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THE RELATIONSHIP OF CENTRAL AND PERIPHERAL ORGAN MASSES TO AEROBIC PERFORMANCE VARIATION IN HOUSE SPARROWS

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Summary

We evaluated the relationship between organ mass and the limits to aerobic metabolism in house sparrows *Passer domesticus*. The results were used to test three models of performance limitation (the central limitation, peripheral limitation and symmorphosis concepts). Basal metabolic rate (BMR) was determined during the rest phase. The maximum rate of oxygen consumption during exercise ($\dot{V}_{O_2max}$) was measured in an enclosed wheel that allowed limited hovering flight. Neither BMR nor $\dot{V}_{O_2max}$ was affected by gender, but adults had significantly higher $\dot{V}_{O_2max}$ and lower BMR than juveniles. The masses of most central organs (gut, gizzard, liver, heart, kidney and reproductive organs) differed significantly between ages. There were no gender differences in organ mass among juveniles, but liver mass differed between male and female adults. In the pooled data, BMR was positively correlated with the mass of three central organs (gut, liver and kidney) and with one peripheral effector (breast muscle); together, these explained more than half the variance in BMR (r^2=0.57). In adults, BMR was positively correlated with the mass of reproductive tissue. The masses of one peripheral effector (breast muscle) and one central organ (the heart) were positively correlated with $\dot{V}_{O_2max}$ (r^2=0.17 for the pooled data set). These results are consistent with a symmorphosis model of aerobic capacity. We found a significant positive relationship between BMR and $\dot{V}_{O_2max}$ in juveniles, but not in adults. Taken together, our data indicate that house sparrows can achieve elevated $\dot{V}_{O_2max}$ without paying a 'penalty' (fitness trade-off) in the form of an increased BMR.

Key words: aerobic capacity, basal metabolic rate, exercise, house sparrow, *Passer domesticus*, symmorphosis.

Introduction

The limits to locomotor performance and energy metabolism are among the most intensively studied organismal-level physiological traits. This interest stems from both mechanistic and ecological perspectives. From a mechanistic viewpoint, locomotor and aerobic traits require the effective and coordinated functioning of a suite of enzymes, organelles, cells, tissues, organs and organ systems and, hence, are useful integrative indices of overall physiological vigor or quality. In an ecological and evolutionary context, whole-animal performance is 'noticed' by selection and hence seems intuitively likely to be related to fitness.

Theoretically, performance limits might be set by peripheral effector organs (primarily skeletal muscles) or by central organs (primarily visceral organs such as the pulmonary, cardiovascular, digestive or excretory systems) that support peripheral effectors. These views represent the 'peripheral limitation hypothesis' and the 'central limitation hypothesis,' respectively (Peterson et al., 1990; Weiner, 1993). An alternative model is that all aspects of performance are optimally scaled such that no one component is limiting, and the system as a whole has no expensive excess capacity (e.g. 'symmorphosis'; Weibel, 1987; Weibel et al., 1991).

One way to investigate these questions is to make use of the natural between-individual variation typical of physiological traits (Bennett, 1987). From a mechanistic perspective, correlative analyses of variation at different levels of integration (e.g. enzymes, organelles, cells, organs, organ systems and the intact animal) can provide useful insights into the functional basis of performance (e.g. Garland, 1984; Bennett et al., 1989). For example, this method can generate predictions of which components may be 'targeted' for evolutionary change if there is selection for increased whole-animal performance.

We used this approach in a study of aerobic performance in house sparrows (*Passer domesticus*), reasoning that a large aerobic capacity is particularly important for birds because of the high power output needed to sustain flight. Despite extensive study (especially of mammalian oxygen transport), there is a surprising lack of consensus on which specific organ systems (or other factors) limit aerobic performance

in vertebrates, although most physiologists believe cardiovascular traits (cardiac output, blood oxygen-carrying capacity, arterial-venous oxygen partial pressure gradients) strongly influence maximal rates of oxygen flux (e.g. Chappell and Snyder, 1984; Taylor et al., 1987).

We explored the influence of organ size on maximal aerobic metabolism in the context of the central limitation, peripheral limitation and symmorphosis models. We also tested the hypothesis that basal metabolic rate (BMR) should be correlated with visceral organ mass (Kersten and Piersma, 1987; Daan et al., 1990). Finally, we examined the concept that BMR and maximal aerobic capacity should be positively correlated (the 'aerobic capacity model'; Bennett and Ruben, 1979; Bennett, 1991). This idea can also be derived from both the symmorphosis and central limitation models, because an ability to support high aerobic capacity should require a large investment in visceral organs, which in turn should elevate BMR (e.g. Daan et al., 1990; Burness et al., 1998).

Materials and methods

Animals and treatment groups

House sparrows *Passer domesticus* L. were introduced into Australia in the late 1850s and subsequently have spread throughout much of the continent. We worked with free-living populations at several locations near Wollongong, New South Wales. Nearby habitats included urban areas, gardens, parks and coastal eucalyptus woodland. Birds were captured in the morning in Potter traps baited with birdseed, placed in cloth bags and transported to the laboratory within 2 h of capture. They were held in a cage with food and water available *ad libitum* until maximal aerobic capacity was determined in the early afternoon (see below), after which they were returned to the holding cage. Food was removed from the holding cage at 15:00 h local time. We measured basal metabolic rate that night (see below), and killed and dissected the birds the following morning.

We captured birds in November and December 1998, which is within the breeding season for house sparrows in the Wollongong area. All adults were in reproductive condition (brood patches and follicles were present in females; males had large testicles). Given the schedule of the local breeding season and the extent of skull ossification, we assume that all juvenile birds were less than 4 months old.

