

COMPARISON OF RUNNING ENERGETICS IN MALE AND FEMALE DOMESTIC FOWL

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SUMMARY

1. Carbon dioxide production (\dot{V}_{CO_2}) and end-exercise venous lactate concentration were compared in intensively-trained, mature male and female domestic fowl running on a treadmill for 10-min periods at maximal and sub-maximal work loads.

2. The relationship between \dot{V}_{CO_2} and running speed was linear and had the same slope in male and female birds. However the maximum sustainable running speed of the males was approximately twice that in the females and the maximum weight-specific \dot{V}_{CO_2} was 60 % higher in males.

3. End-exercise venous lactate concentration rose significantly above resting at work loads above 75 % maximum in females, but only at work loads above 95 % maximum in fully-trained males.

4. The results indicate a greater work capability in male than in female birds in the conditions of the experiments.

INTRODUCTION

The energetics of treadmill running have been investigated in several species of bird including rhea (Taylor, Dm'iel, Fedak & Schmidt-Nielsen, 1971), greylag goose, painted quail, bobwhite quail, chukar partridge, guinea fowl, turkey (Fedak, Pinshow & Schmidt-Nielsen, 1974) emperor penguin (Pinshow, Fedak, Battles & Schmidt-Nielsen, 1976), ostrich (Fedak & Seeherman, 1979), Marabou stork (Bamford & Maloiy, 1980), domestic fowl (Brackenbury & Avery, 1980; Brackenbury, Avery & Gleeson, 1981), Pekin duck (Bech & Nomoto, 1982) and Japanese quail (Nomoto, Rautenberg & Iriki, 1983). The majority of these birds are capable of increasing their metabolic rate by 3–5 times during treadmill exercise, although rhea and domestic fowl achieved increases of 10–11 times and this compares favourably with the metabolic performance of many flying birds. From their studies on seven species of bird Fedak *et al.* (1974) found that the incremental cost of transport, which is equivalent to the slope of the oxygen consumption *versus* running speed relationship, was inversely related to body weight. However, it is clear that both the aerobic scope

of birds and their incremental cost of transport may also be influenced by body geometry and by the degree of cursorial specialization shown. Thus the maximum oxygen consumption rate measured during treadmill exercise in Pekin duck, which is poorly adapted for running, was only 3.5 times the true resting value (Bech & Nomoto, 1982). The cost of transport in the greylag goose was just as high as that in the chukar partridge which weighed eight times less. Similarly, the measured costs of transport in Marabou stork (Bamford & Maloiy, 1980) and penguin (Pinshow *et al.* 1976) were, respectively, six and sixteen times the values predicted on the basis of body weight.

It is therefore evident that running energetics is governed not only by body weight but also by morphological and physiological factors. No studies have yet been carried out to determine whether or not there may also be a sex difference in exercise capability in birds, although such information would clearly be of relevance in the context of the ecological energetics of migrating and breeding populations. Brackenbury *et al.* (1981) noted that the maximum weight-specific oxygen consumption of well-trained female domestic fowl was much less than that previously measured in male birds by Brackenbury & Avery (1980). Such a difference might be expected in sexually mature, actively laying birds in view of the proportion of the total metabolic energy reserve that must be devoted to reproduction. The aim of the present investigation was to assess the effect of reproductive activity on exercise capability by comparing the performance of mature male birds with that of mature females which were in regular laying condition.

METHODS

Animals and training

Experiments were conducted on five male (White Leghorn, mean body weight 2.8 kg) and five female (Warren, mean body weight 1.8 kg) domestic fowl individually selected on the basis of suitability for treadmill running. Both groups were acquired at approximately 16 weeks of age and were subjected to a regular training régime spanning approximately 8 months. During this period the males were caged separately whilst the females were housed in a group. In both cases the birds were fed *ad libitum* on a commercial diet. During the first few months the birds were subjected to endurance training in connection with a separate study of the utilization of dietary energy (Brackenbury & El-Sayed, 1984). At the end of this period the birds were all capable of running continuously for 90 min at approximately 60 % maximum work load. During the remaining 4 months of training each bird was exercised at least once a day for 10 min at gradually increasing work loads. Regular checks were made on both resting and end-exercise blood lactate concentrations (see below). As training proceeded both lactate values gradually declined as the birds became fitter and more familiar with the handling procedures. In addition, the birds were gradually familiarized with the wearing of a loose-fitting mask to be used for the collection of expired gases. During the final 3–4 weeks the intensity of the training was stepped up to at least two runs per day. Laboratory temperatures were maintained below 20 °C to minimize heat stress during exercise. All runs took place on a Woodway Animal treadmill, the running surface of which measured 153 × 43 cm.

