Cardiorespiratory adjustments of homing pigeons to steady wind tunnel flight

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Summary

We made detailed cardiorespiratory measurements from homing pigeons during quiet rest and steady wind tunnel flight. Our pigeons satisfied their 17.4-fold increase in oxygen consumption during flight with a 7.4-fold increase in cardiac output ($\dot{Q}$) and a 2.4-fold increase in blood oxygen extraction. $\dot{Q}$ was increased primarily by increasing heart rate sixfold. Comparisons between our study and those from the only other detailed cardiorespiratory study on flying birds reveal a number of similarities and important differences. Although the avian allometric equations from this earlier study accurately predicted the flight $\dot{Q}$ of our pigeons, this was primarily due to due to compensating discrepancies in their heart rate and stroke volume predictions. Additionally, the measured heart mass (M_H)-specific $\dot{Q}$ ($\dot{Q}/M_H$) of our pigeons during wind tunnel flight was about 22% lower than the estimated value. Compared to running mammals in previous studies, the 1.65-fold $\dot{Q}$ of our pigeons is consistent with their larger heart mass.

Key words: blood gas, metabolism, cardiac output, stroke volume, heart rate.

Introduction

Flying vertebrates are of interest to cardiovascular physiologists because their aerobic metabolic capability is about twice that of running mammals of equal size (Thomas et al., 1987). Because homing pigeons *Columba livia* combine a relatively small body size (allometric variation) with superior athletic ability (adaptational variation) and tractable behavior, they are an excellent animal model for investigating the upper limits of vertebrate cardiorespiratory adaptation and performance during intense metabolic stress.

Over the years, much has been learned about the many aspects of the cardiorespiratory responses of birds to treadmill exercise (Bevan et al., 1994, 1995) and resting hypoxic stress (Maginniss et al., 1997; Novoa et al., 1991). Other studies have investigated various aspects of avian flight physiology that include metabolism and biochemistry (Christensen et al., 1994; George and John, 1993; Schwilch et al., 1996), thermoregulation and water balance (Adams et al., 1997; Carmi et al., 1993, 1994; Hissa et al., 1995; Giladi et al., 1997), and wing cycle and ventilation (Boggs et al., 1997a,b). However, only one in-depth cardiorespiratory study on an avian species during steady flight has been reported (Butler et al., 1977). Consequently, this central aspect of avian physiology remains poorly understood.

Two reasons for the scarcity of detailed avian flight cardiorespiratory data are the need for specialized equipment (e.g. a wind tunnel) and chronic vascular cannulation techniques, which provide access to the bird's circulatory system while allowing normal behavior of the bird. Accordingly, the two primary objectives of this study were: (1) to develop chronic cannulation techniques and blood sampling procedures for the pigeon in order to routinely obtain arterial and mixed venous blood samples from both resting and flying birds, and (2) to comprehensively characterize the basic cardiorespiratory parameters of our population of homing pigeons at calm rest and during steady wind tunnel flight under defined conditions.

Materials and methods

Experimental animals and housing

Homing pigeons *Columba livia* L. to be investigated were of unknown sex and obtained from Dr Melvin Kreithen's outdoor loft at the University of Pittsburgh; mean body mass (± S.D.) was 340±45 g. The birds were housed in individual indoor cages at 21°C under a 12 h:12 h (light:dark) photoperiod with ample commercial pigeon food and water. All data reported in this study were collected between 09:00 h and 01:00 h.

Screening and familiarization
Resting studies

The birds were first screened to determine whether they were

behaviorally acceptable for use in the resting experiments. Screening involved placing the bird inside an open-circuit metabolic chamber (described below) for 1 h while its rate of carbon dioxide production was continuously recorded. Quiet, resting birds produced little variation in carbon dioxide production. These birds were chosen as potential candidates for resting studies. Birds passing this screening test were further familiarized to the chamber during three 1 h sessions on consecutive days before being scheduled for surgery.

Flight studies

After an initial screening for wind tunnel flight competence, birds showing promise were included in the daily training schedule. Each bird was trained to fly in a horizontal wind tunnel for 7 min at a constant air speed of 18.4 m s^{-1} and an ambient air temperature of 10–12°C, while carrying the devices required for a specific experiment (e.g. metabolism mask and tube, blood pressure transducer, or pieces of heavy string simulating cannula extension lines). The trained bird was then scheduled for surgery.

Experimental apparatus

Metabolic chamber

Resting measurements were made from each bird as it sat quietly in a darkened, open-circuit Plexiglas® metabolic chamber (40 cm×20 cm×20 cm L:W:H). This chamber was placed inside an environmental chamber set at 15°C to prevent thermal hyperventilation during the experiment. The environmental chamber kept the internal temperature of the metabolic chamber at 18.0±0.9°C, as monitored by a YSI Scanning tele-thermometer (Model 47, YSI, Yellow Springs, OH, USA) and thermistor probe (Model 427).

Wind tunnel

All flight experiments were performed in a 6.6 m long open-circuit horizontal wind tunnel (Aerolab, Laurel, MA, USA) with test section dimensions and air flow properties that have been described elsewhere (Thomas et al., 1984). All training and each wind tunnel experiment was carried out at an air speed of 18.4 m s^{-1}, and an ambient temperature of 10–12°C to keep the bird from overheating.

Vascular surgery

Resting and flight studies

Surgery was performed on the day before an experiment using 2% Halothane anesthetic metered by a vaporizer (Flurothane, Model FR, Pittsburgh, PA, USA) and carried in a 2:1 ratio of oxygen and nitrous oxide. The total flow rate through the vaporizer was 1.5 l min^{-1}. Mixed venous blood samples were obtained from a silastic cannula (0.030 cm i.d.×0.064 cm o.d.; Dow Corning, Midland, MI, USA) placed in the bird's right atrium through the cervical cutaneous branch of the jugular vein. The position of the cannula's tip in the right atrium was verified by autopsy after completion of the experiments. Data from birds having the cannula tip located outside the right atrium were discarded. Arterial blood samples

were obtained from a second silastic cannula (Dow Corning, 0.051 cm i.d.×0.094 cm o.d.) placed in the bird's right ischiadic artery. An 80% solution of polyvinylpyrrolidone (PVP-40T; Sigma, St Louis, MO, USA) in aqueous heparin [1000 U ml^{-1}; Elkins-Sinns, Inc., Cherry Hill, NJ, USA (hereafter called 'PVP–heparin')] was used to maintain cannulae patency prior to an experiment.