Aerobic capacity

We used open-circuit respirometry to measure rates of oxygen consumption ($\dot{V}_{O_2}$; $ml\,O_2\,min^{-1}$) during intense exercise in an enclosed motorized running wheel. This method reliably elicits maximal $\dot{V}_{O_2}$ ($\dot{V}_{O_2max}$) (Chappell et al., 1996). The wheel (32 cm diameter by 11 cm wide; internal volume 9 l) was supplied with dry air at rates of $5\,l\,min^{-1}$ STP (standard temperature and pressure), metered ±1 % with a Hastings mass-flow controller. Air exiting the wheel was dried, scrubbed of CO_2 and analyzed for O_2 content (Sable Systems FC-1). Oxygen concentrations (±0.002 %) were recorded on a Macintosh computer equipped with an A/D converter (National Instruments Lab-NB) and custom-designed software (WartHog Systems).

To begin a test, we placed birds in the wheel and allowed them a 2 min adjustment period before starting wheel rotation at low speed (approximately $0.3\,m\,s^{-1}$ at the rim). We increased rotation speed in fixed increments of approximately $0.1\,m\,s^{-1}$ every 2 min until the bird could no longer maintain position and $\dot{V}_{O_2}$ did not increase with increasing speed. Several ping-pong balls rolling freely in the wheel helped to motivate the birds and elicit a maximal effort. All sparrows flapped vigorously or hovered at the start of wheel rotation, but as the birds became tired they tended to switch from flight to hopping and jumping. After the end of exercise bouts, we continued to monitor metabolic rate until $\dot{V}_{O_2}$ had clearly begun to decrease from the level during exercise. All birds showed signs of exhaustion at the end of exercise, but none was injured. Tests lasted 6–17 min (2.5–12 min of actual exercise during wheel rotation).

We used the 'instantaneous' calculation (Bartholomew et al., 1981) to compensate for the mixing characteristics of the wheel and to resolve accurately short-term changes in gas exchange. We computed $\dot{V}_{O_2max}$ as the highest instantaneous $\dot{V}_{O_2}$ averaged over a continuous 1 min interval (Chappell et al., 1996). The maximal $\dot{V}_{O_2}$ always occurred during periods of intense flapping, typically early in the testing period when birds often maintained nearly constant hovering flight.

Basal metabolic rate

We measured each bird's basal metabolic rate (BMR; determined as $ml\,O_2\,min^{-1}$) during the night following $\dot{V}_{O_2max}$ evaluation. Birds had been fasted for 3 h at the beginning of BMR measurements, which started at approximately 18:00 h (local time) and continued for an additional 12–14 h until the following morning. Up to four birds were tested simultaneously. Each was kept in a separate respirometer constructed from a 2 l paint can equipped with air inlet and outlet ports, a thermocouple and a perch. The chambers were placed in an environmental cabinet maintaining a temperature of 32.5±1 °C (within the thermoneutral zone for this species; Hudson and Kimzey, 1966). A separate Tylan mass-flow controller maintained a constant flow rate of dry air ($500\,ml\,min^{-1}$ STP) to each chamber. Excurrent air from the chambers was routed to a two-channel O_2 analyzer (Applied Electrochemistry S-3A) through a computer-controlled airstream selector (Sable Systems Respirometry Multiplexer V2.0) such that values for two sparrows were measured simultaneously (one by each S-3A channel). Each bird was monitored for 42 min, followed by a 3 min reference reading, before switching to another sparrow. This system allowed each individual to be monitored approximately 47 % of the time. Data were recorded on a Macintosh computer interfaced with a DataTaker 500 A/D converter (Data Electronics). We computed BMR as the lowest $\dot{V}_{O_2}$ averaged over a continuous 10 min interval during periods when $\dot{V}_{O_2}$ was low and stable.

Morphological data

After removing the birds from the metabolic chambers at the completion of BMR measurements, we returned them to the holding cages for 2 h for rehydration (food was not available). They were then weighed to ±0.05 g (we used this mass for all analyses involving body mass), killed instantly by simultaneous cervical dislocation and thoracic compression, and then dissected. We removed each bird's heart (ventricles only), liver, lungs, gizzard, gut (small and large intestine and cecae), kidneys and reproductive organs (testes in males; ovaries and oviduct in females). Organs were trimmed of fat and connective tissue, emptied of contents (heart, gut), washed in physiological saline, blotted dry and weighed (to ±0.1 mg). They were then dried to constant mass at 60 °C and reweighed. In most juvenile females, the ovaries were too small to be weighed accurately; in these cases, we arbitrarily assigned a mass of 0.1 mg (the resolution limit of the balance).

The entire right breast muscle complex (musculus supracoracoideus and musculus pectoralis) was carefully dissected from the skeleton and processed as described above. We also removed the entire right leg and detached all muscles and tendons proximal to the tibiotarsus–tarsometatarsus joint; these tissues were processed as described above. Essentially all the muscle tissue from both breast and leg was recovered (we estimate that less than 1 % remained attached to the skeleton), and we were careful to dissect each bird in an identical manner.

Statistics

Since avian BMR and $\dot{V}_{O_2max}$ are power functions of body mass (Aschoff and Pohl, 1970; Hinds et al., 1993), we $\log_{10}$-transformed these variables to linearize them prior to analyses, and used mass residuals obtained from double-logarithmic regressions when comparing metabolic rates with body composition. For consistency, we used this method for both BMR and $\dot{V}_{O_2max}$, even though the latter was not significantly correlated with mass in our data set (the use of residuals generated from simple means of $\dot{V}_{O_2max}$ yielded similar qualitative results). Similarly, we converted all organ mass data into residuals from regressions of dry organ mass against fresh body mass. Significance tests for residuals analyses were performed according to Hayes and Shonkwiler (1996). Some authors (Ricklefs et al., 1996) have suggested using 'part-whole' correlations when compensating for the effects of body size. In this technique, body mass is adjusted by subtracting the mass of the dependent variable. Part-whole correlations of the largest organ we studied (breast muscle; approximately 18 % of body mass) led to the same qualitative results as conventional mass correlations. Because of this, and since we used dry organ mass but fresh body mass in our analyses, we employed conventional correlation techniques. We used 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 ± S.D. Analyses were performed using Statistica/Mac software (StatSoft, Inc.).

