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Measurement of Maximum Oxygen Consumption in Guinea Fowl *Numida meleagris* Indicates That Birds and Mammals Display a Similar Diversity of Aerobic Scopes during Running

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ABSTRACT

Judgement of exercise performance in birds has been hampered by a paucity of data on maximal aerobic capacity. We measured the maximal rate of oxygen consumption ($\dot{V}O_{2,max}$) in running guinea fowl *Numida meleagris*, a bird that has been used in several previous studies of avian running. Mean $\dot{V}O_{2,max}$ during level treadmill running was 97.5 ± 3.7 mL O₂ kg⁻¹ min⁻¹ (mean \pm SEM, $N = 5$). $\dot{V}O_{2,max}$ was on average 6% higher when the birds ran uphill compared with the value during level running (paired t -test, $P = 0.041$, $N = 5$). The mean basal rate of oxygen consumption ($\dot{V}O_{2,bmr}$) of the same individuals was 7.9 ± 0.5 mL O₂ kg⁻¹ min⁻¹. Mean factorial aerobic scope based on individually measured values of $\dot{V}O_{2,max}$ and $\dot{V}O_{2,bmr}$ was 13.2 ± 0.6 (mean \pm SEM, $N = 5$). This value was considerably lower than the factorial aerobic scope previously measured during running in *Rhea americana*, a large flightless ratite. The difference in factorial scope between these two running birds likely reflects the effects of body size as well as size-independent differences in the ability to deliver and use oxygen. These data confirm a previous prediction that birds have a diversity of factorial aerobic scopes similar to that exhibited by mammals.

Introduction

The maximum aerobic capacity during locomotion provides an important reference value to which submaximal efforts can

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be compared, but these values are only readily available for certain vertebrate groups. Values for the maximal rate of oxygen consumption ($\dot{V}O_{2,max}$) during running have been determined for a variety of mammalian species (Langman et al. 1981; Taylor et al. 1981; Jones et al. 1989; Longworth et al. 1989; Lindstedt et al. 1991; Hinds et al. 1993) that exhibit a wide range of factorial aerobic scopes (Bishop 1999). In contrast, judging the intensity of energetic effort of birds during locomotion is hampered by a paucity of information on maximal aerobic capacities within this group. The use of birds as a model system to study the mechanics and energetics of running (Fedak et al. 1974; Brackenbury et al. 1981; Roberts et al. 1997, 1998; Gatesy 1999a, 1999b; Buchanan and Marsh 2001; Nassar et al. 2001) makes it particularly important to know the limits of aerobic performance during terrestrial locomotion.

The defining characteristic of measures of $\dot{V}O_{2,max}$ is the leveling off of the rate of oxygen consumption in a locomotor test requiring progressively higher levels of muscular effort. By this criterion, $\dot{V}O_{2,max}$ has been measured in only two bird species, the rhea *Rhea americana* and the jungle fowl *Gallus gallus* (Bundle et al. 1999; Hammond et al. 2000). Although we are primarily interested in maximal aerobic capacities during running, it is worth noting that although rates of oxygen consumption of flying birds are high and may be at, or near, maximal values in some cases (Bishop 1999; Chappell et al. 1999), no flight studies have been able to document a plateau in the rate of oxygen consumption under conditions of increasing exercise intensity. Other studies that have measured the energetic demands of cursorial birds during treadmill running have not documented a plateau in the rate of oxygen consumption (Fedak et al. 1974; Brackenbury and Avery 1980; Brackenbury et al. 1981; Taylor et al. 1982; Roberts et al. 1998), although the values of Brackenbury and coworkers have been considered to be maximal (Bishop 1999).

The factorial aerobic scope, the ratio of $\dot{V}O_{2,max}$ to the basal rate of oxygen consumption ($\dot{V}O_{2,bmr}$), of 36 found by Bundle et al. (1999) for the rhea is higher than that reported in the majority of mammals. These authors speculated that high factorial scopes are typical of birds in general. However, Bishop (1999), using simple indicators of the oxygen carrying capacity of the circulatory system, predicted that the potential range of factorial aerobic scopes should be similar in birds and mammals. Values of $\dot{V}O_{2,max}$ reported for jungle fowl (*G. gallus*; Hammond et al. 2000) appear to support Bishop's analysis.

These authors found mass-specific $\dot{V}O_{2,\max}$ and factorial aerobic scope values much lower than those measured for the rhea. However, because the $\dot{V}O_{2,\max}$ of the jungle fowl was measured while locomoting in a rotating drum, the precise relation of these measurements to those measured during treadmill running might be questioned, especially because Hammond et al. (2000) report that the birds tended to stumble and exhibited vigorous wing movements. Since $\dot{V}O_{2,\max}$ is best considered an activity-specific measurement (see "Discussion"), using a defined locomotor activity is desirable. Additional $\dot{V}O_{2,\max}$ data obtained in progressive treadmill running tests on cursorial birds are necessary to decide whether running birds in general have higher aerobic scopes than mammals or whether they instead exhibit a similar diversity in the expandability of aerobic metabolism, as was predicted by Bishop (1999) and as the comparison between rheas and jungle fowl suggests.

