Metabolic power, mechanical power and efficiency during wind tunnel flight by the European starling *Sturnus vulgaris*

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Summary

We trained two starlings (*Sturnus vulgaris*) to fly in a wind tunnel whilst wearing respirometry masks. We measured the metabolic power (P_{met}) from the rates of oxygen consumption and carbon dioxide production and calculated the mechanical power (P_{mech}) from two aerodynamic models using wingbeat kinematics measured by high-speed cinematography. P_{met} increased from 10.4 to 14.9 W as flight speed was increased from 6.3 to 14.4 m s^{-1} and was compatible with the U-shaped power/speed curve predicted by the aerodynamic models. Flight muscle efficiency varied between 0.13 and 0.23 depending upon the bird, the flight speed and the aerodynamic model used to calculate P_{mech}. P_{met} during flight is often estimated by extrapolation from the mechanical power predicted by aerodynamic models by dividing P_{mech} by a flight muscle efficiency of 0.23 and adding the costs of basal metabolism, circulation and respiration. This method would underestimate measured P_{met} by 15–25 % in our birds. The mean discrepancy between measured and predicted P_{met} could be reduced to 0.1±1.5 % if flight muscle efficiency was altered to a value of 0.18. A flight muscle efficiency of 0.18 rather than 0.23 should be used to calculate the flight costs of birds in the size range of starlings (approximately 0.1 kg) if P_{met} is calculated from P_{mech} derived from aerodynamic models.

Key words: flight, mechanical power, metabolic power, bird, efficiency, oxygen consumption, starling, *Sturnus vulgaris*.

Introduction

Flapping flight is among the most energetically expensive activities that vertebrates perform (Schmidt-Nielsen, 1972; Norberg, 1990). Quantifying the metabolic cost of flight is therefore important in a variety of biological problems. Examples include the estimation of avian daily energy demands (Weathers et al., 1984; Bryant, 1997), reconstruction of the evolution of flight (Norberg, 1990; Rayner, 1991; Ruben, 1991; Speakman, 1993), estimation of the potential flight ranges of migratory birds (e.g. Rayner, 1990; Walsberg; 1990, Carmi et al., 1992; Klaassen, 1995; Klaassen, 1996; Butler et al., 1997; Weber et al., 1994; Weber et al., 1998; Pennycuick, 1998) and calculation of optimum flight speeds (e.g. Lindström and Alerstam, 1992; Hedenström and Alerstam, 1995; Hedenström and Alerstam, 1997) or migratory strategies (e.g. Weber et al., 1994; Weber et al., 1998).

It is technically difficult to make direct measurements of metabolic power (P_{met}) using methods such as the doubly labelled water technique during free flight (for a review, see Masman and Klaassen, 1987) or mask respirometry during wind tunnel flight (for a review, see Butler and Woakes, 1990) or from cardiac output (for reviews, see Bishop and Butler, 1995; Bishop, 1997). A more rapid alternative way to estimate total power consumption during flight is to use a theoretical aerodynamic model to calculate the mechanical component of power output during flight (P_{mech}) and to obtain an estimate of P_{met} from this by:

$$P_{met} = 1.1[(P_{mech}/E_{FM}) + P_{BMR}], \qquad (1)$$

where flight muscle efficiency (E_{FM}) is defined as P_{mech}/metabolic power consumed by the flight muscles and P_{BMR} is basal metabolism (Tucker, 1973; Pennycuick, 1975; Pennycuick, 1989; Norberg, 1990). Predictions of P_{met} made using equation 1 may be in error since they rely on four assumptions: (i) that aerodynamic models predict P_{mech} accurately, (ii) that E_{FM} is fixed (usually at a value of 0.23; e.g. Pennycuick, 1975), (iii) that P_{BMR} is constant, and meaningful, during flight, and (iv) that the extra costs of respiration and circulation during flight each contribute 5 % to P_{met}. Assumptions iii and iv have not been tested since it is not currently possible to partition metabolic rate either experimentally or theoretically, but predicted P_{met} is relatively insensitive to deviations in assumed P_{BMR} or the combined

cost of respiration and circulation. Predicted P_{met} is more sensitive to errors in P_{mech}: a change of 1 % in P_{mech} will alter P_{met} by 0.9 %. Predicted P_{met} is most sensitive to the value of E_{FM}: a change of 0.01 in the assumed E_{FM} will change predicted P_{met} by 4–5 %. Predictions of P_{met} obtained from equation 1 are sensitive to the value of E_{FM} used because P_{mech} represents only a small proportion of flight muscle metabolic rate (Rayner and Ward, 1999; Rayner, 1999). This means that a small change in P_{mech} will correspond to a large change in P_{met} because most of the the metabolic power supplied to the flight muscles is transformed to heat as a by-product of the conversion of chemical to kinetic energy (Hill, 1938).