Results

Metabolic rate

We obtained data from 36 adult (19 male and 17 female) and 30 juvenile (16 male and 14 female) house sparrows ranging in mass from 19.5 to 27.7 g. We discarded $\dot{V}_{O_2max}$ data from four adults because of errors in running wheel operation. Body mass was not significantly related to either age or gender ($P>0.08$), although males were slightly heavier than females.

Regressions of mass *versus* BMR were significantly different from zero ($P<0.0002$; Fig. 1). The relationship between mass and BMR was not affected by gender ($P=0.2$), but differed significantly between ages ($P=0.00005$); the interaction term was not significant ($P=0.14$; ANCOVA). We discarded BMR data from one adult female whose BMR exceeded the predicted value by more than 4 S.D. (see Fig. 2). Juvenile BMR averaged approximately 13 % higher than that of adults of similar mass (1.06 and 0.94 ml O_2 min^{-1}, respectively, for a common mass of 22.5 g). Values for juveniles were virtually identical to predictions from the regression of Aschoff and Pohl (1970) for 22.5 g resting passerines (1.05 ml O_2 min^{-1}).

Unlike the results for BMR, the correlation between mass and $\dot{V}_{O_2max}$ was not significant in either adults or juveniles ($P>0.24$; Fig. 1). $\dot{V}_{O_2max}$ was not affected by gender ($P=0.18$), but differed significantly between ages ($P=0.00045$; ANOVA).

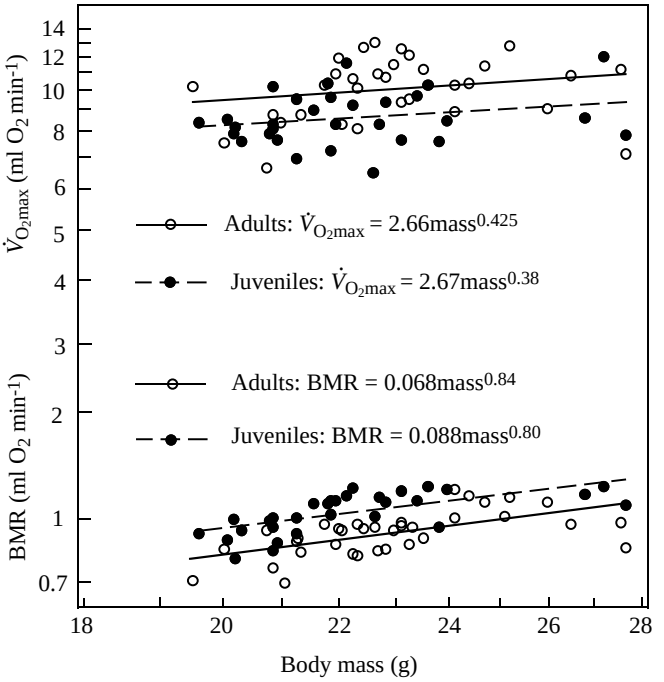

Fig. 1. Allometry of body mass and metabolism in house sparrows. Both axes are logarithmic. Top: maximum rate of oxygen consumption ($\dot{V}_{O_2max}$) during forced exercise. Bottom: basal metabolic rate (BMR). The regressions for BMR are significant ($r^2=0.35$, $P=0.00017$ for adults; $r^2=0.42$, $P=0.00010$ for juveniles). The regressions for $\dot{V}_{O_2max}$ are not significant ($P>0.24$) but, for purposes of consistency, were used to generate mass residuals for subsequent analyses (see text).

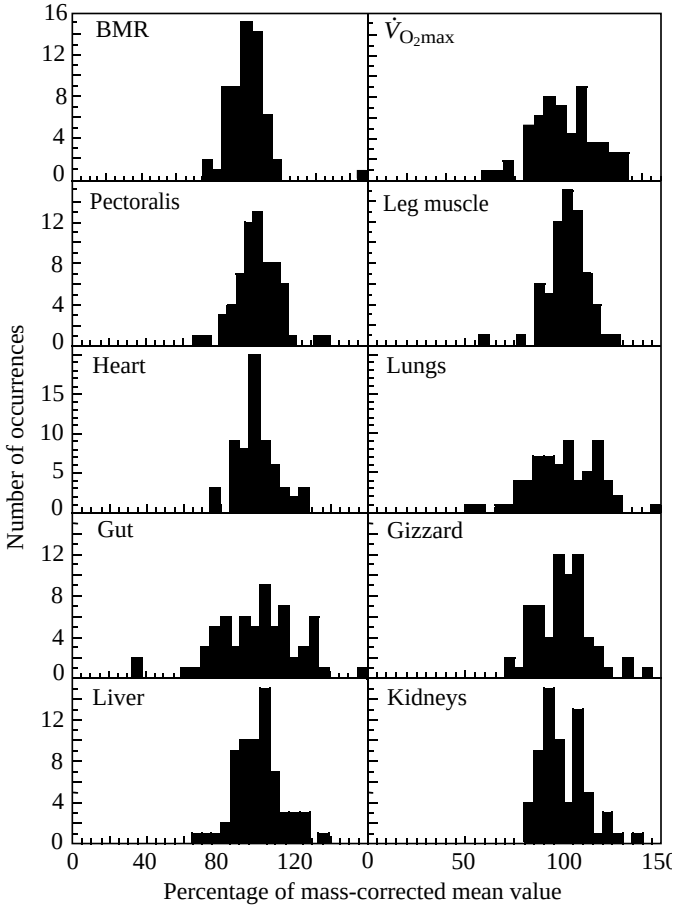

Fig. 2. Variance in aerobic metabolism (basal rate of oxygen consumption, BMR; maximal rate of oxygen consumption, $\dot{V}_{O_2max}$) and organ mass in juvenile and adult house sparrows. To facilitate comparisons, variance is shown as mass residuals, normalized to percentages [100×(observed value)/(predicted value)]. Separate mass regressions were used for juveniles (N=30) and adults (N=36).