We measured $\dot{V}O_{2,\max}$ during treadmill running in helmeted guinea fowl *Numida meleagris*. Typical of many phasianid birds, guinea fowl are capable runners that have strong burst-flight capacities but little endurance in flight. In the wild, members of this species mostly walk and run as part of their daily activities and fly only to escape predation (Ayeni 1982). Domesticated strains of guinea fowl have retained a considerable running capacity and have been used in several laboratory investigations of running (Fedak et al. 1974; Roberts et al. 1998; Gatesy 1999a, 1999b; Buchanan and Marsh 2001; Nassar et al. 2001). However, the level of exercise used in these studies, which include brief runs at speeds up to 4.2 m s^{-1} , cannot be fully evaluated without knowing the $\dot{V}O_{2,\max}$ of these birds. If guinea fowl had a similar factorial aerobic scope to rheas, one would predict a maximal aerobic speed of 10 m s^{-1} in level running, which seems unlikely. The possibility exists that guinea fowl cannot run at speeds on the level that elicit $\dot{V}O_{2,\max}$, and their capacities might be revealed by running them uphill, as was done for rheas (Bundle et al. 1999). However, we predict that factorial aerobic scope of guinea fowl is lower than that of rheas and is more in line with that found for the jungle fowl, another phasianid bird.

Material and Methods

Guinea fowl (*Numida meleagris*) were obtained from the Guinea Farm (New Vienna, Iowa) as hatchlings and cage reared at the Northeastern University Division of Laboratory Medicine. At the time of the measurements, the birds were between 10 and 14 mo old. Birds had ad lib. access to food and water and were maintained on a 12L : 12D cycle. The five birds used to determine $\dot{V}O_{2,\max}$ had a mean body mass of $1.52 \pm 0.05 \text{ kg}$ ($\pm \text{SEM}$, $N = 5$, range 1.41 to 1.66 kg). Of these five subjects, four were males and one was a female. Five additional birds that were part of a separate study were used to measure blood lactate levels at different running speeds. These birds had a

mean mass of $1.44 \pm 0.06 \text{ kg}$ ($\pm \text{SEM}$, $N = 5$, range 1.32 to 1.68 kg).

For 2 mo before measurements of $\dot{V}O_{2,\max}$, the birds were trained to run on a motorized treadmill (Trimline 2600, Trimline, Tyler, Tex., $120 \times 44\text{-cm}$ tread area). The training regime consisted of running for approximately 30 min d^{-1} , 5 d wk^{-1} at speeds ranging from 1.5 to 3.9 m s^{-1} . At the end of the training period, all birds could sustain 30 min of exercise at 2.5 m s^{-1} .

During measurements of $\dot{V}O_2$, the guinea fowl ran inside a three-sided box with a partial top. The box was open at the back and had a mirror mounted on the front facing the running bird. Ambient room temperature was approximately 20°C . A duct brought cool air from an air conditioner to one side of the box. Airflow was controlled with a slide such that sufficient cool air was allowed to flow into the box to prevent the birds from continuously panting. Most birds displayed intermittent panting, particularly at higher speeds.

Respiratory gases were collected using a flow-through respirometry system, with the birds wearing a loose-fitting mask (Fig. 1). The lightweight, transparent mask was constructed from the upper, roughly hemispherical portions of two 2-L plastic bottles. One of these hemispheres was used to create a collar that provided a loose seal around the bird's neck. The smooth surface slanting forward prevented the bird from removing the mask with its feet. The second hemisphere was fastened to the top of the collar with transparent tape and formed the anterior of the mask to which the excurrent flexible plastic tubing was attached. During the measurements, an investigator supported the tubing, which allowed the birds to run with very little additional weight on their heads. A Gast air pump (model 1HAB-25-m100X) drew air into the mask at the neck and out through the tubing above the bird's head. Excurrent air from the mask passed through a column of Drierite to absorb water and then through a notameter-type flow meter (IGO7-RB, Cole Parmer, Vernon Hills, Ill.) with a needle valve on the outlet to control flow. The ambient flow rate was set at 5.0 L min^{-1} and 10.0 L min^{-1} for birds at rest and during exercise, respectively. Gas samples for analysis were withdrawn through sampling tubes placed in the excurrent line from the pump. CO_2 content was measured with a Sable Systems CA-1 CO_2 analyzer. Gas withdrawn for O_2 measurements passed through a column of CO_2 absorbent (Ascarite) and additional Drierite before measurement of O_2 content using an Amtek S-3A/II O_2 analyzer. This dual-channel oxygen analyzer was operated in differential mode, and the expired air from the mask was compared with dry, CO_2 -free room air, which was pumped continuously through the second cell of the analyzer. The reading of the analyzer with dry, CO_2 -free air flowing through both cells was checked before and after each set of measurements. The CO_2 analyzer was calibrated by metering 100% CO_2 into an airstream at a rate that gave a fractional CO_2 content of 0.02. The oxygen analyzer was standardized with dry, CO_2 -free

room air, which was assumed to have a fractional oxygen content of 0.20953. Fractional O₂ and CO₂ contents were recorded into a Macintosh 7100/80 computer via a Powerlab 2e 12-bit A/D converter (AD Instruments, Colorado Springs, Colo.) and displayed using Chart software (version 4.01, AD Instruments).

Oxygen consumption was calculated using the following equation from Withers (1976):

$$\dot{V}_{O_2} = \frac{\dot{V}_E(F_{I_{O_2}} - F_{E_{O_2}})}{1 - F_{I_{O_2}} + R(F_{I_{O_2}} - F_{E_{O_2}})}$$

where \dot{V}_E = flow rate of dry air out of the mask in mL min⁻¹ corrected to STP; $F_{I_{O_2}}$ = fractional concentration of O₂ in dry air entering the mask, which was assumed to be 0.20953; $F_{E_{O_2}}$ = fractional concentration of O₂ in dry, CO₂-free gas exiting the mask; and R = respiratory exchange ratio.

This equation is appropriate for calculating rates of oxygen consumption when water vapor is absorbed before the downstream flow meter and both H₂O and CO₂ are absorbed before the oxygen analyzer (Withers 1976). We routinely used a representative R value of 0.85 in this equation. The R values determined during the course of the experiment were used to evaluate the pattern of change in R with exercise intensity but were not used in these calculations of \dot{V}_{O_2} , because the calculation of \dot{V}_{O_2} by this method is essentially independent of R in the physiological range (Withers 1976).

