in physiological performance traits might be important factors in social behaviour. However, there have been relatively few studies of this question. Garland, Hankins & Huey (1990) showed that one aspect of locomotory performance in *Sceloporus* lizards (sprint speed) was a significant predictor of behavioural dominance in competition for basking sites. Similarly, malaria-infected male *Sceloporus* – which have lower exercise capacity than parasite-free animals – are socially subordinate to males free of infection (Schall, Bennett & Putnam 1982; Schall & Dearing 1987). A recent study of mate choice in Red Jungle Fowl showed that males with high aerobic performance are preferred by females (Chappell *et al.* 1997). Although the mechanism of choice was unclear, such a preference could be advantageous to females in 'good genes' models of sexual selection.

In this study it was predicted that individual differences in aerobic capacity would be a determinant of the social ranking in newly established groups of female Red Jungle Fowl. It was also predicted that changes in aerobic performance during the experiment would be a function of an individual's social rank. However, we found no evidence of any relationship between the social dominance ranking of female jungle fowl and their aerobic performance: aerobic capacity at the beginning of the experiment did not predict the social rank birds attained in test flocks, and changes in aerobic capacity during the experiment were independent of social status.

Why would a crucial physiological trait such as aerobic metabolism be unrelated to a primary aspect of social behaviour? Several possibilities need to be considered. From a theoretical perspective, a predictive relationship between performance and rank might be absent – even if dominance behaviour was highly dependent on sustained exercise capacity – if variance in aerobic capacity was low and lacked repeatability. Female Red Jungle Fowl do show substantial individual differences in aerobic performance, as is typical for vertebrates (e.g. Garland & Bennett 1990; Hayes & Chappell 1990; Chappell & Bachman 1995) including male jungle fowl (Chappell *et al.* 1996). Maximal rates of oxygen consumption varied by as much as two-fold between females (after correcting for body mass), and the average difference from mass-corrected mean values was 14% (Fig. 1). These performance differences were significantly repeatable over

time. However, the repeatability of $\dot{V}_{O_2\max}$ found for females ($r = 0.31$) is much lower than that reported for males ($r = 0.6$–0.9; Chappell *et al.* 1996). We speculate that the lower repeatability may be related to the reduced importance of high $\dot{V}_{O_2}$ in females, as discussed in the next paragraph.

In our view the most likely explanation for the lack of relationship between $\dot{V}_{O_2\max}$ and rank is that the behaviours female jungle fowl use to establish and maintain social dominance (displays and fighting) are not strongly dependent on maximal aerobic performance. Interactions between females, although frequent, are typically of low intensity and are quickly resolved, often without actual combat (Collias 1943). Therefore the outcomes of female–female contests are probably much more dependent on burst activity (or factors other than exercise ability) than on a high capacity for sustained power production. This is in sharp contrast to male–male interactions, which frequently involve intense, sustained fighting (a proclivity humans exploit in staged 'cockfights'). Combatants routinely fight to exhaustion (Ligon *et al.* 1990), and in such contests males with high aerobic capacity are likely to have an advantage. The observations that male $\dot{V}_{O_2\max}$ and factorial aerobic scope are approximately twice that of females in both domestic chickens and Red Jungle Fowl (Brackenbury & El-Sayed 1985; Chappell *et al.* 1996; Table 1), and that repeatability of $\dot{V}_{O_2\max}$ is much lower in females than in males, are consistent with this hypothesis.

If aerobic performance is influenced by overall body condition, why were changes in performance during the experiment unrelated to social rank? A possible explanation is the *ad libitum* food availability during the tests. Our experimental birds – even subordinates – probably did not suffer from food shortage. We speculate that in more natural conditions food resources are often limited and dominant individuals may be able to monopolize them, with detrimental effects on the nutrition and health (and consequently the aerobic performance) of subordinates. Similarly, the *ad libitum* feeding regimen may have minimized the impact of *A. galli* infection, which had no effect on aerobic performance in our

study. In a food-restricted environment this intestinal nematode might have produced significant effects (Ruff 1978).

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Table 1. Basal metabolic rate (BMR), maximal aerobic metabolism $\dot{V}_{O_2\max}$) and factorial aerobic scope ($\dot{V}_{O_2\max}$/BMR) for male and female Red Jungle Fowl. BMR and male $\dot{V}_{O_2\max}$ data were obtained from Chappell *et al.* 1996 and Chappell *et al.* 1997. These values are standardized to mean masses of 894 g for females (this study) and 1357 g for males (Chappell *et al.* 1997); both means are for birds not infected with *Ascaridia galli*

Sex	BMR (ml O_2 min^{-1})	$\dot{V}_{O_2\max}$ (ml O_2 min^{-1})	Aerobic scope
Males	12·7	127	10·0
Females	9·80	57·9	5·9

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