Adult $\dot{V}_{O_2max}$ averaged approximately 17 % higher than that of juveniles (10.1 and 8.61 ml O_2 min^{-1}, respectively, for a common mass of 22.5 g).

Factorial aerobic scope ($\dot{V}_{O_2max}$/BMR) was not influenced by mass in either age group (P>0.13). Factorial scope was not affected by gender (P=0.20), but was significantly influenced by age (P<0.00001), with no significant interaction (P=0.12; ANOVA). Adult factorial scope was approximately 30 % higher than that of juveniles (10.8±2.11 and 8.33±1.15, respectively). Similarly, the 'absolute' scope ($\dot{V}_{O_2max}$ minus BMR, or the portion of total aerobic scope available for exercise, regulatory thermogenesis or other aerobic activities) was not affected by mass (P=0.38, ANCOVA) or gender (P=0.14), but it was strongly influenced by age (P=0.0001), with no significant interaction between these variables (P=0.29; ANOVA). The absolute scope of adults was approximately 20 % greater than that of similarly sized juveniles (9.2 *versus* 7.7 ml O_2 min^{-1}, respectively).

Variation in metabolic rate (coefficients of variation) averaged 15.9 % for $\dot{V}_{O_2max}$ and 11.2 % for BMR (Fig. 2) and was not affected by age or gender.

Organ mass

The fractional contribution of organ mass to total body mass differed significantly between adults and juveniles (Table 1). Juveniles had larger digestive organs (gut, liver, gizzard) and kidneys, and smaller hearts, gonads and leg muscles than adults. In addition, there was a trend for smaller breast muscles in juveniles, although this did not attain significance (P=0.57). Fractional organ masses of males and females were statistically indistinguishable in juveniles, but adult females had a larger liver and showed a trend towards a larger gizzard and kidneys than in adult males.

Water contents of organs ranged from 72.6 % (gizzard) to 81.6 % (reproductive organs). There were no gender differences in water content (P=0.25), and only two organs showed significant (but small) differences between juveniles and adults (heart, P=0.0008, 78.0 % *versus* 77.1 %, respectively; leg muscle, P=0.004, 78.2 % *versus* 76.8 %, respectively). In contrast to leg muscle, there was no age difference in the water content of breast muscle (74.2 % *versus* 74.1 %, respectively; P=0.79).

Because of the significant age difference in the mass allometry of BMR and $\dot{V}_{O_2max}$ (Fig. 1), we used separate regressions for adults and juveniles when computing organ mass residuals for comparison with metabolic rates. There was substantial variation in the size of all organs and muscles (Figs 2, 3). Unsurprisingly, age differences and variance were largest for reproductive organs (Table 1; Fig. 3). The large variation in adult females resulted from reproductive states ranging from individuals with small oviducts and ovaries with minimal follicular activity to birds with multiple large follicles and hypertrophied oviducts. Coefficients of variation in the

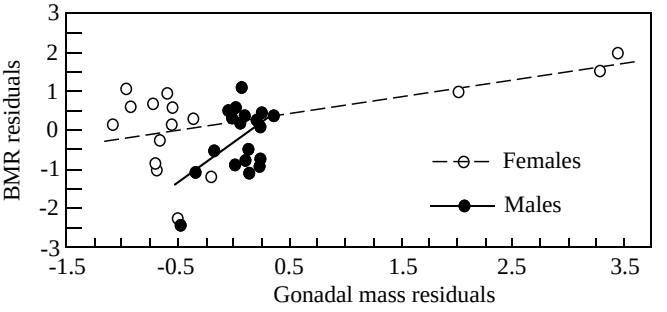

Fig. 3. Variance in reproductive organ size in adult female (N=17) and adult male house sparrows (N=19) and its relationship to basal metabolic rate (BMR). Reproductive organs included testes (males) or ovaries and oviducts (females). Organ size and BMR are expressed as mass residuals; the size variation was much larger in females than in males. Both regressions are significant (r^2=0.27, P=0.022 for males; r^2=0.30, P=0.03 for females). Regression lines do not go through the origin because BMR residuals came from a regression including both males and females (Fig. 1), while residuals for reproductive organ mass came from separate regressions for each sex.

Table 1. *Gender and age effects on organ masses of house sparrows (ANCOVA with fresh body mass as covariate)*

Organ	Adult females, *N*=17	Adult males, *N*=19	Juveniles, *N*=30	*P* (M *versus* F; adults)	*P* (adults *versus* juveniles)
Gut	0.097 (1.97±0.36)	0.088 (1.82±0.46)	0.14 (2.90±0.53)	0.32	<0.00001*
Gizzard	0.25 (4.15±0.65)	0.225 (3.53±0.64)	0.29 (4.75±0.53)	0.033	<0.00001*
Liver	0.18 (2.96±0.36)	0.15 (2.55±0.49)	0.21 (3.52±0.48)	0.00099*	<0.00001*
Heart	0.057 (1.09±0.15)	0.062 (1.18±0.15)	0.053 (1.08±0.11)	0.11	0.0015*
Lung	0.0455 (1.06±0.16)	0.047 (1.07±0.26)	0.047 (1.13±0.09)	0.65	0.39
Kidney	0.054 (1.14±0.13)	0.047 (0.96±0.10)	0.062 (1.28±0.09)	0.050	<0.00001*
Gonadal tissues	0.068 (1.03±1.70)	0.076 (2.13±0.39)	0.003 (0.017±0.034)	0.77	0.00005*
Breast muscles	0.52 (17.5±1.05)	0.54 (18.0±2.21)	0.49 (16.9±1.15)	0.43	0.057
Leg muscles	0.23 (8.84±0.80)	0.22 (8.26±0.77)	0.20 (8.03±0.70)	0.32	0.00001*

Dry organ mass (g) is adjusted to a common body mass of 22.5 g. For comparison, wet organ mass (as a percentage of fresh body mass; mean ± S.D.) is given in parentheses.