Birds were run at a steady speed until \dot{V}_{O_2} stabilized for at

least 1 min. The time to 100% response of our system was less than 40 s. Despite some oscillations, the attainment of an average stable value was readily apparent on the record (Fig. 2). The $\dot{V}_{O_{2,max}}$ was defined as the plateau value when \dot{V}_{O_2} no longer increased as treadmill speed was increased. Birds were run on the level and on slopes of 10% and 20% (angles of 6° and 11°, respectively). The plateau value during level running was determined two or three times on separate days for each of the five birds, and the $\dot{V}_{O_{2,max}}$ was expressed as the mean of the separate determinations. Three birds reached a plateau running on both the 10% and 20% slopes, one bird reached a plateau on only the 10% slope, and one bird did not reach a convincing plateau on either slope. For the birds that reached $\dot{V}_{O_{2,max}}$ on both slopes, the values were averaged to determine the $\dot{V}_{O_{2,max}}$ during inclined running. The values for $\dot{V}_{O_{2,max}}$ measured during inclined running were compared with those measured during level running using a paired t -test (Statview, version 5.0, SAS Institute).

To allow accurate calculations of factorial aerobic scope, we also measured the basal metabolic rate of the guinea fowl. The resting rate of oxygen consumption was determined using the same basic respirometry system as during exercise. The principal modification was that the bird was placed in a 35 × 20 × 34-cm chamber for collection of respiratory gasses. Air was drawn through the chamber via holes in the base at a rate of 5.0 L min⁻¹. The chamber was in turn placed in a temperature-controlled cabinet (Revco, Asheville, N.C.). This

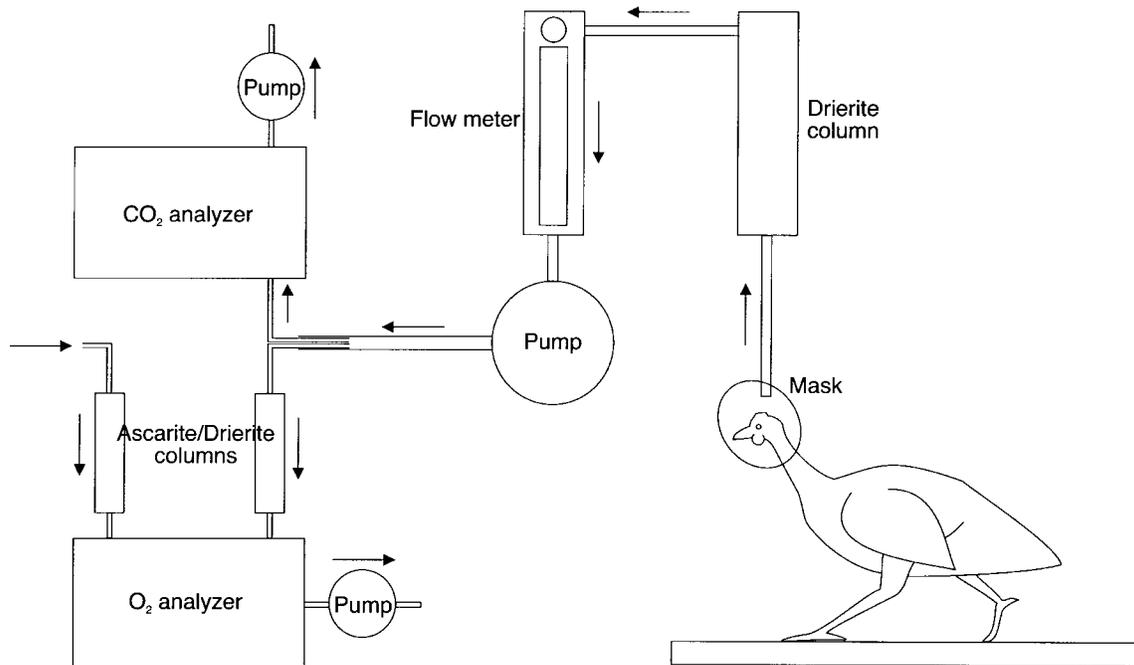


Figure 1. Schematic diagram of the apparatus used to measure rates of oxygen consumption; arrows indicate direction of airflow

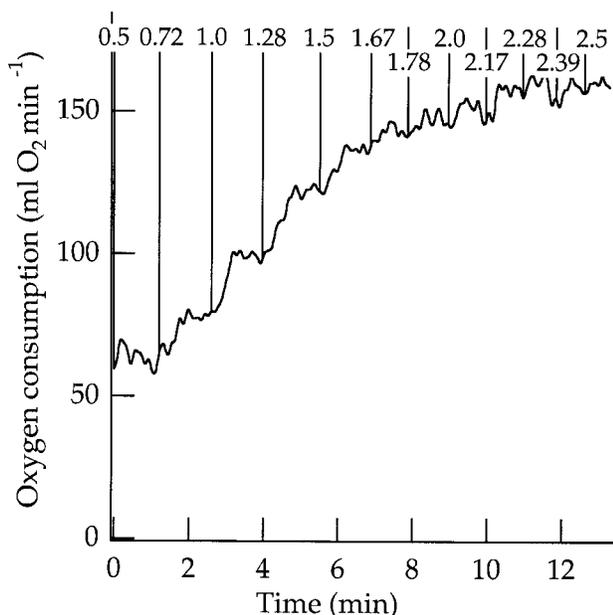


Figure 2. Example trace of rate of O_2 consumption during progressive increases in running speed on a slope of 20%. The numerical markers indicate running speed in m s^{-1} and the approximate time at which the given speed was reached.

allowed the rate of oxygen consumption to be determined at a range of temperatures. In this way, the thermoneutral zone at which resting oxygen consumption is minimized was identified (typically 22° – 28°C). Birds were placed in the chamber at the end of the daylight phase and remained in the chamber, without access to food, for at least 6 hr before measurements were taken. This time period was assumed to be sufficient to allow the birds to reach a postabsorptive state.