Measurements

Metabolism

Resting studies. Conventional open circuit methods and equation 2 from Tucker (1968) were used to determine the oxygen consumption rate ($\dot{V}_{O_2}$) of each bird. A mass flow controller (Model FM-4587, Linde-Union Carbide, Danbury, CT, USA) maintained a constant air flow rate of 0.80±0.01 l min^{-1} (STPD) through the metabolic chamber. The composition of gas entering and leaving the metabolic chamber was continuously sampled by a pump (Model R-2, Applied Electrochemistry, Pittsburgh, PA, USA) and monitored by oxygen and carbon dioxide analyzers (Applied Electrochemistry, Models S-3A-N-22M and CD-38, respectively). Analyzers were calibrated with dry air and a carbon dioxide (5.00% CO_2 in nitrogen) Primary Standard grade gas mixture (Linde-Union Carbide, Jackson Welding, Pittsburgh, PA, USA). Individual oxygen consumption rates were calculated from the mean values of the oxygen and carbon dioxide gas analyzers while blood samples were being drawn.

Flight studies. The rate of oxygen consumption for five pigeons was determined using the open-circuit method and flight training procedures similar to those previously described by Thomas et al. (1984). Briefly, the birds were trained to fly in the wind tunnel for 7 min wearing a custom-fit celluloid mask and molded latex hood. A vacuum source was connected to the mask by a flexible tube that trailed below the flying bird and pulled room air through the mask at a rate of 13.1 l min^{-1} (STPD). Composition of the expired gas was continuously measured as described above, and the oxygen consumption rate was calculated using mean data from the sixth minute of each flight.

To detect if leakage of expired gas occurred from the mask at the flow rate that was to be used for the flight oxygen consumption experiments, several lower flow rates were used during preliminary tests on each bird, and the rate of oxygen consumption ($\dot{V}_{O_2}$) calculated. These tests revealed that no unintended mask leakage occurred (i.e. there was no decrease in the bird's apparent $\dot{V}_{O_2}$) until the flow rate was reduced to 16% below the flow rate used in the actual $\dot{V}_{O_2}$ flight experiments.

The flight mass-specific oxygen consumption rate ($\dot{V}_{O_2}$ kg^{-1}) of each homing pigeon used in the cardiovascular series of measurements was calculated from the mean mass-specific oxygen consumption rate measured from a different but equivalent group of homing pigeons (N=5). These were separate experiments carried out during the same times of the day (09:00 h–11:30 h), months of the year (summer) and wind

tunnel conditions used for the cardiorespiratory measurements (i.e. horizontal flight at 18.4 m s^{-1} and 10–12°C). This two-group approach was used to increase wind tunnel training success. Switching back and forth between normal flight and training a given pigeon to fly with the mask (oxygen consumption measurements) and the pressure transducer back pack (heart rate measurements) confused most birds, and resulted in substantially lower training success rates.

Body temperature

Resting and flight studies. Body temperature was measured to the nearest 0.1°C by inserting a thermistor probe (YSI, Model 427) 5 cm into the bird's cloaca. The probe was calibrated immediately before each experiment using a thermostatically controlled water bath (Isotemp Bath Model 8000, Fisher, Hanover Park, IL, USA) and a precision mercury thermometer (Fisher, 15-000A).

Blood gas tension, total oxygen content and pH

Resting and flight studies. Arterial (a) and mixed venous ($\bar{v}$) blood samples were analyzed for oxygen tension (Pa_{O_2}, $P\bar{v}_{O_2}$) carbon dioxide tension (Pa_{CO_2}, $P\bar{v}_{CO_2}$) and pH (pHa, pH$\bar{v}$) using a blood gas analyzer (Instrumentation Laboratories Model 1306, Lexington, MA, USA). Total oxygen content (Ca_{O_2}, $C\bar{v}_{O_2}$) for the arterial and mixed venous blood samples was measured using a Model K analyzer (Lex-O$_2$-Con, Chestnut Hill, MA, USA). Oxygen and carbon dioxide tensions and pH values were corrected using the measured cloacal temperature and equations supplied in the blood gas analyzer manual. Blood samples were stored in glass syringes (Model 1750-LTN, Hamilton Gastight®, Reno, NV, USA) and chilled in an ice–water slurry to quench the red cells' metabolism before analysis. Hematocrit (Hct) was measured for each blood sample to determine if contamination had occurred by saline admixing. Arterial and mixed venous blood gas tensions and pH analyses were completed within 5 min after the sample was collected. Total oxygen content analyses were completed within 7 min after the sample was collected.

Heart rate

Resting studies. Heart rate (f_H) was recorded during the blood sampling period with silver cutaneous electrodes connected to a heart monitor equipped with a chart recorder (Model 1700, Mennen Medical, Trevose, PA, USA).

Flight studies. Heart rate during flight was determined from the arterial pressure waveform measured with a small (3.0 cm×4.2 cm×1.3 cm W:L:H) 9.4 g pressure transducer (NAMIC, Glens Falls, NY, USA) attached to the bird's back with Velcro™ patches. The transducer's output was recorded by a MacLab analog-to-digital converter controlled by a Macintosh computer running MacLab Chart software.

Experimental protocols
Resting studies

On the day of the experiment, the venous cannula was cleared of the PVP–heparin solution, and the bird systemically

heparinized with 0.3 ml of heparinized saline (50 U ml^{-1}) through the venous cannula. The venous cannula was then attached to a saline-filled extension line (0.051 cm i.d.×0.150 cm o.d.×90 cm L; S-54-HL, Tygon, Akron, OH, USA) connected to one port of a saline-filled three-way manifold. A Tuberculin syringe used to remove saline from the extension line before collecting the blood sample, and a Hamilton syringe used to collect the blood sample, were each attached to the remaining two manifold ports by 1.3 cm lengths of silastic tubing (Dow Corning, 0.051 cm i.d.×0.094 cm o.d.). The arterial cannula was prepared the same way, except that 0.3 ml of saline was used in place of the heparinized saline. After the electrocardiographic leads were attached to the bird it was placed inside the metabolic chamber that was placed inside the environmental chamber.

After a 45 min equilibration period, heart rate and carbon dioxide readouts were monitored for stability to determine an appropriate time for blood sample collection. Just before collecting the blood samples, the extension lines were simultaneously cleared of saline using the Tuberculin syringes. The silastic segments of the Tuberculin syringes were clamped and a 0.5 ml sample of arterial and mixed venous blood was collected simultaneously in each Hamilton syringe over 3 min while heart rate and metabolic rate information were simultaneously recorded. Immediately after collecting the blood samples, the extension lines were clamped near the manifolds, the silastic tubing segments on the Hamilton syringes were clamped and separated from the manifolds, then immersed in an ice–water slurry to quench the red cells' metabolism. The 3 min sampling period was chosen because preliminary tests revealed that faster blood sampling rates were detected by the birds as indicated by higher heart rates and increased oxygen consumption values. Total oxygen content analyses were completed within 7 min after sample collection, and arterial and mixed venous blood gas tensions and pH were completed within 5 min after sample collection. Deep body temperature was measured within 1 min after sample collection was completed. Cardiac output ($\dot{Q}$) and stroke volume (Vs) were calculated for each experiment using the Fick equation.