There were no significant gender differences in wet or dry organ masses among juveniles.

'Gonadal' tissues are testes (males) or ovary and oviduct (females). In most juvenile females, the gonads were too small to weigh accurately and were assigned a mass of 0.0001 g (the resolution limit of the balance).

Values significant after Bonferroni correction are indicated with asterisks.

other morphological variables ranged from 12.7 % in leg muscle to 23.2 % in gut.

We examined correlations between organ masses in both adults and juveniles (Table 2). Both age classes showed consistent positive correlations between liver and gut, and between breast muscles, heart and lungs.

Correlations between organ mass and metabolic rate

Heart, liver and breast muscle mass showed consistently high and significant correlations with BMR in both juveniles and adults (r>0.4; Table 3); in addition, BMR was strongly correlated with gut mass in juveniles and with lung mass in adults. Multiple regressions incorporating heart, liver and breast muscle mass explained 56 % of the variance in adult BMR (P=0.000015) and 46 % of the variance in juvenile BMR (P=0.00098). Adding gut mass to the equation for juveniles substantially increased r^2 to 0.70 (P<0.00001), but adding lung mass to the equation for adults had a negligible effect on explanatory power (r^2=0.57).

Because of large gender differences in the variance of gonadal mass in adults, we evaluated its metabolic effects separately in males and females. Gonadal mass was not significantly correlated with $\dot{V}_{O_2max}$ or with factorial or absolute scope in either sex. However, it was significantly positively correlated with BMR in both males (r^2=0.27, P=0.022; Fig. 3) and females (r^2=0.30, P=0.03). The relationship for females results from three birds that had large oviducts; if these individuals are removed from the regression, the significance disappears.

Correlations with organ mass were weaker for $\dot{V}_{O_2max}$ than for BMR (Table 3). Although heart, lung and leg muscle residuals were positively correlated with $\dot{V}_{O_2max}$ residuals in adults, only breast muscle was substantially correlated with $\dot{V}_{O_2max}$ in both age classes, although the correlations were not significant after Bonferroni correction (in juveniles, heart mass was ranked second to breast muscle in explanatory power). Multiple regression incorporating lung and either heart or breast muscle masses explained 22 % of the variance in adult $\dot{V}_{O_2max}$ (P=0.025–0.028). A regression including all three terms explained slightly more variance but had marginal significance (P=0.05).

No organ mass was correlated with factorial scope in either age group. However heart, lung and breast muscle mass were correlated with absolute scope in adults, and breast muscle mass was correlated with absolute scope in juveniles (Table 3), although the correlations were not significant after Bonferroni correction.

Since we used age-specific regressions to generate metabolic

Table 2. *Correlations (*r *values) between organ mass residuals in adults (top right) and juveniles (bottom left)*

Organ	Gut	Gizzard	Liver	Heart	Lung	Kidney	Gonadal tissue	Breast muscle	Leg muscle
Gut		0.29	0.35 (0.041)	0.002	0.076	0.23	0.13	0.14	0.37 (0.029)
Gizzard	–0.19		0.26	–0.36 (0.040)	0.054	0.13	–0.28	–0.021	0.23
Liver	0.43* (0.0020)	0.29		–0.082	0.16	0.425 (0.011)	0.23	0.030	0.16
Heart	0.15	0.23	0.18		0.61* (0.00013)	0.073	–0.021	0.52* (0.0017)	0.23
Lung	–0.009	0.34	–0.001	0.37 (0.047)		0.21	0.18	0.55* (0.00058)	0.48 (0.0024)
Kidney	0.165	0.29	0.014	0.16	0.305		0.28	0.10	0.275
Gonadal tissue	0.18	–0.30	–0.058	–0.22	–0.38	–0.28		0.063	–0.015
Breast muscle	0.305	0.25	0.12	0.65* (0.00012)	0.58* (0.00087)	0.17	–0.19		0.39 (0.020)
Leg muscle	0.17	0.25	0.22	0.36 (0.054)	0.55* (0.00018)	–0.25	–0.15	0.27	

'Gonadal' tissues are testes (males) or ovary and oviduct (females).
For cells with $P<0.06$, the P level is given in parentheses.
Values significant after a Bonferroni correction are indicated with asterisks.

and organ size residuals for juveniles and adults, and because the overall relationships between these variables were similar in the two age classes (Table 3), it was appropriate to pool the two data sets. We excluded gonadal mass from the combined analysis since it was more than 60 times greater in adults than in juveniles (Table 1). In the combined data (Table 4), seven organ masses (gut, liver, heart, lung, kidney, breast muscle and leg muscle) were positively and significantly correlated with BMR; a multiple regression incorporating these variables explained 60 % of the variance in BMR ($P<0.00001$). However, the partial correlations of only four of these variables (gut, liver, kidney and breast muscle) were significant, and in combination they explained 57 % of the variance in BMR.

The masses of two organs (heart and breast muscle) were substantially correlated with $\dot{V}_{O_2max}$, and a multiple regression incorporating these two variables explained 17 % of the variance in the pooled $\dot{V}_{O_2max}$ data ($P=0.004$). No organ mass was significantly correlated with factorial scope in the combined data (Table 4). However, absolute scope was significantly positively correlated with breast muscle mass, and heart mass showed a positive trend prior to Bonferroni correction.