Blood lactate concentrations were obtained during a protocol used in a separate study of blood flow. In this protocol, the birds ran for 2 min at each speed followed by 2 min of walking at 0.5 m s^{-1} . The highest speeds used exceeded the maximum aerobic speed for the individual as measured in this study. Blood was withdrawn from an indwelling arterial cannula immediately following the 2-min run at each speed. Lactate concentration was measured using an enzymatic UV kit from Sigma Chemical (kit 826-UV).

Results

The $\dot{V}\text{O}_2$ of the birds changed rapidly with each change in treadmill speed until they reached their maximum aerobic speed. In the example shown in Figure 2, taken from a bird running on a slope of 20%, $\dot{V}\text{O}_2$ increased with running speed up to a speed of 2.17 m s^{-1} . Above this speed, there was no further increase in $\dot{V}\text{O}_2$. The oscillations in the curve are ap-

parently the result of intermittent panting by the bird, with $\dot{V}\text{O}_2$ increasing slightly during the bout of panting.

The mean $\dot{V}\text{O}_2$ in birds running on a level treadmill plateaued at speeds above 2.78 m s^{-1} (Fig. 3). The gradual leveling off of mean $\dot{V}\text{O}_2$ at speeds above 2.78 m s^{-1} is partly an artifact of the decreasing sample size at these speeds. Individual birds often showed a more abrupt transition to the plateau at speeds above their maximum aerobic speed (see level running in Fig. 4), but in many cases, particularly during running on a gradient, the slope of $\dot{V}\text{O}_2$ versus speed was shallower at speeds near the maximum aerobic speed (see values for 20% grade in Fig. 4). The $\dot{V}\text{O}_{2,\text{max}}$ for level running ranged from 89.5 to $106.4 \text{ mL O}_2 \text{ kg}^{-1} \text{ min}^{-1}$, with a mean value of $97.5 \pm 3.7 \text{ mL O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ (mean \pm SEM, $N = 5$).

Multiple values for $\dot{V}\text{O}_2$ are shown at 0 m s^{-1} (Fig. 3). The highest and middle values represent rates of oxygen consumption measured with the mask system just before the exercise values were obtained, with birds standing quietly and lying on the darkened treadmill, respectively. The lowest resting value is the basal metabolic rate $\dot{V}\text{O}_{2,\text{bmr}}$ measured at night in post-absorptive birds. The mean $\dot{V}\text{O}_{2,\text{bmr}}$ averaged $7.9 \pm 0.5 \text{ mL O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ (mean \pm SEM, range 7.2 to 8.6, $N = 5$). The mean

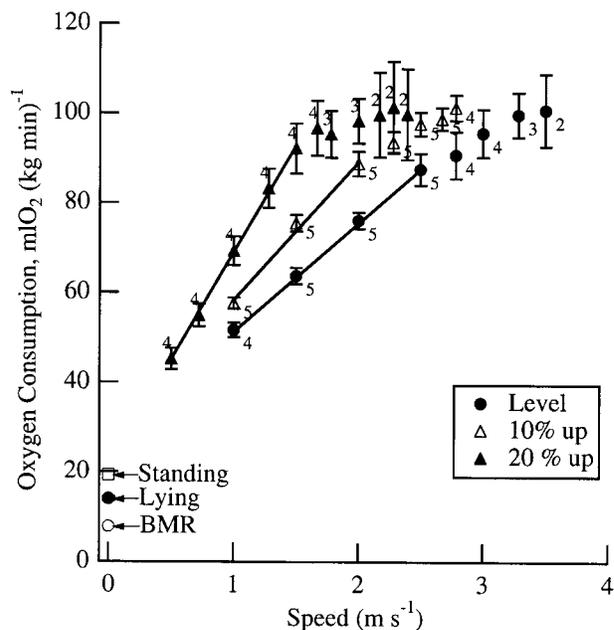


Figure 3. Mean oxygen consumption (± 1 SEM) of running guinea fowl. The numbers beside each plotted value indicate the number of individuals measured at that speed and slope. The solid lines are regressions calculated using the individual values for each animal over the range of speeds spanned by the line (see Table 1 for the equations). At 0 m s^{-1} , the three values plotted are mean $\dot{V}\text{O}_2$'s for the following conditions: basal metabolic rate (*open circle*), lying in a darkened box on the treadmill (*solid circle*), and standing quietly on the treadmill in a darkened box (*open square*).

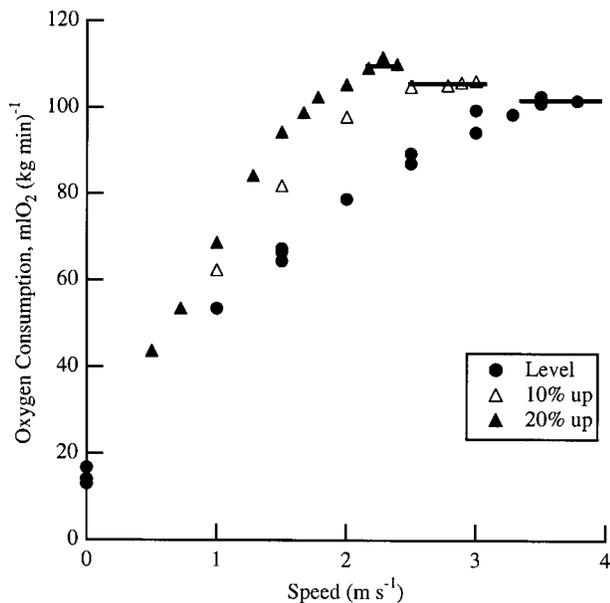


Figure 4. Example data for one bird showing the relation of oxygen consumption to speed on three different slopes. Data are shown for both level and inclined running. The maximum rate of O_2 consumption was taken as the mean of the values on the plateau, as shown by the horizontal lines.

factorial aerobic scope obtained for each bird based on individual measurements of $\dot{V}O_{2,max}$ during level running and BMR for each bird was 13.2 ± 0.6 (mean \pm SEM, range 11.3 to 14.5, $N = 5$). R values ranged from 0.83 to 1.09 and showed an increase with running speed, typically exceeding a value of 1 at the speeds at which $\dot{V}O_2$ leveled off.