The value of E_{FM} is normally assumed to be 0.23 (Pennycuick, 1975), although sometimes a different constant value in the range 0.20–0.25 is used (Norberg, 1990). These values of E_{FM} have not been measured directly; instead, the value 0.23 is the value taken from typical values for vertebrate muscle *in vitro* and lies approximately in the middle of the range of partial efficiency (E_P, defined as the change in P_{mech} for potential energy/change in P_{met}) of animals in ascending or descending flight in wind tunnels (budgerigar *Melopsittacus undulatus*, mass 0.035 kg, E_P 0.19–0.28; laughing gull *Larus atricilla*, mass 0.30 kg, E_P 0.30, Tucker, 1972; fish crow *Corvus ossifragus*, mass 0.275 kg, E_P 0.20–0.29, Bernstein et al., 1973; white-necked raven *Corvus cryptoleucos*, mass 0.48 kg, E_P 0.32–0.40, Hudson and Bernstein, 1983; 0.13–0.40 for two species of bat *Phyllostomus hastatus*, mass 0.093 kg, and *Pteropus gouldii*, mass 0.78 kg, Thomas, 1975). There are two problems with the assumption that E_{FM}=0.23 on the basis of the data from these studies. First, wingbeat kinematics, and therefore drag, alter to compensate for the change in thrust required to fly up- or downhill (Rayner, 1986), so E_{FM} may differ from E_P. Second, the wide range in values of E_P suggests that it may be invalid to assume that efficiency is constant across species, individuals and flight speeds.

Efficiency is much lower than 0.23 when calculated from simultaneous estimates of P_{mech} and P_{met}: 0.11 during forward flight and 0.15 during hovering in the 0.0117 kg nectar-feeding bat *Glossophaga soricina* (Norberg et al., 1993) and 0.10 and 0.11–0.13, respectively, for ruby-throated hummingbirds *Archilochus colubris* (mass 0.0035 kg) hovering in heliox (Chai and Dudley, 1995) and in air (Chai et al., 1998). Currently, the major limitation in applying equation 1 to bird flight performance is that the assumption that a fixed value of 0.23 for E_{FM} is appropriate for all birds is unreliable.

If E_{FM} is invariant with flight speed, P_{met} should approximate a fixed multiple of P_{mech} as a function of speed (since P_{BMR} is relatively small). Aerodynamic models predict that P_{mech} will have a U-shaped relationship with flight speed (Tucker, 1973; Pennycuick, 1975; Pennycuick, 1989; Rayner, 1979; Rayner, 1999). In contrast to this prediction, P_{met} often has a much flatter relationship with flight speed in most birds and bats during wind tunnel flight (for a review, see Rayner, 1994). Measurements of mechanical power production by the M. pectoralis muscle in magpies also suggest a flat power/speed relationship over most forward flight speeds (Dial

et al., 1997). These measurements are from the largest muscles used during flight, so they include the majority of P_{mech}, although the data do not necessarily reflect the trend in P_{mech} across flight speeds for the entire animal. The measured values of M. pectoralis power production in magpies do not differ significantly from predicted P_{mech} (Rayner, 1999). The discrepancy between P_{met} predicted by equation 1 and that measured by respirometry during wind tunnel flight may be caused by variation in E_{FM} with flight speed. Alternatively, P_{mech} produced by the flying animal may differ from that predicted by aerodynamic theory either because of changes in wingbeat kinematics due to carrying the respirometry mask or because of variation in kinematics across individuals and flight speeds that is not accounted for in some aerodynamic models.