Relationships between BMR, $\dot{V}_{O_2max}$ *and aerobic scope*

The 'aerobic capacity model' (Bennett and Ruben, 1979) predicts a constant factorial scope because of a putative functional linkage between BMR and $\dot{V}_{O_2max}$. Accordingly, we tested for correlations between these two variables using mass residuals in both age groups and for the pooled data. Only juveniles showed a significant relationship, with BMR explaining approximately 19 % of the variance in $\dot{V}_{O_2max}$ ($P=0.016$). For the pooled data, the correlation was positive ($r=0.23$) but did not attain significance ($P=0.069$).

A priori, it might be expected that inter-individual variation in factorial scope is equally likely to result from variation in BMR or in $\dot{V}_{O_2max}$. However, in house sparrows of both age classes, factorial scope was more tightly correlated with $\dot{V}_{O_2max}$ than with BMR ($r=0.73$ in juveniles and $r=0.75$ in adults for $\dot{V}_{O_2max}$; the corresponding values for BMR are $r=-0.28$ and $r=-0.45$). Therefore, differences in the factorial expansibility of aerobic power output in this species are largely attributable to variation in $\dot{V}_{O_2max}$ as opposed to variation in BMR.

Unsurprisingly, absolute scope ($\dot{V}_{O_2max}$ minus BMR) is strongly influenced by $\dot{V}_{O_2max}$ ($r>0.98$ in both juveniles and adults), but it is interesting to ask whether variation in BMR has any significant effect on variation in absolute scope. In fact, there was a significant relationship between these variables in juveniles ($r=0.4$, $P=0.026$), but not in adults ($P=0.28$).

Discussion

This study asked three main questions. First, does organ mass predict maximal aerobic performance? Second, does organ mass predict basal metabolic rate? Finally, are basal metabolic rate and maximal aerobic performance correlated? Before addressing these issues, it is appropriate to comment briefly on the measurement technique.

Measurement validity

Measurements of the aerobic capacity of volant birds are difficult because $\dot{V}_{O_2max}$ is probably attained only during flight. Our running wheel protocol is an effective and highly repeatable method for determining $\dot{V}_{O_2max}$ in red junglefowl *Gallus gallus* (Chappell et al., 1996), but that species is primarily terrestrial and does not fly except in brief bursts (mainly to escape predators). In contrast, house sparrows are strong fliers that routinely fly for long distances. Although measurements during sustained flight were not possible in the wheel, several lines of evidence make us confident that our method reliably elicited maximal aerobic performance, at least over periods of a few minutes. First, when wheel rotation started, all birds flapped vigorously (and most hovered nearly continuously) for 1–3 min; the measured $\dot{V}_{O_2max}$ was always achieved during these periods of intense wing motion. Since hovering is believed to be the most expensive mode of flight (Pennycuick, 1968), it seems logical that this represented a maximal effort. Second, our data are well within the range of aerobic scopes of birds in flapping flight (Tucker, 1973; Brackenbury, 1984; Gessaman and Nagy, 1988) and substantially greater than maximal avian thermogenic scopes (e.g. Marsh and Dawson, 1989). Fourth, our $\dot{V}_{O_2max}$ values from summer-acclimatized birds, when scaled to a common mass, are 11–42 % higher than the maximal thermogenic $\dot{V}_{O_2}$ reported for winter-acclimatized house sparrows (Koteja, 1986; Dutenhoffer and Swanson, 1996). Finally, the exercise regime produced obvious behavioral evidence of exhaustion in all individuals tested, indicating that $\dot{V}_{O_2max}$ had been attained.

Organ mass and aerobic capacity

The three models of performance limits assume that the maximal aerobic capacity of the intact animal scales with the functional capacity of skeletal muscle effectors (peripheral limitation model), with the visceral support organs for gas or nutrient transport (central limitation model) or with both (symmorphosis). We used dry organ mass as an index of functional capacity. Dry organ mass is also an index of the birds' investment in central and peripheral components, assuming that mass is proportional to both the construction (growth) and operational (maintenance) costs of organs. Although mass does not account for individual variation in organ composition (e.g. lipid or connective tissue content, enzyme activity, etc.; Piersma et al., 1996), we feel that this approach is a reasonable approximation.

Given these assumptions, the peripheral limitation model predicts strong correlations between effector organ mass (skeletal muscle) and aerobic performance, but not between

Table 3. *Correlations (*r *values) between organ mass and aerobic performance in adults and juveniles*

	Adults				Juveniles			
	BMR	$\dot{V}_{O_2max}$	F Scope	A Scope	BMR	$\dot{V}_{O_2max}$	F Scope	A Scope
Gut	0.25	0.31	0.15	0.30	0.70* (0.000024)	0.21	–0.19	0.17
Gizzard	–0.066	–0.067	0.002	–0.080	0.090	–0.10	–0.16	–0.11
Liver	0.53* (0.0015)	0.061	–0.23	0.033	0.40 (0.033)	–0.058	–0.029	–0.089
Heart	0.45* (0.0088)	0.38 (0.040)	–0.003	0.45 (0.013)	0.54* (0.0032)	0.23	–0.090	0.20
Lung	0.45* (0.0083)	0.44 (0.014)	0.30	0.44 (0.015)	0.165	–0.067	–0.15	–0.084
Kidney	0.39 (0.023)	0.31	0.022	0.29	0.31	–0.039	–0.23	–0.060
Gonadal tissue					–0.11	0.043	0.092	0.054
Breast muscle	0.49* (0.0034)	0.38 (0.039)	0.01	0.36 (0.054)	0.56* (0.0021)	0.44 (0.017)	0.12	0.44 (0.017)
Leg muscle	0.375 (0.035)	0.365 (0.050)	0.08	0.35	0.22	–0.094	–0.25	–0.11

BMR, basal metabolic rate; $\dot{V}_{O_2max}$, maximum rates of O_2 consumption during intense forced exercise; F Scope, $\dot{V}_{O_2max}$/BMR; A Scope, $\dot{V}_{O_2max}$ minus BMR.