The $\dot{V}O_{2,max}$ during uphill running was on average 6% higher than that found for level running and was reached at lower speeds than in level running (Figs. 3–5). Although the difference in $\dot{V}O_{2,max}$ is small, the value when running uphill was consistently higher (Fig. 5), and the difference was statistically significant in a paired comparison (paired t -test, $P = 0.04$, $N = 4$). We lacked sufficient data to determine whether the values at slopes of 10% and 20% were significantly different.

At rates of oxygen consumption below approximately 90% of $\dot{V}O_{2,max}$, guinea fowl exhibited the typical linear relationship between oxygen consumption and running speed (Figs. 3, 4; Table 1). Assuming an energy equivalent of $20.1 \text{ J mL}^{-1} O_2$, the slope of the relationship between rate of oxygen consumption and running speed during level running translates into a net cost of transport of $8.1 \text{ J kg}^{-1} \text{ m}^{-1}$, a value similar to the values obtained for guinea fowl in previous studies ($9.4 \text{ J kg}^{-1} \text{ m}^{-1}$; Fedak et al. 1974; $8.4 \text{ J kg}^{-1} \text{ m}^{-1}$; Roberts et al. 1998). The y -intercept value for $\dot{V}O_2$ of 27.2 is statistically indistinguishable from the value of $23.4 \text{ mL } O_2 \text{ kg}^{-1} \text{ min}^{-1}$ obtained by Fedak et al. (1974).

Blood lactate concentrations remained low at rest and moderate running speeds (Fig. 6). In birds run at their maximum aerobic speeds, there was a substantial increase in lactate levels. The highest measured lactate concentration was 9.3 mmol L^{-1} .

Discussion

To our knowledge, the $\dot{V}O_{2,max}$ measurements presented here represent the second time that $\dot{V}O_{2,max}$ has been documented for a species of bird during a precisely defined locomotor task and only the third time that an avian $\dot{V}O_{2,max}$ has been definitively measured under any conditions (Bundle et al. 1999; Hammond et al. 2000). The attainment of $\dot{V}O_{2,max}$ is defined here as the leveling off of the rate of oxygen consumption in a progressive locomotor task and is specific to the locomotor task performed. A rise in plasma lactate levels has been considered a supplementary measure of the attainment of $\dot{V}O_{2,max}$ (Seeherman et al. 1981). Guinea fowl show a substantial rise in lactate production when run for only 2 min at their maximum aerobic speed (Fig. 6). The blood lactate values measured in guinea fowl are lower than those found in the rhea (Bundle et al. 1999) and a range of mammal species (Seeherman et al. 1981) after running at speeds above their maximum aerobic speed. However, the overall pattern observed is similar, with lactate accumulating at running speeds where oxygen consumption has leveled off. The lower peak accumulations of lactate in guinea fowl can probably be attributed to the shorter time course of the exercise regime used to obtain lactate measurements in this study and the fact that the highest speed used during the lactate measurements was only slightly in excess of

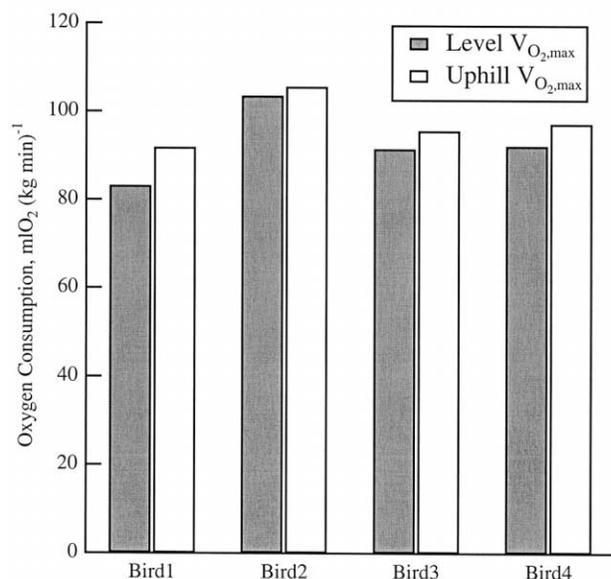


Figure 5. Maximal oxygen consumption of individual birds when running on the level treadmill (shaded bars) and uphill (open bars) slopes.

Table 1: Regression statistics on the linear portion of the relation between oxygen consumption and speed

% Grade	Intercept (<i>a</i>)	Slope (<i>b</i>)	SEM, Intercept	SEM, Slope	<i>n</i>	<i>r</i> ²
0	27.2	24.0	3.4	1.8	21	.90
10	27.6	30.7	4.4	2.8	16	.90
20	21.3	47.7	4.6	4.3	20	.91

Note. Data were fitted to the equation $\dot{V}O_2 = a + bv$, where $\dot{V}O_2$ has units of milliliters oxygen per kilogram per minute and v is in meters per second.

the maximum aerobic speed. For the lactate measurements, guinea fowl were run at a given speed for only 2 min, alternating with 2 min at a walking speed. The combination of rising *R* values, lactate accumulation, and a plateau in $\dot{V}O_2$ are all indicative of an increasing reliance on anaerobic metabolism and a reaching of maximal aerobic capacity at high running speeds.