We measured P_{met} by mask respirometry and wingbeat kinematics by high-speed cinematography of European starlings *Sturnus vulgaris* (hereafter referred to as starlings) during wind tunnel flight across a range of flight speeds to assess whether flight costs form a U-shaped curve relative to flight speed. We calculated P_{mech} from two aerodynamic models, a relatively simple model developed from fixed-wing aerodynamic theory (Pennycuick, 1989) and a more complex one based on the generation of vortex rings (Rayner, 1979), which corresponds to the observed flight pattern and wake vortex geometry of starlings (Rayner and Swaddle, 2000). Flight muscle efficiency was calculated from P_{met} and P_{mech} by rearranging equation 1. We subsequently assessed how much P_{met} would differ from our measurements if it were predicted from P_{mech} determined by aerodynamic modelling assuming an efficiency of 0.23.

Materials and methods

Wind tunnel

Starlings *Sturnus vulgaris* were flown in a closed-section Göttingen-type variable-speed wind tunnel at the University of the Saarland, Saarbrücken, Germany (Biesel et al., 1985; Nachtigall, 1997). Birds were prevented from leaving the 1 m×1 m×1 m flight chamber upwind by wire mesh (25 mm hexagonal, 1 mm diameter) and downwind by vertical plastic chords (1 mm diameter, 1 cm apart). The top and one side wall of the flight chamber were made of glass to allow filming of lateral and dorsal images. The floor and walls of the chamber and the tunnel sections immediately up- and downwind of the flight chamber were made of wood. Air speed was monitored downwind of the flight chamber with a pitot-static tube connected to a manometer. Air speed in this position was linearly related to that in the centre of the flight chamber. Air speed could be controlled to within ±0.2 m s^{-1} and was measured to ±0.1 m s^{-1}. Turbulence (where turbulence= 100×standard deviation of air speed/mean air speed at each point) was measured using a DISA hot-wire anemometer at 11 points (in the centre of the flight chamber, half-way between the centre and each corner and at the mid points between the centre and the floor and ceiling). Mean turbulence at air speeds between 6 and 14 m s^{-1} was 1.80–1.95 % (S.D. 0.5–0.6) and did

not vary consistently with flight speed. Air speed measured at 32 points at 10 cm intervals horizontally and vertically from the centre of the flight chamber varied by less than 4 % from that measured in the centre of the flight chamber. Air temperature within the flight chamber averaged 18.5±0.2 °C. Air humidity was 63.0 ±0.7 %. Air density was 1.18 ±0.002 kg m^{-3}.

Birds and training

Starlings (seven hand-reared and eight wild-caught adult birds captured under licence from Scottish Natural Heritage in Aberdeenshire, UK) were housed in groups of 3–4 birds in indoor cages (approximately 2 m×2 m×2 m) and fed *ad libitum* on a mixture of moistened puppy pellets (Eukanuba), poultry pellets and cage bird egg food supplemented with mealworms and cage bird vitamin and mineral supplement. The birds were accustomed to the wind tunnel by placing them individually in the flight chamber, where they preferred to stand on a perch rather than on the smooth floor of the chamber. Birds flew spontaneously when the perch was retracted into the floor of the chamber. The perch was returned after progressively longer periods of flight until the birds that were trained successfully (four wild-caught adult female birds) would fly continuously for up to 1 h twice daily. The birds normally flew in the top half of the flight chamber looking straight ahead, but they learnt that they could show when they were tired by consistently flying close to the place where the perch would emerge from the floor of the chamber and looking at the trainer. The perch was returned to allow the bird to rest during training sessions when it showed this behaviour.

Two of the birds learnt to fly wearing masks from which exhaled respiratory gases were extracted through a flexible tube. The starlings were accustomed to flight in the wind tunnel for 10 months before the data reported here were collected to minimise the effects of stress upon metabolic rate. Each bird was flown three times at approximately 1 m s^{-1} increments in flight speed within the range of speed that each bird would fly wearing the mask (6.3–13.2 m s^{-1} for bird 15, mass 0.080±0.0008 kg; 8.3–14.4 m s^{-1} for bird 19, mass 0.089±0.0002 kg). Although the starlings could fly in the wind tunnel for 1 h without the respirometry mask, they would only fly for 12–15 min whilst carrying the mask before they showed that they were ready to land. All masked flights from which data are reported were therefore of 12 min duration. The order of the speeds at which the birds were flown was assigned randomly.