Adults (N=35; N=32 for $\dot{V}_{O_2max}$); juveniles (N=30).

Body mass residuals were used for BMR, $\dot{V}_{O_2max}$ and organ mass.

We evaluated the effects of adult gonadal mass (testes in males and ovary plus oviduct in females) separately because of much higher variance in females than in males (see text).

For cells with P<0.06, the P level is given in parentheses.

Values significantly different after a Bonferroni correction are indicated with asterisks.

Table 4. *Correlations (*r *values) between organ mass and aerobic performance for all birds combined*

	BMR	$\dot{V}_{O_2max}$	F Scope	A Scope
Gut	0.46* (0.00014)	0.26 (0.037)	0.03	0.23
Gizzard	–0.003	–0.09	–0.09	–0.097
Liver	0.47* (0.00010)	0.003	–0.17	–0.028
Heart	0.43* (0.00044)	0.34 * (0.0089)	0.06	0.31 (0.016)
Lung	0.32* (0.011)	0.21	0.04	0.185
Kidney	0.355* (0.0039)	0.15	–0.06	0.12
Breast muscle	0.52* (0.000010)	0.41* (0.0014)	0.05	0.38* (0.0031)
Leg muscle	0.30* (0.015)	0.14	–0.02	0.12

BMR, basal metabolic rate; $\dot{V}_{O_2max}$, maximum rate of O_2 consumption during exercise; F Scope, $\dot{V}_{O_2max}$/BMR; A Scope, $\dot{V}_{O_2max}$ minus BMR.

N=62 for $\dot{V}_{O_2max}$; N=65 for BMR.

Body mass residuals were used for BMR, $\dot{V}_{O_2max}$, organ mass and A Scope.

For cells with P<0.06, the P level is given in parentheses.

Values significant after a Bonferroni correction are indicated with asterisks.

the mass of associated visceral organs (particularly heart and lungs) and performance. The converse is expected under the central limitation hypothesis, while symmorphosis predicts that aerobic performance will correlate with both skeletal muscle and visceral organ masses. Although our results with house sparrows are not clear-cut, they are most consistent with the symmorphosis model: in the pooled data set, $\dot{V}_{O_2max}$ is significantly correlated with the size of the primary peripheral effector (breast muscle) and with the size of the heart – the central organ most closely associated with oxygen transport (Table 4). The same general pattern was apparent in both adults and juveniles (although lung mass was strongly correlated with $\dot{V}_{O_2max}$ in the adults but not the juveniles; Table 3). These results, and the symmorphosis model, are also consistent with the strong covariance of heart, lung and breast muscle mass seen in both adults and juveniles (Table 2).

The most stringent interpretation of the basic symmorphosis concept, that there is no excess capacity in the system, would require that all correlations between component variables are close to 1.0 (i.e. there should be no residual variation). Our data fail that requirement, and in that sense do not provide unambiguous support for symmorphosis. It should be emphasized that four-fifths of the variation in $\dot{V}_{O_2max}$ is not explained by heart and breast muscle mass. Presumably, differences in other factors (e.g. aerobic enzyme activity, mitochondrial density, capillary geometry, etc.; Weibel, 1984, 1987; Weibel et al., 1991) account for the remaining variance.

Organ mass and basal metabolism

Several authors (e.g. Kersten and Piersma, 1987; Peterson et al., 1990; Daan et al., 1990; Piersma et al., 1996; Burness et al., 1998) have suggested that much of the energy used in basal metabolism is consumed by visceral organs (especially the heart, liver, kidneys and intestine). These organs have a relatively high metabolic intensity (power consumption per unit mass) compared with resting muscle (e.g. Krebs, 1950; Martin and Fuhrman, 1955; Leblond and Messier, 1958; Cairnie and Bentley, 1967; Ferraris, 1994). Accordingly, visceral organs should be the primary determinants of BMR, and variation in BMR should be correlated with variation in the mass of these organs.

In general terms, our results support that hypothesis. However, the specific organs that predict BMR differ among studies. Daan et al. (1990) report that heart and kidney mass explained approximately half of the variance in BMR in a sample of 22 bird species. Burness et al. (1998) also found kidney mass to be positively correlated with BMR in tree swallows (*Tachycineta bicolor*). However, in that species, the correlation with heart mass was not significant, and the mass of the small intestine was significantly negatively correlated with BMR (the combination of kidney and intestine mass explained approximately 21 % of the variation in BMR). In house sparrows, we found the mass of most visceral organs to be positively correlated with BMR, and the mass of three of these (kidney, gut and liver) remained significant in a multiple regression. Thus, only kidney mass is a consistent predictor of BMR in all three studies. A potentially more important contrast between our results and most previous studies is our finding that the mass of a peripheral effector – breast muscle – is strongly correlated with BMR, in addition to the three visceral organs (a similar correlation was reported by Weber and Piersma, 1996). It could be argued that, because breast muscle and heart masses are covariant (Table 2), it is difficult to determine which has the primary influence on BMR. However, our analyses suggest that breast muscle is the more important determinant, since it has a higher correlation coefficient in both age classes and in the pooled data (Tables 3, 4) and its partial correlation remains significant in a multiple regression. It is unsurprising that variation in breast muscle mass should affect BMR, since this muscle constitutes 17–18 % of total body mass in house sparrows, as much as all the visceral organs combined.

We were particularly interested in the influence of reproductive tissue on BMR. Avian reproductive organs undergo a profound regression in non-reproductive adults. However, they become quite large during the breeding season and are the sites of considerable cell division and secretory activity, so it is logical to assume that they would have some influence on energy metabolism. Our data are consistent with this hypothesis: we found significant positive correlations between reproductive tissue mass and BMR in both sexes (Fig. 3). It should be noted that, in females, the positive correlation is due to three birds with very large oviducts. Nevertheless, it is instructive to consider the

apparent energy cost of maintaining reproductive condition in house sparrows.