The higher $\dot{V}O_{2,max}$ measured when the birds run up a slope confirms the suggestion of others that the measured $\dot{V}O_{2,max}$ is activity specific and can be changed by altered muscle recruitment. The $\dot{V}O_{2,max}$ can change with altered recruitment because the rate of oxygen consumption at maximal levels is limited by multiple systems involved in oxygen delivery and use. The dogma has been that in humans, and by extension in other animals as well, $\dot{V}O_{2,max}$ is set by a central limitation on oxygen transport by the cardiovascular system (e.g., Bassett and Howley 2000). However, others have suggested that the oxygen transport system represents a linked series of oxygen conductances, and changes at any level can influence the capacity of the whole system (Wagner 1996, 2000). The 6% increase in oxygen consumption found when guinea fowl run uphill is approximately equal to the modest increments found in three studies comparing humans running on level and sloped treadmills (Taylor et al. 1955; Hermansen and Saltin 1969; Paaavolainen et al. 2000). These increments could be due to recruiting different muscles, or muscle compartments, with higher capacities for diffusion or use of oxygen. When running uphill, the leg muscles also shorten more when active (Roberts et al. 1997), and this could potentially influence blood flow and thus oxygen transport.

The increased gradient of the linear portion of the relationship between $\dot{V}O_2$ and running speed during uphill running undoubtedly reflects the greater muscle volume recruited when running uphill. The increased cost of running uphill is due to the increase in mechanical work done to lift the body and the increased cost of producing force to support the body weight by muscles undergoing shortening (Roberts et al. 1997). We calculated the efficiency of performing work to lift the body up the slope after subtracting out the cost of standing quietly on the treadmill. Efficiency was approximately 8% and 12% on the 10% and 20% grades, respectively. These values are similar to those predicted, given the combined effects of body size and slope (P. Weyand, personal communication).

Combined with previous data, the results of this study sug-

gest that birds may show as great a diversity of aerobic scopes as do mammals. Mammals vary greatly in factorial aerobic scope (Langman et al. 1981; Taylor et al. 1981; Jones et al. 1989; Longworth et al. 1989; Lindstedt et al. 1991; Hinds et al. 1993). This variation reflects differential investment in the morphological and physiological adaptations required for aerobic metabolism (Weibel et al. 1991; Bishop 1999). Bundle et al. (1999) reported a factorial aerobic scope during treadmill running of 36 for the rhea, a flightless ratite bird, and speculated that birds, unlike mammals, might in general have high factorial scopes. The estimated factorial scope for the rhea was based on a basal rate of oxygen consumption predicted by the equation for non-passerine birds of Lasiewski and Dawson (1967). Using the measured basal metabolic rate for rheas (Crawford and Lasiewski 1968), the factorial scope is 32. The factorial aerobic scope of 13 for guinea fowl is considerably lower than this

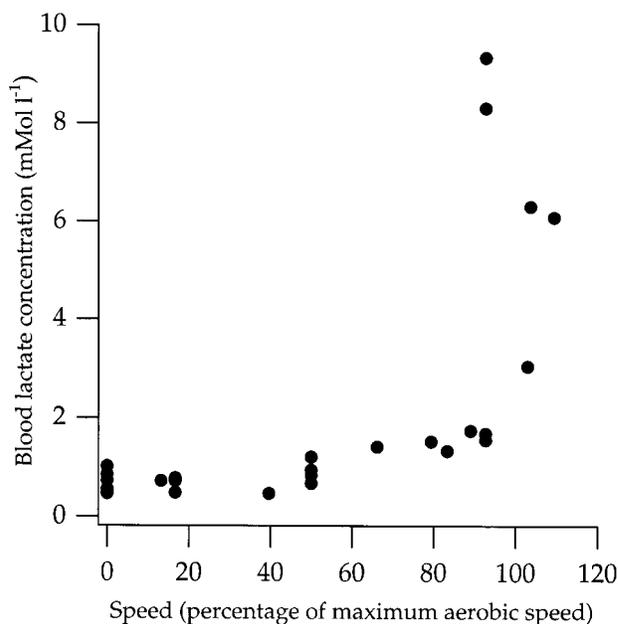


Figure 6. Blood lactate concentrations during level running. Lactate concentrations were measured in blood samples obtained from an arterial cannula after 2 min of running at a given speed. Speeds are expressed as a percentage of the maximum aerobic speed. Zero speed refers to a bird lying down in the dark. Data are from five individuals.

value for rheas. The only other $\dot{V}O_{2,\max}$ value reported for a bird is for another phasianid species, the jungle fowl *Gallus gallus* (Hammond et al. 2000), exercising in a rotating drum that elicited wing movements as well as leg movements. Equations derived by Hammond et al. (2000) relating $\dot{V}O_{2,\max}$ and BMR to body mass for male jungle fowl predict a factorial aerobic scope of approximately 14 for 1.5-kg birds (females have a lower factorial aerobic scope, approximately 7 for 1.5-kg birds). The jungle fowl used by Hammond et al. (2000) were not subjected to endurance training, as were our birds, but were group housed in large outdoor pens under conditions that elicited locomotor activity due to social interactions. However, despite differences in methodology, the two species of phasianid, helmeted guinea fowl and jungle fowl, have similar factorial aerobic scopes, and these scopes are less than one-half of the value found for the rhea. On the basis of the available empirical data, it appears that the variation in factorial aerobic scope of birds is similar to that exhibited by mammals.