Flight studies

Blood sampling and blood gas measurements. For these experiments, the arterial and venous cannulae were first prepared as described above. The three-way manifold, Tuberculin syringe, and the Hamilton glass sample syringe associated with each cannula's 90 cm long extension line were secured to a custom-built 'dual-sampling device' that allowed all four syringes to be filled by using a single hand. By applying small clamps to the appropriate silastic tubing segments during the flight, a single researcher could first simultaneously clear saline from the lines into the Tuberculin syringes and then draw arterial and venous blood samples into the Hamilton glass syringes. During an experiment, the sampling device was held in a position 0.5 m downstream from the flying bird by a researcher lying on top of the wind tunnel with his arms protruding through snug-fitting arm holes in the ceiling of the

wind tunnel's test section. Arterial and mixed venous blood (0.5 ml) was collected simultaneously in each Hamilton syringe during the sixth minute of flight. As soon as the bird landed on a perch lowered to signal the end of the flight, the extension lines were clamped near the manifolds, the silastic tubing segments on the Hamilton syringes were clamped and separated from the manifolds, and then submersed in an ice–water slurry to quench the red cells' metabolism prior to analysis. Blood gas tension and pH analyses were completed within 5 min after sample collection, and total oxygen content analyses were completed with in 7 min after sample collection. Deep body temperature was measured within 1 min after the bird landed by the previously described procedure. Cardiac output and stroke volume were calculated for each experiment using the Fick equation.

Heart rate measurements. Measurement of a bird's heart rate during flight was made on the day following the blood gas sampling experiment using the same wind tunnel conditions (horizontal flight at 18.4 m s^{-1} and ambient temperature of 10–12°C). The PVP–heparin solution was removed from the arterial cannula and the bird systemically heparinized as previously described. The arterial cannula was then connected to the pressure transducer attached to the back of the bird with a Velcro$^{\circledR}$ square. The heart rate reported for each bird is the mean value calculated from data collected throughout the sixth minute of flight, to coincide with the same time in the flight when blood samples were collected.

After these measurements were completed, the bird was killed and the position of the tip of the venous cannula in the right atrium was checked. The heart was then excised, its chambers were open and blotted free of blood and the mass of the heart was (M_{H}) was determined to the nearest 0.01 g using a Mettler balance.

Assessment of protocols used for collecting and storing whole blood samples

These tests were carried out for two reasons: (1) to learn the best method of preserving the blood gas tensions of whole blood samples during collection and temporary storage, and (2) to determine whether whole blood metabolism and/or tubing permeability were factors to consider in reporting final blood gas tensions and pH values.

Collection of blood samples and extension line permeability

Mixed venous pigeon blood (0.5 ml) was collected in a Hamilton syringe at room temperature (22°C) and a sample immediately injected into the blood gas analyzer for analysis. The Hamilton syringe was then attached to an extension line of equal length and composition used in the resting experiments. The extension line was filled with blood and its free end was clamped to prevent contaminating the blood with room air. Samples of blood from the free tip of the extension line were then injected into the analyzer every 5 min until the syringe was empty. This procedure was repeated at 12°C (i.e. the ambient temperature of the environmental chamber and wind tunnel). Oxygen tension

data were plotted against time and the slope was calculated for both temperatures.

Whole blood metabolism and storage

A 0.5 ml sample of mixed venous pigeon blood collected in a Hamilton syringe was immediately injected into the blood gas analyzer for assay. After sealing off the syringe's needle with a short segment of silastic tubing, the syringe was submersed in an ice–water slurry. Injections were repeated every 5 min until the syringe was empty. This procedure was carried out at the temperatures of 22 and 12°C, and with the Hamilton syringe submersed in the ice-water slurry (1°C) during injections. Oxygen tension results were plotted against time and the slope was calculated for each temperature.

Results

Assessment of protocols used for collecting and storing whole blood samples

Results from these preliminary tests are summarized in Table 1. As expected, lowering the temperature of the blood sample from 22°C to 1°C substantially decreased the metabolic rate of the whole blood samples as reflected in the slopes (Table 1). The similarity between the slopes of the Hamilton syringe and the extension line data at 22°C show that the effect of the extension line permeability on measured oxygen tension values was minimal during sample collection. The question then turned to influence of the whole blood's metabolic rate on oxygen tension during the collection and storage time before analysis.

During both resting and flight experiments, preservation of the oxygen tension of blood samples during collection is seen by the notable reduction of the $\Delta P_{\mathrm{O_2}}$ rate in going from 22°C to 12°C (Table 1). This reduction in blood temperature takes place as the blood passes through the extension line, which acts as a heat exchanger and brings the blood into thermal equilibrium with the air of environmental chamber or wind tunnel, preserving the oxygen tension of each arterial and mixed venous blood sample used in our results.

Using an ice–water slurry for storage of blood samples prior

Table 1. *Assessment of blood storage and collection methods using the rate of change in pigeon whole blood oxygen tension for each temperature and holding receptacle*

Method of storage	Temperature (°C)	$\Delta P_{\mathrm{O_2}}$ (mmHg min^{-1})
Hamilton syringe	22	−1.3
Extension line	22	−1.2
Hamilton syringe	12	-6.6×10^{-2}
Extension line	12	-5.2×10^{-2}
Hamilton syringe	Ice–water slurry	4.1×10^{-3}

$\Delta P_{\mathrm{O_2}}$ slopes were calculated from data points collected over a 30 min period.

Table 2. *Mean resting and flight metabolic and cardiovascular data, and the factor by which each parameter increased when going from rest to flight*

Value	Rest (*N*=12)	Flight (*N*=7)	F/R
$\dot{V}_{O_2}/M_b$ (ml kg^{-1} min^{-1})	17.8±3.9	309.6±37.4*	17.4
$\dot{Q}/M_b$ (ml kg^{-1} min^{-1})	302±67	2244±269	7.43
f_H (beats min^{-1})	110±19	663±33[†]	6.03
V_s/M_b (ml kg^{-1})	2.75±0.04	3.38±0.08	1.23

R, rest; F, flight.

Values are means ± S.E.M.

*Value was determined from a different but equivalent group of pigeons (see text).

[†]Only 5 values were used to calculate the mean ± S.E.M.

Table 3. *Mean resting and flight pigeon cardiorespiratory data, and the factor by which each parameter increased from rest to flight*

Value	Rest (*N*=12)	Flight (*N*=7)	F/R
C_{aO_2} (Vol%)	18.8±2.4	18.6±1.8	0.99
$C_{\bar{v}O_2}$ (Vol%)	12.9±3.5	4.8±0.9	0.37
P_{aO_2} (mmHg)	111±9	106±10	0.96
$P_{\bar{v}O_2}$ (mmHg)	60±11	35±5	0.58
P_{aCO_2} (mmHg)	36.2±2.5	27.2±2.0*	0.75
$P_{\bar{v}CO_2}$ (mmHg)	43.3±2.8	45.8±3.6*	1.06
pHa	7.473±0.030	7.522±0.046*	–
pH$\bar{v}$	7.429±0.030	7.380±0.055*	–
E_B (%)	31±15	74±3	2.4
Hct$_a$ (%)	53±8	51±4	0.96
Hct$_{\bar{v}}$ (%)	54±9	51±4	0.94

R, resting; F, flight.