Metabolic power

Expired gases were collected using masks (0.7 g) made of transparent acetate film which covered the entire head and bill of the bird. Air was extracted from the mask at 3.0±0.1 l min^{-1} through a polyurethane tube (internal diameter 1.6 mm, external diameter 2 mm) which led over the back of the bird to the top of the downwind end of the flight chamber. Birds supported 1.6 g of tubing when they flew in the centre of the flight chamber. Expired gases did not escape from the mask since gas exchange measurements did not decline when air flow through the mask was reduced to 1.5 l min^{-1}. All measurements involved 5 min of

perching prior to flight so that the effects of handling upon metabolic rate were not superimposed upon flight costs, 12 min of flight and a further 5 min of perching. Gas concentrations in the measuring system took 1 min to reach steady state after the mask had been placed on or removed from the bird and after flight had begun or ended because of mixing of expired gases within the tubing of the analysis system. Data collected in the first minute of flight were therefore excluded from analyses. Gas concentrations were measured by a paramagnetic oxygen analyser (Taylor Servomex OA180) and an infrared carbon dioxide analyser (Hartmann and Braun URAS MT). Data from the gas analysers was recorded using a BASIC program running on a BBC B+ computer. The rate of air extraction from the mask was measured with a wet test gas flow meter (Wrights DM3A, accuracy ±0.1 %). Gases from the mask were dried with silica gel before and after passing through the flow meter. The gas analysers were calibrated daily by zeroing with oxygen-free nitrogen gas and spanning the oxygen analyser with ambient air and the carbon dioxide analyser with a gas mixture of known carbon dioxide content (Messer Griesheim). The rate of oxygen consumption ($\dot{V}_{O_2}$) was calculated from equation 3b of Withers (Withers, 1977). $\dot{V}_{O_2}$ and the rate of carbon dioxide production ($\dot{V}_{CO_2}$) were used to calculate metabolic power (P_{met}, W) from:

$$P_{met} = 16.18\dot{V}_{O_2} + 5.02\dot{V}_{CO_2}, \qquad (2)$$

in which $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ are expressed in ml s^{-1} STPD (Romijin and Lokhorst, 1961).

Wingbeat kinematics

We used two Photo-Sonics series 2000-1PL 16 mm cameras (255 frames s^{-1}; 16 mm Agfa XTR 250/XTS 400 colour negative film) at near-perpendicular viewing angles to film simultaneous lateral and dorsal views of bird 15. The films were used to measure wing morphology and wingbeat kinematics by stereophotogrammetric resection (Möller, 1998) during the middle of one respirometry flight at approximately 1 m s^{-1} increments in flight speed during phases in which the bird flew steadily and maintained position within the wind tunnel. Wingbeat frequency was calculated by counting the number of frames required to complete between 34 and 71 complete wing beats. Wingbeat amplitude was calculated from projected dorso-ventral excursions of the wing tip over five consecutive wingbeats. Wingspan was measured from the maximum extension of the wings in the dorsal view during the downstroke. A lateral view of the entire flight by each bird was also recorded on Hi8 tape at 50 fields s^{-1} using a Sony VX1 video camera. The Hi8 video recordings were subsequently viewed to assess the position and stability of the bird during each 12 min flight.

Mechanical power

Two aerodynamic models, the vortex ring model (Rayner, 1979) and the lifting line/momentum jet (Pennycuick, 1989) model, were used to calculate P_{mech}. The lifting line model was chosen because computation is simple and it is used widely for calculating flight costs (e.g. Carmi et al., 1992; Speakman, 1993; Klaassen, 1995; Klaassen, 1996; Pennycuick, 1998;

Weber et al., 1998; Spaar et al., 1998). The vortex ring model more closely reflects the aerodynamics of lift production by the wings and explicitly incorporates values of wingbeat kinematics as they change with flight speed (or as a consequence of flying in a wind tunnel carrying a respirometry mask), while in Pennycuick's lifting line model these changes are implicit in the assumption of constant profile power. The mass of the respirometry mask and tube (3.2 g) were added to the bird mass, which was the average of bird mass measured at the beginning and end of each flight. The drag of the mask with 0.60 m of tube (the length of tube supported by the starlings when they flew in the centre of the flight chamber) was measured at 6, 8, 10, 12 and 14 m s^{-1} using a one-component strain gauge and a plastic model of a gliding starling moulded from coordinates determined by three-dimensional stereophotogrammetry (Butz et al., 1985; Gesser et al., 1998a; Gesser et al., 1998b). Mask and tube drag were added to estimated body parasite drag during calculation of P_{mech} by both models.