The difference in factorial aerobic scopes between guinea fowl and rheas in part reflects the effects of body size. Bishop (1999) found that in birds and mammals, $\dot{V}O_{2,\max}$ scales to body mass with an exponent significantly higher than that of BMR. This scaling was based on standardized $\dot{V}O_{2,\max}$ data in which interspecific differences in heart mass and hemoglobin concentrations were accounted for by scaling the data to a relative heart mass of 1% of body mass and a blood hemoglobin concentration of 15 g 100 mL⁻¹. Bishop (1999) derived the following equation relating standard factorial aerobic scope (AS_{st}) to body mass: $AS_{st} = 23.3M_b^{0.151}$, where M_b is body mass in kilograms. The rheas for which factorial aerobic scope data are available had a mean body mass of 21.8 kg (Bundle et al. 1999) compared with 1.52 kg for the guinea fowl in this study. Standard factorial aerobic scopes based on these body masses are 37.0 and 24.8 for rhea and guinea fowl, respectively. Thus, on the basis of body mass alone, a considerably lower factorial aerobic scope is predicted for guinea fowl than for rheas. However, the predicted difference is less than that actually measured, and additional factors need to be considered.

In addition to the effects of body size, guinea fowl and rheas appear to differ in their investment in morphological and physiological systems for oxygen delivery and use. Bishop (1997) showed that relative heart mass is a reasonable predictor of aerobic capacity. Across a range of bird and mammal species, 78% of the variability in $\dot{V}O_{2,\max}$ can be accounted for by differences in relative heart mass (Bishop 1999). Guinea fowl heart mass is 0.67% ± 0.04% of body mass (mean ± SEM, range 0.50 to 0.90, $N = 9$; D. J. Ellerby, unpublished data) compared with a heart mass of approximately 1.2% of body mass in the rhea (Bundle et al. 1999). The difference in heart mass suggests that rheas have a greater capacity than guinea fowl to deliver oxygen to their tissues. Correlating with this difference in cardiovascular capacity is a difference in the amount of leg muscle mass available to consume oxygen during running. Presumably,

the leg muscles consume the majority of oxygen utilized during treadmill running. Guinea fowl leg muscle mass is 20.5% ± 0.5% of body mass (mean ± SEM, range 19.1 to 21.4, $N = 4$; D. J. Ellerby, unpublished data) compared with 30% in the rhea (Bundle et al. 1999). One reason for the higher value for leg muscle mass as a percentage of total body mass in rheas as compared with guinea fowl is undoubtedly the lower relative investment in flight muscle mass by the rhea. Of course, the active muscle mass per se does not determine the consumption of oxygen because aerobically supported contractile activity depends on the metabolism of the mitochondria in the muscles (Mathieu et al. 1981). Thus, a number of factors—including body mass, the capacity of the cardiovascular system to deliver oxygen, and the relative mass and aerobic capacity of active muscles—likely combine to account for the large difference in factorial aerobic scope between rheas and guinea fowl.

The modest aerobic capacities of guinea fowl and jungle fowl are probably typical of cursorial phasianid birds that have good burst-flight abilities but low endurance in flight. In general, these birds have less hindlimb muscle mass and smaller heart masses than do the large flightless ratites (Hartman 1961). In contrast to the ratites, these phasianid runners have large amounts of body mass devoted to the flight muscles, which they use for powerful escape flights (Askew and Marsh 2001). However, these muscles have a very low aerobic capacity in typical members of this group, including the guinea fowl (MacNaughtan 1974; Kiessling 1977; R. L. Marsh, unpublished data). Thus, the contribution of the flight muscles to organismal aerobic scope in these birds, even if combined with leg activity as in the study by Hammond et al. (2000), is likely to be small. However, some small phasianids, for example, *Coturnix coturnix*, are migratory and might be expected to have higher aerobic scopes during flight than running due to the high cost of flight (Bishop 1997). This migratory species has a higher heart mass than is typical of most phasianids (Hartman 1961). Finally, we would emphasize that our data apply specifically to domestic helmeted guinea fowl subjected to a treadmill endurance-training regime. Whether free-living members of this species have similar capacities remains to be determined.

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Literature Cited

Askew G.R. and R.L. Marsh. 2001. The mechanical power output of the pectoralis muscle of blue-breasted quail (*Coturnix chinensis*): the in vivo length cycle and its implications for muscle performance. *J Exp Biol* 204:3587–3600.