Values are means ± S.E.M.

*Six samples were used to calculate the means ± S.E.M.

to analysis proved to be the most effective method of preserving the oxygen tension of blood samples (Table 1).

Although not measured, we would expect similar drifts in the carbon dioxide tension and pH values of whole blood samples using the methods of collection and storage described here.

In summary, these preliminary tests indicated that under the sampling and temporary storage conditions used in this study, the influences of cannula extension line permeability and whole blood metabolism prior to analysis on the blood gas tensions and pH of analyzed samples was negligible. Accordingly, no attempt was made to correct the final measured values for these influences.

Resting and flight cardiorespiratory data

Resting and flight data are presented in Tables 2, 3 and 4.

Adjustments of pigeons to flight

Our pigeons satisfied their 17.4-fold increase in $\dot{V}_{O_2}$ with a 7.4-fold increase in cardiac output ($\dot{Q}$) and a 2.4-fold increase in blood oxygen extraction (E_B). Cardiac output was increased primarily by an increase in the heart rate (f_H) (sixfold), and stroke volume (V_s) increased only modestly (Table 2). The similarity of the resting and flight P_{aO_2} and C_{aO_2} values indicates a close matching of respiratory adjustments and metabolic requirements (Table 3). The fall in P_{aCO_2} and the associated respiratory alkalosis that accompanied flight, however, indicate hyperventilation during flight (Table 3). These data suggest some exchange limitations for oxygen during flight that required the higher relative ventilation to maintain P_{aO_2}.

Discussion

Overview

As indicated previously, only one in depth cardiorespiratory study has heretofore been reported for an avian species undertaking steady flight (Butler et al., 1977). Whereas Butler's group also investigated the pigeon, both the resting conditions and the flight speed they utilized differed

substantially from those of the present study (see below). An in depth understanding of avian cardiorespiratory physiology is clearly central to advancing our knowledge of avian flight physiology and adaptation. Accordingly, we will begin our discussion by examining how closely the resting and flight data obtained from these two studies agree. In so doing, particular attention will be given to evaluating which data set for this 'bird model' most closely approximates the cardiorespiratory adjustments of a pigeon flying in nature.

Aside from these two studies, all other cardiorespiratory studies on flying birds have been of limited scope in the sense that they did not *directly* measure all of the Fick equation parameters needed to fully assess a given animal's cardiorespiratory performance (Bishop, 1997; Bishop and Butler, 1995). To circumvent this problem, various researchers have combined data from incomplete studies on different avian species flying at disparate flight conditions in order to derive allometric equations for estimating the various Fick equation parameters for a generalized bird (Bishop, 1997; Bishop and Butler, 1995). In the second part of our discussion, we will evaluate how accurately Bishop's allometric equations (Bishop, 1997) can estimate the cardiorespiratory parameters that we measured from our flying pigeons.

Because of their different evolutionary histories, birds and mammals use different cardiorespiratory designs and resources to satisfy their metabolic requirements. Nevertheless, the maximal aerobic capabilities ($\dot{V}_{O_2max}$) of flying birds and bats are essentially the same, but are about twice those of running mammals of similar size (Thomas, 1975). This is because flying vertebrates combine the $\dot{V}_{O_2max}$-enhancing influences of small body size (allometric variation) and an athletic lifestyle (adaptational variation), whereas similar-sized non-flying mammals (e.g. mice and rats) have consistently adapted 'non-athletic' lifestyles. Only after body size exceeds about 2 kg do examples of 'highly athletic' running mammals begin to appear. Finally in our discussion, we consider what Fick

Table 4. *Selected resting and flight metabolic, cardiovascular and cardiorespiratory values obtained from pigeons in the present study compared to those reported by Butler et al. (1977)*

Value	Present study		Butler		PS/B	
	R	F	R	F	R	F
$\dot{V}_{O_2}/M_b$ (ml kg^{-1} min^{-1})	17.8	309.6	25.5	200	0.70	1.55
$\dot{Q}/M_b$ (ml kg^{-1} min^{-1})	303	2244	555	2410	0.54	0.93
f_H (beats min^{-1})	110	663	171	670	0.64	0.99
V_S/M_b (ml kg^{-1})	2.75	3.38	3.24	3.60	0.85	0.94
Ca_{O_2} (Vol%)	18.8	18.6	15.1	13.7	1.24	1.36
$C\bar{v}_{O_2}$ (Vol%)	12.9	4.8	10.5	5.4	1.23	0.98
$Ca_{O_2}-C\bar{v}_{O_2}$ (Vol%)	5.9	13.8	4.6	8.3	1.28	1.66
Hct (%)	53	51	42	41	1.26	1.24
E_B (%)	31	74	30	61	1.26	1.21

R, resting; F, flight; PS, present study; B, Butler et al. (1977).

parameter adaptations and adjustments distinguish our exercising pigeons from those of running mammals of various sizes. Particular attention will be given to how the heart-mass-specific stroke volumes, cardiac outputs and cardiac work capabilities of our flying pigeons compare with those of exercising mammals of different body masses and aerobic capabilities.

Comparison of the current resting and flight data with previous studies

Resting data

Resting data from the present study ('PS') are compared in Table 4 with corresponding pigeon data reported by Butler et al. (1977) ('B'). As is readily apparent from the PS/B ratios, the resting $\dot{V}_{O_2}/M_b$, $\dot{Q}/M_b$, f_H and V_S/M_b values of our pigeons are substantially lower than those reported by Butler. One important reason for this discrepancy is the difference in 'resting' conditions that were used. While Butler's resting data were obtained from masked pigeons perched inside a wind tunnel, our data were collected from birds quietly resting in a darkened chamber to which they were previously familiarized. Consistent with this interpretation are the $\dot{V}_{O_2}/M_b$ and $\dot{Q}/M_b$ values reported by Grubb (1982) for pigeons resting at conditions similar to those of the present study. Grubb's values agree to within 3% and 12%, respectively with our values. A second probable reason for discrepancies in these PS/B ratios is that the $\dot{V}_{O_2}/M_b$ value used by Butler in his 1977 study to calculate resting $\dot{Q}/M_b$ and V_S/M_b came from his earlier study (Butler, 1970), which used resting conditions different from those in his later study. Finally, the different hematocrit values measured in these two studies are an important factor accounting for the observed Ca_{O_2} and $C\bar{v}_{O_2}$ discrepancies, as indicated by the similarity of the PS/B ratios for Hct, Ca_{O_2}, $C\bar{v}_{O_2}$ and $Ca_{O_2}-C\bar{v}_{O_2}$ (Table 4). The hematocrit value reported by Butler's group is substantially lower than the weighted mean value of 55.2% that we calculated from data reported for a total of 293 pigeons by five different groups of investigators (Gayathri and Hegde, 1994; Kalomenopolou and Koliakos, 1989; Viscor et al., 1985; Bond and Gilbert, 1958; Kaplan,

1954). In summary, differences in resting conditions used, methodologies concerning the source of the oxygen consumption value used in the Fick equation, and very different hematocrit values, appear to be primary factors contributing to the observed PS/B ratio discrepancies observed in these two studies (Tables 4 and 5).