Experimental procedures

Two series of runs were performed on the fully trained birds. In the first series 1-ml blood samples were drawn from the wing vein before and immediately after the 10-min exercise period. The blood was immediately de-proteinized in 0.6 mol l^{-1} perchloric acid, centrifuged, refrigerated and analysed within 18 h for lactate concentration (Boehringer Mannheim). In the second series the birds were fitted with masks and expired gases were collected continuously at flow rates of $19\text{--}35 \text{ l min}^{-1}$ depending on work load. The masks were made of plastic and weighed 15 g (males) and 10 g

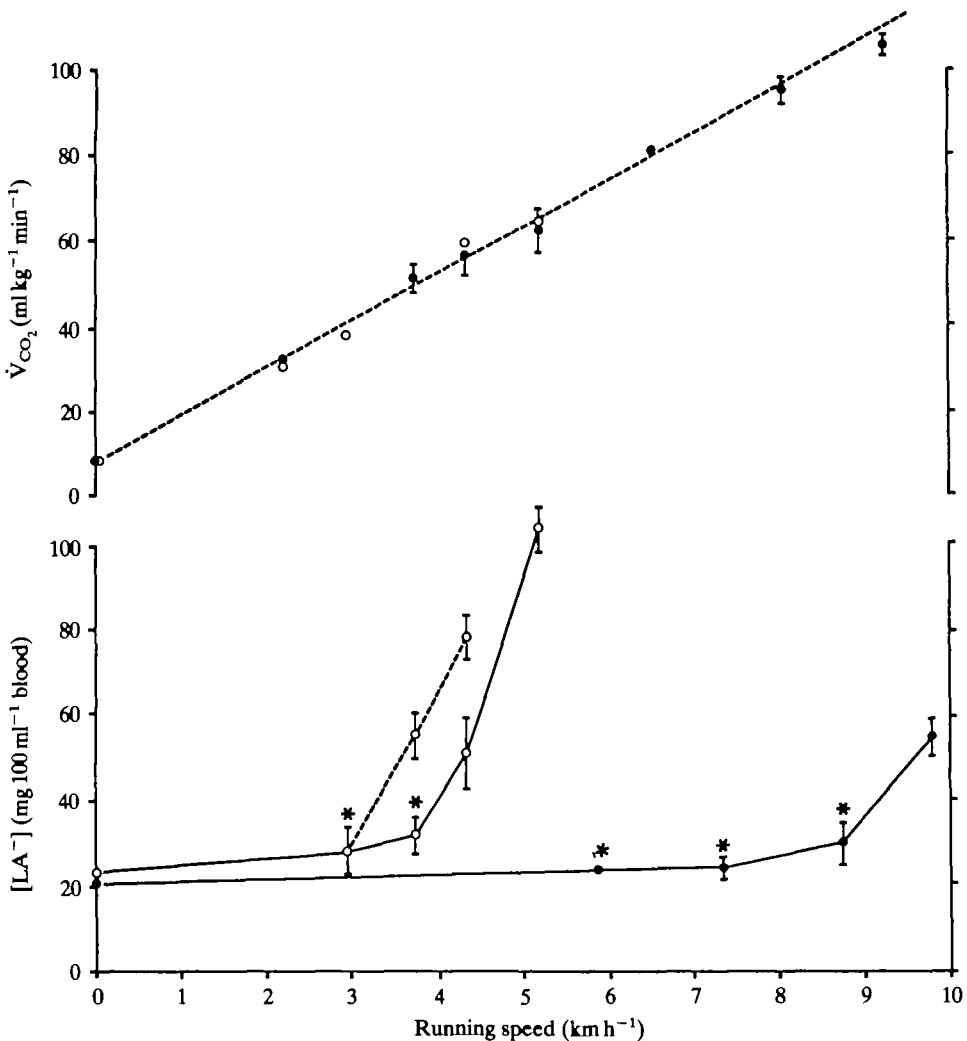


Fig. 1. Carbon dioxide production (\dot{V}_{CO_2}) and end-exercise venous lactate concentration (LA^-) in domestic fowl (filled circles, male; unfilled circles, female) during treadmill exercise at different speeds. Mean values ± 1 s.e.m. Values marked by asterisks are not significantly different from rest ($P \leq 0.05$). Dotted line in lower graph indicates values obtained in female birds before the final period of intensive training.