- Ayeni J.S.O. 1982. Home range size, breeding behavior, and activities of helmeted guinea fowl *Numida meleagris* in Nigeria. *J West Afr Ornithol Soc* 5:37–43.
- Bassett D.R. and E.T. Howley. 2000. Limiting factors for maximum oxygen uptake and determinants of endurance performance. *Med Sci Sports Exercise* 32:70–84.
- Bishop C.M. 1997. Heart mass and the maximum cardiac output of birds and mammals: implications for estimating the maximum aerobic power input of flying animals. *Philos Trans R Soc Lond B Biol Sci* 352:447–456.
- . 1999. The maximum oxygen consumption and factorial aerobic scope of birds and mammals: getting to the heart of the matter. *Proc R Soc Lond B Biol Sci* 266:2275–2280.
- Brackenbury J.H. and P. Avery. 1980. Energy consumption and ventilatory mechanisms in the exercising fowl. *Comp Biochem Physiol* 66A:439–445.
- Brackenbury J.H., P. Avery, and M. Gleeson. 1981. Respiration in exercising fowl. I. Oxygen consumption, respiratory rate and respired gases. *J Exp Biol* 93:317–325.
- Buchanan C.I. and R.L. Marsh. 2001. Effects of long-term exercise in the biomechanical properties of the Achilles tendon of guinea fowl. *J Appl Physiol* 90:164–171.
- Bundle M.W., H. Hoppeler, R. Vock, J.M. Tester, and P.G. Weyand. 1999. High metabolic rates in running birds. *Nature* 397:31–32.
- Chappell M.A., C. Bech, and W.A. Buttemer. 1999. The relationship of central and peripheral organ masses to aerobic performance variation in house sparrows. *J Exp Biol* 202:2269–2279.
- Crawford E.C., Jr., and R.C. Lasiewski. 1968. Oxygen consumption and respiratory evaporation of the emu and rhea. *Condor* 70:333–339.
- Fedak M.A., B. Pinshow, and K. Schmidt-Nielsen. 1974. Energy cost of bipedal running. *Am J Physiol* 227:1038–1044.
- Gatesy S.M. 1999a. Guineafowl hind limb function. I. Cineradiographic analysis and speed effects. *J Morphol* 240:115–125.
- . 1999b. Guineafowl hind limb function. II. Electromyographic analysis and motor pattern evolution. *J Morphol* 240:127–142.
- Hammond K.A., M.A. Chappell, R.A. Cardullo, R. Lin, and T.S. Johnsen. 2000. The mechanistic basis of aerobic performance variation in red junglefowl. *J Exp Biol* 203:2053–2063.
- Hartman F.A. 1961. Locomotor mechanisms of birds. *Smithson Misc Collect* 143:1–91.
- Hermansen L. and B. Saltin. 1969. Oxygen uptake during maximal treadmill and bicycle exercise. *J Appl Physiol* 26:31–37.
- Hinds D.S., R.V. Baudinette, R.E. Macmillen, and E.A. Halpern. 1993. Maximum metabolism and the aerobic factorial scope of endotherms. *J Exp Biol* 182:41–56.
- Jones J.H., K.E. Longworth, A. Lindholm, K.E. Conley, R.H. Karas, S.R. Kayar, and C.R. Taylor. 1989. Oxygen transport during exercise in large mammals. I. Adaptive variation in oxygen demand. *J Appl Physiol* 67:862–870.
- Kiessling K.H. 1977. Muscle structure and function in the goose, quail, pheasant, guinea hen and chicken. *Comp Biochem Physiol* 57B:287–292.
- Langman V.A., R.V. Baudinette, and C.R. Taylor. 1981. Maximum aerobic capacity of wild and domestic canids compared. *Fed Proc* 40:432.
- Lasiewski R.C. and W.R. Dawson. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13–23.
- Lindstedt S.L., J.F. Horkanson, D.J. Wells, S.D. Swain, H. Hoppeler, and V. Navarro. 1991. Running energetics in the pronghorn antelope. *Nature* 353:748–750.
- Longworth K.E., J.H. Jones, J.E.P.W. Bicudo, C.R. Taylor, and E.R. Weibel. 1989. High rate of O₂ consumption in exercising foxes: large P_{O₂} difference drives diffusion across the lung. *Respir Physiol* 77:263–276.
- MacNaughtan A.F. 1974. An ultrastructural and histochemical study of fibre types in the pectoralis thoracica and iliobtibialis muscles of the fowl (*Gallus domesticus*). *J Anat* 118:171–186.
- Mathieu O., R. Krauer, H. Hoppeler, G.G. Ehr, S.L. Lindstedt, R.M. Alexander, C.R. Taylor, and E.R. Weibel. 1981. Design of the mammalian respiratory system. VII. Scaling mitochondrial volume in skeletal muscle to body mass. *Respir Physiol* 44:113–128.
- Nassar P.N., A.C. Jackson, and D.R. Carrier. 2001. Entraining the natural frequencies of running and breathing in guinea fowl (*Numida meleagris*). *J Exp Biol* 204:1641–1651.
- Paavolainen L., A. Nummela, and H. Rusko. 2000. Muscle power factors and $\dot{V}O_{2,max}$ as determinants of horizontal and uphill running performance. *Scand J Med Sci Sports* 10:286–291.
- Roberts T.J., R. Kram, P.G. Weyand, and C.R. Taylor. 1998. Energetics of bipedal running. I. Metabolic cost of generating force. *J Exp Biol* 201:2745–2751.
- Roberts T.J., R.L. Marsh, P.G. Weyand, and C.R. Taylor. 1997. Muscular force in running turkeys: the economy of minimizing work. *Science* 275:1113–1115.
- Seeherman H.J., C.R. Taylor, G.M. Maloiy, and R.B. Armstrong. 1981. Design of the mammalian respiratory system. II. Measuring aerobic capacity. *Respir Physiol* 44:25–37.
- Taylor C.R., N.C. Heglund, and G.M.O. Maloiy. 1982. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J Exp Biol* 97:1–21.
- Taylor C.R., G.M.O. Maloiy, E.R. Weibel, V.A. Langman, J.M.Z. Kamau, H.J. Seeherman, and N.C. Heglund. 1981. Design of the mammalian respiratory system. III. Scaling maximum aerobic capacity to body mass: wild and domestic mammals. *Respir Physiol* 44:25–37.
- Taylor H.L., E. Buskirk, and A. Henschel. 1955. Maximal oxygen

- intake as an objective measure of cardio-respiratory performance. *J Appl Physiol* 8:73–80.
- Wagner P.D. 1996. A theoretical analysis of factors determining $\dot{V}_{O_{2,max}}$ at sea level and altitude. *Respir Physiol* 106:329–343.
- . 2000. Diffusive resistance to O_2 transport in muscle. *Acta Physiol Scand* 168:609–614.
- Weibel E.R., C.R. Taylor, and H. Hoppeler. 1991. The concept of symmorphosis: a testable hypothesis of structure-function relationship. *Proc Natl Acad Sci USA* 88:357–361.
- Withers P.C. 1976. Measurement of \dot{V}_{O_2} , \dot{V}_{CO_2} , and evaporative water loss with a flow-through mask. *J Appl Physiol* 42:120–123.

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