Flight data

The flight $\dot{V}_{O_2}/M_b$ of our pigeons was about 1.6 times that of Butler's pigeons (Table 4). A reason for this difference could be the substantially different wind tunnel air speeds used in the current study (18.4 m s^{-1}) and Butler's study (10 m s^{-1}). Most birds, however, show little change in oxygen consumption over the range of air speeds at which they fly in a wind tunnel (Ellington, 1991). Grippler and Grivuni strains of pigeons show only a 10% change in $\dot{V}_{O_2}/M_b$ over a range of wind tunnel flight speeds from 8 to 14 m s^{-1} (Rothe et al., 1987). These investigators reported a $\dot{V}_{O_2}/M_b$ value of 310 ml (kg min)$^{-1}$ for their pigeons flying at 10 m s^{-1}, a value 1.6 times greater than Butler's value despite the same air speed, but essentially the same as that measured from our pigeons flying at 18 m s^{-1}.

Concerning flight speed, pigeons have been reported flying in nature at speeds of 16.1 m s^{-1} (LeFebvre, 1964), 18.3 m s^{-1} (Skutch, 1991), 19.1 m s^{-1} (Polus, 1985), and 19.7 m s^{-1} (Levy, 1986). Record-holding homing pigeons have achieved average flight speeds of 22 m s^{-1} during long distance races in calm air (Levy, 1986). Thus, the air speed used in the current study (18.4 m s^{-1}) is within the range of air speeds that pigeons normally fly at in nature. The highest speeds that unencumbered Grippler pigeons will fly at in a wind tunnel is 18 m s^{-1} (Rothe and Nachtigall, 1987). Our birds, however, were equipped with a mask and associated gas sampling tubes (metabolic determinations), or pressure transducers (heart rate determinations), or cannula extension lines (blood sampling), which contributed extra drag during these measurements. Based on determinations from other species of flying vertebrates (Thomas, 1975), we assume that the metabolic rates of our pigeons may have been about 10% to 15% higher than those expected during unencumbered flight at the same air

speed, but may approximate the metabolic requirements of unencumbered flight at the higher speeds that these bird sometimes achieve in nature (Levy, 1986).

There are reasons to believe that the flight $\dot{V}_{O_2}$ value reported in Table 2 for our pigeons is near the maximal value that these birds are capable of achieving in nature. The flight $\dot{V}_{O_2}$ of our birds is only 10% less than the highest specific $\dot{V}_{O_2}$ that Rothe et al. (1987) were able to measure from their somewhat smaller sized Grippler and Grivuni strains of pigeons during flight at their maximum encumbered speed ($14\ \mathrm{m\ s^{-1}}$). Also, most of our pigeons would only fly steady for a maximum period of about 10 min while carrying the various types of measuring and blood sampling equipment. Accordingly, we will hereafter assume that our homing pigeons were operating either very close to, or at their $\dot{V}_{O_2max}$ capability, and the flight cardiorespiratory data we obtained represent the maximal, or very near the maximal, values that these birds are capable of.

Flight f_H, V_S, Ca_{O_2}–$C\bar{v}_{O_2}$ and $\dot{Q}$

Despite the substantially higher flight $\dot{V}_{O_2}/M_b$ of our pigeons, the flight f_H, V_S/M_b and thus, the specific $\dot{Q}$ of our birds, are generally similar to those of Butler's birds (Table 4). This relationship appears to be primarily attributable to the higher hematocrits (Hct) of our birds, as previously discussed, that allow them to achieve a much higher Ca_{O_2} (Table 4). This, along with their somewhat lower $C\bar{v}_{O_2}$, allowed our pigeons to deliver 1.6 times more oxygen to their tissues per unit blood flow compared to Butler's pigeons (Table 4). Thus, our pigeons' higher Ca_{O_2}–$C\bar{v}_{O_2}$ value allowed them to satisfy their substantially higher flight $\dot{V}_{O_2}/M_b$ with approximately the same $\dot{Q}/M_b$ as Butler's pigeons.

Pigeon flight/rest ratio data

How do the factors by which our pigeons increase their resting cardiorespiratory parameters to accommodate the increased metabolic requirement of flight compare with those of Butler's pigeons? Flight/Rest (F/R) ratios for these two studies are summarized in Table 5. As expected from the foregoing relationships, each Fick parameter F/R ratio shown in Table 5 is higher for our birds than for those in Butler's study (Butler et al., 1977).

Table 5. *Comparison of selected flight/rest ratios obtained from the present study with those reported by Butler et al. (1977)*

Value	Present study	Butler	PS/B
$\dot{V}_{O_2}/M_b$ (ml kg^{-1} min^{-1})	17.4	7.84	2.22
$\dot{Q}/M_b$ (ml kg^{-1} min^{-1})	7.42	4.34	1.71
f_H (beats min^{-1})	6.03	3.92	1.54
V_S/M_b (ml kg^{-1})	1.23	1.11	1.11
Ca_{O_2}–$C\bar{v}_{O_2}$ (Vol%)	2.34	1.80	1.30
E_B (%)	2.38	2.03	1.17
Hct (%)	0.96	0.98	0.98

R, resting; F, flight; PS, present study; B, Butler et al. (1977).

Comparison of cardiorespiratory data obtained in the current study to those predicted from allometric equations

Allometric equations are a powerful tool for understanding fundamental relationships between the physiological capabilities and the morphological dispositions and design constraints of different animals (Taylor and Weibel, 1991). Bishop (1997) has recently published a very comprehensive allometric evaluation of the maximum cardiorespiratory capabilities of exercising birds and mammals. He concluded that avian heart muscle has the same biomechanical performance as that of a terrestrial animal. Accordingly, by making some simplifying assumptions about the magnitude of the Ca_{O_2}–$C\bar{v}_{O_2}$ term in the Fick equation, Bishop (1997) showed that heart mass (M_H) and $\dot{V}_{O_2max}$ data from mammals could be used to calculate reasonable estimates of a flying bird's $\dot{V}_{O_2max}$.