The estimated BMR of a 22.5 g adult female with regressed gonads (1/50 the measured mean gonadal mass) is $0.920\,ml\,O_2\,min^{-1}$ [based on a multiple regression predicting log(BMR) from log(mass) and dry gonadal mass]. For a similarly sized female with average gonadal mass, the estimated BMR is $0.943\,ml\,min^{-1}$, or 2.5 % larger than for a non-reproductive female. For a bird with five times the mean gonadal mass (as occurred in females with large oviducts), the estimated BMR is $1.07\,ml\,min^{-1}$, or approximately 16 % more than that of a non-reproductive female. For males, the effects are larger, although the observed range of gonadal mass was smaller than in females (maximum gonad mass was only 1.5 times the mean mass). The estimated BMRs are $0.781\,ml\,min^{-1}$ for a non-breeding male, $0.929\,ml\,min^{-1}$ (19 % greater than a non-breeder) for males having the mean observed gonadal mass and $1.01\,ml\,min^{-1}$ (29 % greater than a non-breeder) for males having gonads 1.5 times the mean mass. These costs are substantial, but additional work is needed to determine whether they are due to the maintenance cost of large reproductive organs, to the systemic morphological, physiological or behavioral effects of high levels of gonadal hormones or to other factors. However, we do not believe that the differences in male BMR are associated with differences in circulating testosterone level *per se* because BMR is apparently unaffected by this hormone in male white-plumed honeyeaters (*Lichenostomus penicillatus*; W. A. Buttemer and L. B. Astheimer, unpublished data).

Relationship between basal metabolic rate and aerobic capacity

Across a wide size range of vertebrate ectotherms and endotherms, $\dot{V}_{O_2max}$ averages approximately 10-fold higher than the minimum 'normothermic' metabolic rate (MMR; i.e. exclusive of hypometabolic states such as torpor or hibernation; Bartholomew, 1982). On the basis of this observation and other data, Bennett and Ruben (1979) proposed that $\dot{V}_{O_2max}$ and MMR are functionally linked, so that selection for high aerobic capacity to support intense sustained activity will indirectly generate a concomitant increase in MMR. Most attempts to test this 'aerobic capacity model' have involved searching for positive correlations between MMR and $\dot{V}_{O_2max}$, both interspecifically (e.g. Lechner, 1978; Taylor et al., 1981; Hinds and Rice-Warner, 1992; Bozinovic, 1992; Sparti, 1992; Dutenhoffer and Swanson, 1996) and intraspecifically (e.g. Hayes, 1989; Garland and Else, 1987; Chappell and Bachman, 1994). The results have been inconclusive, with some studies reporting significant correlations and others failing to find a relationship (for a review, see Hayes and Garland, 1995). The results from our study of house sparrows are also ambiguous: juveniles showed the expected positive correlation between minimal metabolic rate (BMR) and $\dot{V}_{O_2max}$, but there was no correlation in adult birds.

In analyzing relationships between organ mass, BMR and aerobic capacity, it is important to consider the time scale over which maximal metabolic rate is measured. Our estimate of $\dot{V}_{O_2max}$ is derived from brief bouts of acute intense exercise and represents the maximal power output possible over short periods (minutes). Accordingly, it may not be reasonable to expect it to scale with the mass or activity of central support organs such as the digestive system, whose regulatory functions operate over much longer time spans. Since these organs are probably large contributors to BMR (Daan et al., 1990; Burness et al., 1998; Table 4), it is not surprising that we found no significant correlations between short-term $\dot{V}_{O_2max}$ and BMR in adults and in the pooled data. When determined over long periods (days or weeks), sustained metabolic power output is considerably lower than our short-term $\dot{V}_{O_2max}$ values (Drent and Daan, 1980; Peterson et al., 1990; Hammond and Diamond, 1997) and is more likely to be affected by all components of the visceral organ 'infrastructure' and, hence, is more likely to be correlated with BMR.

In conclusion, as predicted by the symmorphosis concept, we found positive correlations between maximal aerobic metabolic rate and the masses of both the primary effector organ for exercise (breast muscle) and the primary central organ of oxygen transport (the heart). If these correlations are the result of heritable functional linkages, then selection for increased aerobic capacity in house sparrows should produce increases in the mass of both heart and breast muscle, but not in the size of other visceral organs or leg muscle. This is consistent with our findings that adults (which have a higher $\dot{V}_{O_2max}$ than juveniles) have significantly larger hearts than juveniles and show a trend towards larger breast muscles (Table 1). However, maturational increases in the mass of these organs do not completely account for the age-related differences in $\dot{V}_{O_2max}$. This suggests that attaining a higher $\dot{V}_{O_2max}$ may entail qualitative as well as mass changes to organs (e.g. enzyme activities, mitochondrial density, capillary density, etc.). The maturational decrease in water content we observed in leg muscle and heart is an example of such a change (Ricklefs and Webb, 1985).

Since we also found positive correlations between heart and breast muscle mass and basal metabolic rate, it might be expected that selection for increased aerobic performance would entail a 'trade-off', or fitness cost, in higher BMR. However, we did not find the expected correlation between BMR and $\dot{V}_{O_2max}$ in our sample of house sparrows (perhaps because BMR is affected by many visceral organs whose mass does not covary with breast muscle mass or $\dot{V}_{O_2max}$). Also, adult sparrows achieved a higher $\dot{V}_{O_2max}$ and aerobic scope than juveniles even though adults had a lower BMR. Taken together, these results suggest that house sparrows do not have to pay a higher maintenance energy cost (elevated BMR) to attain an increased aerobic capacity.

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