(females). Each mask was connected to the air pump by means of a 1.5-m length of flexible tube (i.d. 0.5 cm) and the flow rate was monitored by a dry gas meter. A sample of the collected gas was drawn into a Beckman LB2 CO₂ analyser after passage through Drierite. The flow rate of the pump was adjusted at each running speed to maintain the measured change in CO₂ concentration within the range 0.5–1.0 % thereby ensuring that no expired gas escaped from the mask. The whole apparatus was calibrated by ducting measured concentrations of CO₂ directly into the mask. Finally, the measured carbon dioxide production of the birds (\dot{V}_{CO_2}) was reduced to STPD conditions taking into account the slight reduction in pressure within the flow meter caused by the resistance of the tube along which the air was drawn from the mask.

RESULTS

The measured \dot{V}_{CO_2} reached a plateau within the first 5–6 min of exercise and mean values are based on readings taken during the last 4–5 min of each run. The mean \dot{V}_{CO_2} and end-exercise venous lactate concentrations at different treadmill speeds are shown in Fig. 1. The maximum sustainable speed of the male birds (9.7 km h⁻¹, 2.7 m s⁻¹) was approximately double that of the females (5.0 km h⁻¹, 1.4 m s⁻¹). In both cases, although faster speeds could be achieved, these were sustainable only for 2–3 min. The maximum weight-specific \dot{V}_{CO_2} of the males was approximately 60 % greater than that of the females. These maximum values represented increases of 11 times and 7 times respectively in males and females compared to rest. Blood lactate concentration only began to rise significantly above rest at work loads equivalent to 75 % maximum in the females and 95 % maximum in the males. At the maximum work load the end-exercise venous lactate concentration had risen by 4.5 times in the females but by only 2.5 times in the males. Fig. 1 also shows, by way of comparison, the end-exercise venous lactate concentration in females just before they were subjected to the final 4-week period of intensive training. It can be seen that at this time the values were at least 50 % higher at the heavier work loads than they were after intensive training. During the same period the females were able to extend the length of uninterrupted exercise at the top speed of 5.0 km h⁻¹ from 2–3 min to the full period of 10 min required to obtain a steady-state power output.

DISCUSSION

Effects of training

Gleeson & Brackenbury (1983) have noted the importance of adequate training in establishing reliable physiological responses to exercise in small animals. Birds subjected to treadmill exercise increase both ventilation and energy expenditure much more at any given speed during the initial training runs as a result of stress. The present study has shown that even after stress has been reduced to a minimum as a result of prolonged exposure to the experimental procedures it is still necessary for the birds to undergo a final period of intensive training before a reliable maximum performance can be elicited. It is the uppermost 5–10 % of performance that is the most difficult to extract by training and this peak is rapidly lost if training is interrupted. This pattern became particularly evident in the males whose performance during the later

stages of training continuously exceeded expectations. End-exercise venous lactate concentration would rise at each work load increment only to be followed in further sessions by a reduction to the resting value. Finally, a stable increase in end-exercise venous lactate concentration was obtained but only at the highest work load (Fig. 1).

Gleeson & Brackenbury (1984) found that in female domestic fowl that had been trained three times daily for 6 weeks end-exercise blood lactate concentration already showed a significant rise at work loads of 60 % maximum. The disposal of lactate by these birds was therefore comparable to that of the group used in the present study up to the time of intensive training. This does not necessarily mean that additional training lowered the rate of lactate production at the same physiological stress. Donovan & Brooks (1983) have shown that lactate turnover rates were the same in endurance-trained and untrained rats but that the lactate clearance was much greater in the trained individuals. They concluded that, although lactate removal is directly correlated with blood lactate concentration under any given metabolic condition, trained animals are capable of matching the rate of lactate removal to that of lactate production at a lower concentration than are untrained animals.

The only other report of changes in blood lactate concentration during treadmill exercise in birds is that by Kiley, Kuhlmann & Fedde (1982), who found an approximate doubling in value in the Pekin duck during 20 min exercise at a speed of 1.47 km h^{-1} . This contrasts markedly with the findings of the present study. It may be that, since ducks are only poorly adapted for cursorial locomotion, the leg muscles are unable to sustain aerobic work at higher running speeds. It is equally likely, however, that the high lactate concentration found in ducks resulted from experimental technique. These birds appear to have received only minimal preliminary exposure to a treadmill and were breathing through an acutely implanted tracheal cannula, conditions that in our estimation would contribute to excess lactacidosis.