Bishop (1997) presented two different methods for predicting a flying bird's $\dot{V}_{O_2max}$. Method 1 takes a hierarchical approach, and has the reader use his allometric equations to estimate f_H from M_b (equation 3) and V_S from M_H (equation 6), if they are not known, and to estimate Ca_{O_2}–$C\bar{v}_{O_2}$ from blood hemoglobin concentration (Hgb). Bishop's Method 2 simply assumes that $\dot{Q}_{max}$ is a function of M_H and that there is no difference between birds and mammals during maximal cardiac performance. Thus, for both birds and mammals, Bishop's equation 10 (Bishop, 1997) is used to calculate $\dot{Q}_{max}$ from the animal's M_H, and Ca_{O_2}–$C\bar{v}_{O_2}$ is estimated from Hgb as in Method 1. How precisely do Bishop's Method 1 and Method 2 allometric equations (Bishop, 1997) estimate the cardiorespiratory parameters that we directly measured from our flying pigeons?

Heart rate (Method 1)

The flight f_H from our pigeons our pigeons is about 12% greater than the predicted value (Table 6, Row 1). This underestimation is expected, since Bishop's equation 3 is from an earlier study (equation 9 of Bishop and Butler, 1995), which summarized the minimum metabolic requirements of flying birds, and which included some low-quality (e.g. non steady-state, non $\dot{V}_{O_2max}$ avian f_H data. Bishop pointed out that the data he used to formulate equation 3 may not represent true maximal f_H values, but he assumed that hey were close to maximal values for the purpose of his analysis since better data were unavailable (Bishop, 1997). Some of this discrepancy may also reflect real inter-species differences in maximum heart rate, and that pigeons may be a species with a high maximum. Using Bishop's M_b exponent and adjusting its coefficient to be consistent with our data, yields the following relationship between M_b (kg) and maximum f_H (beats min^{-1}) for highly athletic birds like pigeons flying at $\dot{V}_{O_2max}$ conditions:

$$f_H = 545.7(M_b^{-0.187})\,. \tag{1}$$

Heart mass

Most of Bishop's allometric equations (Bishop, 1997) relate the cardiorespiratory parameter to heart mass, rather than to

Table 6. *Comparisons between pigeon flight cardiorespiratory data obtained in the present study and those predicted for a flying bird of same body mass by Bishop's allometric equations (Bishop, 1997)*

Row	Bishop equation no.	Parameter (units)	Predicted value (error)	Measured value (present study)	PS/Pred	Comments
1	3	f_H (beats min^{-1})	593 (–6.0%)*	663	1.12	Calculated from M_b
2	11	M_H (g)	3.66 (–18%)*	4.48	1.23	Calculated from M_b
3	6	V_S (ml beats^{-1})	1.45 (21.8%)*	1.19	0.82	Calculated from M_H using PS pigeon value (4.48 g)
4	None	Ca_{O_2}–$C\bar{v}_{O_2}$ (ml O_2 ml^{-1})	0.154	0.138	0.90	Estimated from mean avian [Hgb]
5	10	$\dot{Q}$ (ml min^{-1})	795 (0.4%)*	792	1.00	Calculated from M_H, using PS pigeon M_H value (4.48 g)
6	15	$\dot{V}_{O2max}$ (ml min^{-1})	123.5 (13.0%)*	109.3	0.88	Calculated from M_H using PS pigeon M_H (4.48 g)

PS, present study; Pred., predicted.

*Values are calculated error estimates for predicted values from Bishop's equations (Bishop, 1997).

body mass, so M_H is an important attribute to consider (Table 6). Bishop's equation 11, in turn, lets one calculate a mean population M_H of a bird from its M_b. The calculated M_H for our pigeons is more than 20% less than the measured value (Table 6, Row 2). Concerning our M_H value Magnan (1922), in his comprehensive study of birds, reported a mean pigeon M_H of 1.294% of M_b, which corresponds to a mean M_H of 4.57 g for the 0.353 kg flying pigeons we studied. This differs by only 2% from our measured M_H value (Table 6).

The large discrepancy between allometrically calculated and measured M_H for a bird like a homing pigeon is not surprising for the following reasons. Heart mass is importantly influenced by adaptive specialization. As Bishop's study (Bishop, 1997) clearly demonstrates, you need to know an animal's M_H before any reliable predictions can be made. Homing pigeons are clearly a 'highly athletic' species of bird since they can fly for over 10 h a day at very high speeds (Levy, 1986). Thus, homing pigeons share with other highly athletic birds (e.g. humming birds, swifts, starlings and wild ducks) disproportionately large specific heart masses (Hartman, 1961; Magnan, 1922). In formulating equation 11, Bishop used data from Magnan's comprehensive study (Magnan, 1922) that included both athletic and substantially less athletic species of birds. Accordingly, his equation tends to underestimate the M_H of highly athletic avian species. Using the same M_b exponent that Bishop used in his equation 11, and adjusting its coefficient to fit our data, yields the following relationship between M_b (kg) and M_H for our pigeons (and perhaps other highly athletic birds):

$$M_H = 11.80(M_b^{0.93}) . \tag{2}$$

Stroke volume

Bishop's equation 6 (Bishop, 1997) predicts a flying bird's maximal V_S from M_H. Substituting our pigeon's mean measured M_H into this equation yields a predicted V_S that is almost 20% higher than our measured value (Table 6, Row 3). What are the reasons for this discrepancy? Bishop's equation 6 (Bishop, 1997) also comes directly from an earlier study (Bishop and Butler, 1995) that used V_S data for pigeons flying *at minimum power speed* (Bishop et al., 1977) to estimate the

coefficient of this equation. As was discussed previously, even though the flight $\dot{V}_{O_2}$ of Butler's pigeons was only about two-thirds that of our birds, their Fick-calculated V_S value was about 6% higher than our value because of their low Ca_{O_2} value, which in turn, resulted from the abnormally low Hct values in their birds (Table 4). Accordingly, only part of the observed 20% discrepancy is explained by the V_S value that Bishop and Butler used to determine their equation's coefficient.