Body parasite drag in both models was estimated from the equations of Pennycuick (Pennycuick, 1975; Pennycuick, 1989). Equivalent flat plate area (A_{fp}, m^2) is:

$$A_{fp} = 2.85 \times 10^{-3} M^{2/3}, \qquad (3)$$

where M is body mass in kg. Parasite power (P_{par}) is then given as a function of flight speed (V, m s^{-1}) by:

$$P_{par} = \tfrac{1}{2}\rho A_{fp} V^3 \qquad (4)$$

(Pennycuick, 1975; Rayner, 1979), where ρ is air density (kg m^{-3}). Possible effects of tilting of the body on parasite drag were not included. The profile drag coefficient in the vortex ring model was 0.02 (Rayner, 1979); the profile drag factor X_1 in the lifting line model was 1.2 (Pennycuick, 1975; Pennycuick, 1989). Alternative models of body drag are considered in the Discussion.

Efficiency

We used our measurements of P_{met} and P_{mech} to calculate E_{FM} using equation 1, with basal metabolic rate P_{BMR} (=0.9 W) predicted allometrically from mean bird mass (Aschoff and Pohl, 1970). It might be more appropriate to express flight costs as a multiple of the resting component of metabolic rate during the active phase (1.2 W; Aschoff and Pohl, 1970) and to use this value for P_{BMR} in equation 1 for calculation of E_{FM} since data were collected during the active period. This would also require reassessment of the hypothesized 1.1 factor on mechanical flight power accounting for non-flight metabolism during flight. To be consistent with previous work, resting-phase P_{BMR} was used in equation 1, and P_{met} during flight was expressed relative to resting-phase P_{BMR}.

Statistical analyses

Data were analysed using Minitab version 12.22. Analyses of covariance (ANCOVA) were performed by GLM ANCOVA. Tukey *post-hoc* comparisons were used following analyses of covariance to assess the significance of differences between birds. The level of probability at which results were regarded as significant was $P=0.05$. Means are presented ±

s.e.m. unless stated otherwise. Most other calculations, including power calculations with the lifting line and vortex ring aerodynamic models, were performed in MS Excel97.

Results
Metabolic power

$\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$, and hence P_{met}, increased abruptly from the resting level at the start of flights and decreased at the end of flights (Fig. 1). $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$ and P_{met} declined during flight; P_{met} declined by 0.030±0.002 W min^{-1} (GLM ANCOVA, flight speed, $F_{1,1979}=1317.9$, $P<0.001$; time, $F_{1,1979}=355.9$, $P<0.001$; bird, $F_{1,1979}=110.3$, $P<0.001$). The respiratory exchange ratio (RE) averaged 0.84±0.01 ($N=45$) across all flights. RE declined during flights from 0.87±0.01 ($N=24$) for bird 15 and 0.91±0.01 ($N=21$) for bird 19 during the second minute of flight to 0.80±0.01 ($N=24$) for bird 15 and 0.79±0.01 ($N=21$) for bird 19 in the eleventh minute. RE varied primarily with time into flight, although RE was greater for bird 19 than for bird 15 and greater during faster flight (GLM ANCOVA, time, $F_{1,1979}=465.1$, $P<0.001$; flight speed, $F_{1,1979}=286.3$, $P<0.001$; bird, $F_{1,1979}=11.0$, $P=0.001$; Tukey *post-hoc* comparison, RE of bird 19 was 0.01 greater than that of bird 15 taking into account differences between flight speeds and time into flight).

P_{met} was greater for bird 19 (mean 12.7±0.2, $N=21$, range 11.1–14.9 W) than for bird 15 (mean 11.7±0.2, $N=24$, range 10.4–13.5 W). The difference in P_{met} between the birds was partly accounted for by the difference in range of flight speed, since P_{met} increased with flight speed (Fig. 2) and bird 19 flew within a faster range of flight speed (8–14 m s^{-1}) than bird 15 (6–13 m s^{-1}) (GLM ANCOVA of the effects of the factor bird and the co-variate flight speed upon P_{met}, flight speed, $F_{1,44}=47.0$, $P<0.001$; bird, $F_{1,44}=1.1$, $P=0.3$). Bird 19 was 10 g heavier than bird 15. The higher range of flight speed of bird 19 was consistent with the requirement of heavier animals to fly more quickly (see Pennycuick, 1989). Averaged across both birds, P_{met} was equivalent to 13.5±0.2 (range 11.5–16.5) times resting-phase P_{BMR}.