Comparison of running energetics in male and female

A linear relationship between metabolic rate, as measured by oxygen consumption, and running speed has now been described in several species of bird, the slope of the relationship being referred to as the incremental cost of locomotion (Taylor, 1977). Previous studies in domestic fowl have shown that the incremental cost of locomotion is approximately the same in the male and in the mature, laying female (Brackenbury & Avery, 1980; Brackenbury *et al.* 1981; Fig. 2), although the female was only capable of 60 % of the maximum sustainable metabolic rate of the male. In both these studies the measured respiratory quotient (RQ) during 10 min exercise was very close to unity (0.96–0.97) and there was little variation in RQ at the different speeds. Fig. 2 indicates that the \dot{V}_{CO_2} -speed relationship obtained in the present study lay only marginally below the \dot{V}_{CO_2} -speed relationship described in earlier studies, as would be anticipated if the exercise RQ were marginally less than 1.

The measured \dot{V}_{CO_2} did not appear to be significantly affected by variations in the CO_2 pool resulting from egg-shell secretion or from lactacidosis at the highest metabolic rates (Fig. 1). Estimates of each of these effects can be obtained. Approximately 2 g of CO_2 is secreted into the developing egg-shell during the period whilst the egg is in the shell gland. If the mean rate of secretion is assumed to be 0.2 g h^{-1} , this is equivalent to only 3 % of the \dot{V}_{CO_2} measured at the lowest exercise

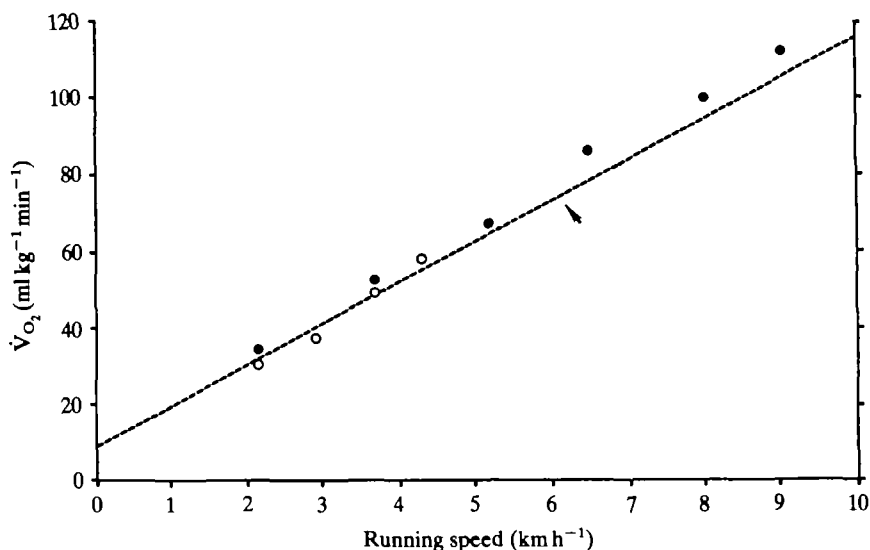


Fig. 2. Oxygen consumption ($\dot{V}O_2$) during treadmill exercise at different speeds in male (filled circles) (Brackenburg & Avery, 1980) and female (unfilled circles) (Brackenburg, Avery & Gleeson, 1981) domestic fowl. The dotted line represents $\dot{V}CO_2$ data from Fig. 1.

speed (2.2 km h^{-1}) and 1.5% of the $\dot{V}CO_2$ measured at the highest speed (5.0 km h^{-1}). Buffering of blood lactic acid by bicarbonate at the highest running speed in females (Fig. 1) could produce approximately 2 mmol of additional CO_2 but this would represent only 4% of the total CO_2 measured during the 10-min run.

The precise physiological reasons for the more limited aerobic capacity of the mature, laying female shown in the present and in earlier studies on domestic fowl (Figs 1, 2) cannot be decided from the data available. It is possible that in all cases the females were simply unwilling to run at higher speeds than those which were achieved in the experimental conditions. This is unlikely; after 10 min exercise at 5.0 km h^{-1} the females were obviously as exhausted by their efforts as were the males at the end of a 9.7 km h^{-1} run. Moreover, despite persistent training, the females were never able significantly to lower the end-exercise blood lactate levels measured at the highest speed, indicating an inability of the muscles to sustain power output at this level by aerobic means alone.

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