Because Butler et al. (1977) did not measure the M_H of their pigeons, Bishop and Butler (1995) assumed their M_H was 1.1% of M_b, as reported by Grubb (1982). This value is lower than the 1.23% we measured from our birds. Accordingly, the lower M_H that Bishop and Butler (1995) used to formulate the coefficient of their flight V_S equation resulted in a higher coefficient magnitude, which results in an overestimation of V_S when our (higher) measured pigeon M_H value is substituted into Bishop's equation 6. In summary, the higher V_S value and the lower M_H value that Bishop and Butler (1995) used to formulate their avian flight V_S equation both contribute to its overestimation of our pigeons flight V_S value (Table 6, Row 3). Based on our data, a more appropriate form of Bishop's equation 6 that relates maximum flight V_S (ml beat^{-1}) to M_H (g) is:

$$V_S = 0.25(M_H^{1.05}) . \tag{3}$$

Arterio–venous oxygen content difference (Method 1 and Method 2)

In the absence of actual flight Ca_{O_2}–$C\bar{v}_{O_2}$ measurements (remembering that only pigeon values are currently available), Bishop used blood hemoglobin concentration data ([Hgb]; g ml^{-1}) to estimate blood oxygen carrying capacity ([Hgb]×1.36 ml O_2 ml^{-1} blood). When [Hgb] data were unavailable, Bishop assumed the mean value of 0.1513 g ml^{-1} reported by Prinzinger and Miscovic (1994) from a comprehensive survey of birds. Bishop then estimated Ca_{O_2} by assuming that the arterial blood of a bird flying at $\dot{V}_{O_2max}$ conditions was 94% saturated with oxygen, which is the mean value reported for seven species of mammals (mostly of large body size) running at $\dot{V}_{O_2max}$ conditions (Bishop, 1997). Bishop

estimated the flying bird's $C\bar{v}_{O_2}$ by assuming a value of 0.038 ml O_2 ml^{-1}, which again is the mean value for seven species of mammals running at $\dot{V}_{O_2max}$ conditions. These assumptions are embedded in the two methods Bishop used for estimating the $\dot{V}_{O_2max}$ of a flying bird. How closely do these largely mammalian-based assumptions and the resulting Ca_{O_2}–$C\bar{v}_{O_2}$ estimates correspond to those measured from our homing pigeons flying at what we assume are $\dot{V}_{O_2max}$ conditions?

While we did not measure [Hgb] for our birds, McGrath (1971) reported a mean blood hemoglobin of 15.6 g% for his pigeons whose mean Hct was similar to our value (i.e. 52.6% *vs* 51% in our study). Proportional scaling and units conversion indicates a [Hgb] of 0.151 g ml^{-1} for our birds, which is in excellent agreement with the default avian [Hgb] that Bishop assumes in his equations (see above). According to Bishop's assumptions, this [Hgb] would translate to an estimated flight Ca_{O_2} of 0.193 ml O_2 ml^{-1} for our pigeons, which is only slightly higher than our measured value of 0.188 ml O_2 ml^{-1} (Table 3). Finally, our finding that the Ca_{O_2} values of our resting and flying pigeons are almost the same (Table 3) indicates that arterial blood saturation does not fall as these birds go from quiet rest to heavy exercise.

Based on Bishop's assumptions, our pigeons should be capable of an estimated flight $C\bar{v}_{O_2}$ of 0.038 ml O_2 ml^{-1}; a value about 20% lower than the measured value (Table 3). Again, it is not known whether this difference reflects the possibility that our pigeons were not flying at $\dot{V}_{O_2max}$ conditions (as we have assumed) or the possibility that flying birds, for thermoregulatory or other reasons, may be incapable of achieving $C\bar{v}_{O_2}$ values as low as highly athletic exercising larger-size mammals. In summary, the predicted Ca_{O_2}–$C\bar{v}_{O_2}$ measured from our pigeons flying at $\dot{V}_{O_2max}$ is about 10% lower than the calculated value (Table 6, Row 4).

Cardiac output (Method 1 and Method 2)

Method 1: Our measured $\dot{Q}$ is 18% lower than the value predicted by multiplying our measured f_H by the V_S value estimated from Bishop's equation 6 (Bishop, 1997; i.e. Method

1, see Table 6, Row 5). Surprisingly, our measured $\dot{Q}$ is more accurately predicted by multiplying the f_H value estimated from Bishop's equation 3 by the V_S value estimated from his equation 6. In the latter case, our measured $\dot{Q}$ is only about 8% lower than the predicted value. These overestimates of $\dot{Q}$ are primarily attributable to the previously discussed fact that Bishop's equation 6 (Bishop, 1997) overestimates the V_S of our pigeons (Table 6, Row 3).

Method 2: Bishop's Method 2 (equation 10; Bishop, 1997), however, very precisely predicts the flight $\dot{Q}$ of our pigeons (Table 6, Row 5). Accordingly, our $\dot{Q}$ data provide strong support for Bishop's assumption that $\dot{Q}_{max}$ is simply a function of M_H (Bishop, 1997).

Maximum rate of oxygen consumption (Method 1 and Method 2)

How accurately do Bishop's two methods (Bishop, 1997) estimate the mean $\dot{V}_{O_2max}$ value we determined for our flying pigeons? Our measured $\dot{V}_{O_2max}$ value is about 18% less than the value predicted by Bishop's Method 1 when our M_H value was used to estimate V_S, and all other variables were estimated by Method 1 procedures. Our measured $\dot{V}_{O_2max}$ value is only about 11% less than that predicted by Bishop's Method 2, however (Table 6, Row 6). This level of agreement is quite good considering all the variables that can influence $\dot{V}_{O_2max}$. This discrepancy might reflect an inaccuracy in our assumption that our pigeons were flying at $\dot{V}_{O_2max}$ conditions, or inaccuracies in one or more of the previously discussed assumptions or relationships that Bishop used to formulate his equation 10. These relationships support Bishop's (Bishop, 1997) suggestion that his Method 2 is the preferred way to estimate a flying bird's $\dot{V}_{O_2max}$.

Relations between cardiorespiratory parameters measured in the current study and those predicted by allometric equations for running mammals

How do the cardiorespiratory parameters of our flying pigeons compare with those predicted by Bishop's allometric

Table 7. *Comparison between flight cardiorespiratory data obtained in the present study and those predicted for a running mammal of the same body mass by Bishop's allometric equations (Bishop, 1997)*

Row	Bishop equation no.	Parameter (units)	Predicted value	Measured value (present study)	PS/Pred	Comments
1	4	f_H (beats min^{-1})	565 (–14.8%)*	663	1.17	Calculated from M_b
2	12	M_H (g)	2.52 (–43.8%)*	4.48	1.78	Calculated from M_b
3	8	V_S (ml $beats^{-1}$)	0.96 (–19.3%)*	1.19	1.24	Calculated using eq. 12, predicted mammalian M_H, value 2.52 g
4	4	Ca_{O_2}–$C\bar{v}_{O_2}$ (ml O_2 ml^{-1})	0.154	0.138	0.90	Estimated from mean mammalian [Hgb], see text
5	10	$\dot{Q}$ (ml min^{-1})	478.7 (–39.6%)*	792.1	1.65	Calculated using eq. 12, predicted mammalian M_H, value 2.52 g
6	15	$\dot{V}_{O_2max}$ (ml min^{-1})	74.5 (–31.9%)	109.4	1.47	Calculated using eq. 12, predicted mammalian M_H, value 2.52 g

PS, present study; Pred., predicted.

*Values are calculated error estimates for predicted values from Bishop's equations (Bishop, 1997).

equations for a mammal of this size running at $\dot{V}_{O2max}$ conditions (Bishop, 1997)? These relationships are summarized in Table 7 and the findings are reported below.