Variation in P_{met} across flight speeds (Fig. 2) was compatible with the U-shaped power/speed curve predicted by aerodynamic models (Pennycuick, 1975; Pennycuick, 1989; Rayner, 1979; Tucker, 1972; this study). Curves of the form $P=\alpha V^{-1}+\beta V^3+\gamma$, where V is flight speed (m s^{-1}) and P is power (W), were fitted to the data for each bird to illustrate the expected approximate power/speed relationship in which induced power is proportional to V^{-1}, parasite (and sometimes profile) power to V^3 and basal metabolic rate (and sometimes profile power) are constant. Coefficients α, β and γ for the fitted curves are given in the caption to Fig. 2; the curves differed between birds (ANCOVA of residuals, $F_{1,41}=12.67$, $P=0.001$). For bird 19, P_{met} increased at flight speeds both greater and less than an intermediate minimum power speed (V_{mp} 9.9 m s^{-1}, minimum P_{met} 12.0 W), although most of the data correspond to the right-hand portion of this curve. Bird 15 would not sustain slow flight for sufficiently long (at least
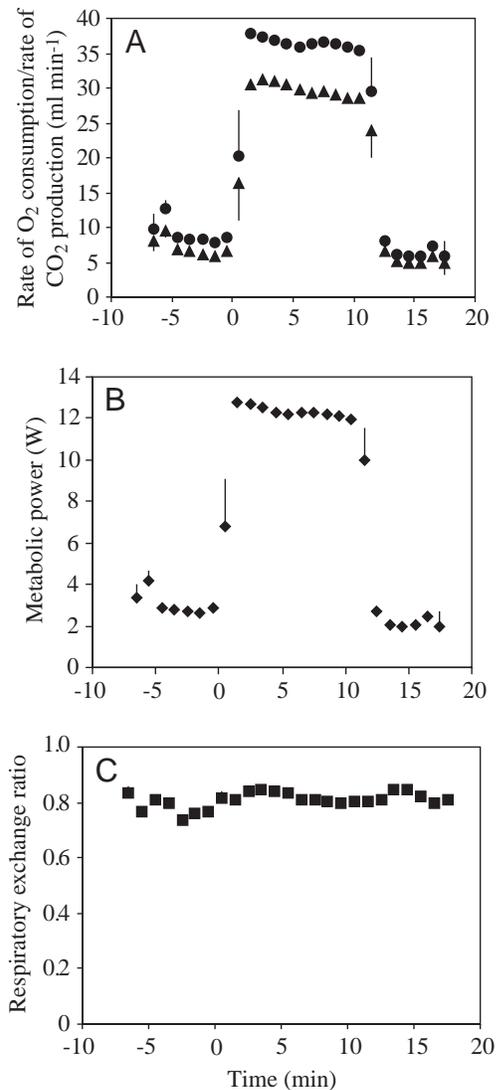
Fig. 1. Time course of (A) the rates of oxygen consumption ($\bullet$) and carbon dioxide production ($\blacktriangle$), (B) metabolic power and (C) respiratory exchange ratio during a wind tunnel flight by starling 15 at 13.3 m s^{-1}. Error bars show the standard error of four measurements made each minute (each of which was the mean value over 15 s). The printed symbols are larger than the error bars during most minutes. The bird flew for 12 min, starting at time 0. Metabolic rate increased when the bird was placed into the flight chamber immediately after the mask had been attached and when the bird was caught to remove the mask at the end of the measurement.
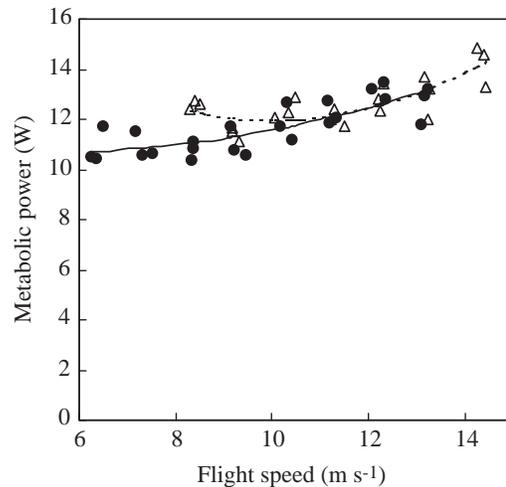