Fick parameters

The $\dot{V}_{O2max}$ of our pigeons was about 1.5× that predicted for an athletic running mammal of the same size (Table 7, Row 6). Of course, very few (if any) running mammals of this size are athletic, so this $\dot{V}_{O2max}$ differential is usually significantly greater when a typical small running mammal is compared to our pigeons. For example, the mass-specific $\dot{V}_{O2max}$ of our pigeons is more than 3× greater than that of a trained running rat (Gleeson et al., 1983).

The higher (1.5-fold) $\dot{V}_{O2max}$ of our pigeons is associated with a disproportionately larger (1.8-fold) heart mass, and $\dot{Q}$ (1.7-fold) compared to values predicted for an athletic running mammal of this size (Table 7, Row 5). The higher $\dot{Q}$ of our pigeons results from its ability to achieve f_H and V_s values that are both about 20% higher than those expected for a running mammal of the same size (Table 7, Rows 1 and 3). The fact that the ratio of 'present study/predicted' for M_H and $\dot{Q}$ in Table 7 are generally similar supports Bishop's assumption that M_H is a valid indicator of an animal's maximum $\dot{Q}$ capability (Bishop, 1997).

In summary, the superior blood oxygen convection capabilities of our pigeons over running mammals of equivalent size are primarily attributable to their ability to achieve higher heart rates and greater stroke volumes simultaneously from their larger size hearts.

Heart mass-specific cardiorespiratory performances of flying pigeons and exercising mammals

As stated previously, a primary underlying assumption of Bishop's comprehensive analysis was that avian heart muscle has the same maximal physiological performance capability as mammalian heart muscle (Bishop, 1997). In this final part of our discussion, we will examine how closely the heart mass-specific cardiac performances of our flying pigeons correspond to those reported for certain non-athletic and highly athletic mammals exercising at or near $\dot{V}_{O2max}$ conditions.

It has been known for some time that high M_b-specific heart mass (M_H/M_b) distinguishes highly athletic animals from their less athletic counterparts. The 4.6-fold M_H/M_b difference between the pigeon and the exercise-trained rat is particularly striking (Table 8), and reflects the fact that the body mass-specific $\dot{V}_{O2max}$ of our pigeons is more than three times greater than that of a rat (Gleeson et al., 1983). Although M_H/M_b is generally similar in highly athletic mammals of very different body sizes, our pigeons' value is the highest of any of the animals shown in Table 8.

The relatively high flight f_H of our pigeons compared to a flying bird or a running mammal of the same size has been discussed previously (Tables 6 and 7). The latter relationship is further supported by the fact that our pigeon's flight f_H exceeds the running rat's maximum value despite the latter's substantially smaller body mass (Table 8).

Data summarized in Table 8 show no consistent relationship between athletic ability or body size and M_H-specific V_s (V_s/M_H). Since available data indicate that running mammals and flying birds have similar mean systemic arterial blood pressures (Bishop, 1997), the data in Table 8 suggest that the maximum M_H-specific stroke work capability of our pigeons is somewhat less than that of a running rat. Perhaps this is a trade-off that pigeons have had to accept in gaining the advantages of having a relatively large size heart that can achieve a relatively high f_H.

Due in part to the inverse relationship between maximum f_H and body mass, M_H-specific $\dot{Q}$ ($\dot{Q}/M_H$) decreases with increasing body mass (Table 8). Accordingly, the most valid

Table 8. *Comparison of the body mass specific heart masses and the specific stroke volumes and cardiac outputs of different athletic and non-athletic birds and mammals*

Animal	Body mass (kg)	M_H/M_b (g kg^{-1})	f_H (beats min^{-1})	V_s/M_H ml (beats g)$^{-1}$	$\dot{Q}/M_H$ ml (min g)$^{-1}$	Comments/Source
Non-athletic animals						
White rat	0.278	2.77	613	0.35	214.4	Gleeson et al., 1983
Goat	30	3.87	266	0.54	143.8	Karas et al., 1987
Steer	474	4.13	216	0.35	73.0	Jones et al., 1989; H. Hoppeler (personal communication)
Athletic animals						
Flying vertebrates						
Bat (*P. hastatus*)	0.101	9.41	779	0.28[i]	221.8[i]	Thomas et al., 1984
Bat (*P. poliocephalus*)	0.669	8.00	476	0.34[i]	162.7[i]	Carpenter, 1985
Homing pigeon	0.353	12.69	663	0.27	176.7	Present study
Running mammals						
Dog	28.8	7.12	271	0.45	121.9	Karas et al., 1987
Standard bred racehorse	453	7.78	202	0.40	80.7	Jones et al., 1989; H. Hoppeler (personal communication)

[i]$Ca_{O_2}–C\bar{v}_{O_2}$ value used to calculate V_s and V_b was estimated from blood oxygen capacity or hemoglobin concentration per Bishop (1997).

$\dot{Q}/M_H$ comparisons are between animals of generally similar body mass. There is reasonably close correspondence between the pigeon's $\dot{Q}/M_H$ value and that reported for the running rat or estimated for two species of flying bats (Table 8). Since flying birds and running mammals have similar mean systemic arterial blood pressures (Bishop, 1997), the M_H-specific cardiac work rate capabilities (W_H/M_H) of birds and smaller size mammals also appear to be generally similar. In summary, $\dot{Q}/M_H$ data from our pigeons provide additional direct support for one of Bishop's central assumptions, that avian heart muscle has the same maximal physiological and biomechanical performance as that from terrestrial mammals. Particularly impressive to us is the ability of 1 g of pigeon myocardium to achieve a $\dot{Q}/M_H$ value that approaches that of a running rat, even though this bird is operating at a $\dot{Q}/M_b$ level during flight that is about four times greater than that of the running rat. The physiological mechanisms that enable homing pigeons to achieve such a high level of cardiovascular performance are still not completely understood. Some important contributing factors, however, may be the robust plasma catecholamine response that accompanies pigeon flight (Liang and Thomas, 1994), and the possibility that flying pigeons maintain advantageous phase relationships between their cardiac and pectoral muscle (wing-beat) cycles (Thomas et al., 1996).

List of symbols

a	arterial blood
Ca_{O_2}, $C\bar{v}_{O_2}$	total oxygen content
E_B	blood oxygen extraction
f_H	heart rate
Hct	hematocrit
M_b	body mass
M_H	heart mass
Pa_{CO_2}, $P\bar{v}_{CO_2}$	carbon dioxide tension
Pa_{O_2}, $P\bar{v}_{O_2}$	oxygen tension
pHa, pH$\bar{v}$	pH
$\dot{Q}$	cardiac output
$\bar{v}$	mixed venous blood
$\dot{V}_{O_2}$	rate of oxygen consumption
V_S	stroke volume

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