Fig. 2. Metabolic power (P_{met}) of two starlings during wind tunnel flight carrying a respirometry mask measured from the rates of oxygen consumption and carbon dioxide production [bird 15, $\bullet$, solid line $P_{met}=(2.03\pm12.6)V^{-1}+(0.0013\pm0.0005)V^3+(10.10\pm1.87)$; bird 19, $\triangle$, broken line $P_{met}=(59.0\pm27.7)V^{-1}+(0.0020\pm0.0006)V^3+(4.07\pm3.42)$] (means $\pm$ s.e.m., $N=24$ for bird 15 and 21 for bird 19), where V is flight speed.

1 min) for P_{met} to be measured at flight speeds as low as the V_{mp} of 4.8 m s^{-1} (minimum P_{met} 10.7 W) predicted from the fitted curve. The V_{mp} of bird 15 was unlikely to be as low as this prediction, and this technique does not estimate V_{mp} or the values of the coefficients with any accuracy. From visual inspection of Fig. 2, V_{mp} for bird 15 could lie within the range 6–9 m s^{-1}, but is lower than that for bird 19.

Wingbeat kinematics

The Hi8 video showed that birds alternated between steady flight, during which they remained relatively still in the upper third of the flight chamber, and undulating (flap-gliding) flight, during which they moved position within the flight chamber. We analysed wingbeat kinematics in steady flight using high-speed cinematography and used these to estimate mechanical power. Movements within the wind tunnel flight chamber in undulating flight were similar to those analysed in detail during unmasked flight by bird 19 (Rayner et al., 2001). The birds tended to flap upwards and forwards in the flight chamber, gaining speed, until they were close to the chamber roof. They then switched to gliding, with wings flexed, during which they decelerated and descended towards the rear of the flight chamber. The bird then began to flap to accelerate forwards, repeating the cycle. Each cycle during undulating flight involved 10–16 wingbeats interspersed with gliding or partial-bounding (Tobalske, 1995) and involved horizontal and vertical excursions of the flight path of 45–60 and 20–35 cm, respectively, depending on flight speed (Rayner et al., 2001). Flights were defined as steady when more than 16 wingbeats were performed without intermittent glides and without pauses between consecutive flaps during which the wings were flexed and in which the location of the bird's beak moved within the wind tunnel by less than ±2 cm in any direction at the same point in consecutive wing beats.

Across both birds, flight was steady for 58±6 % of the time during the sixth minute of each 12 min flight ($N=44$); however, bird 19 flew steadily more often (88±2 %, $N=21$) than bird 15 (33±7 %, $N=24$) (ANOVA, $F_{1,43}=46.6$, $P<0.001$). Bird 15 flew steadily more frequently during slow than fast flight, whilst bird 19 flew steadily most frequently during flight at intermediate speeds (Fig. 3). The proportion of steady flight did not influence P_{met} (GLM ANCOVA of the effects of flight speed and the arcsine-transformed proportion of the flight spent
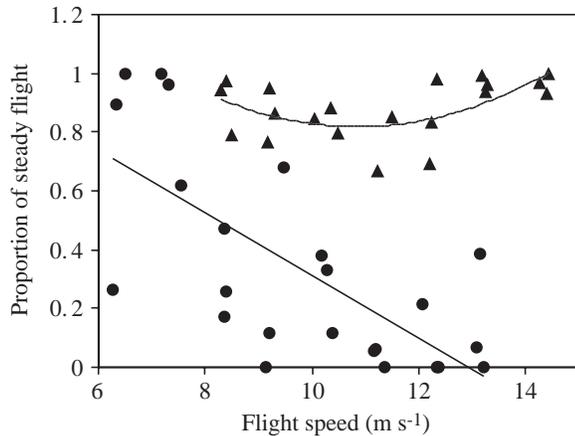
Fig. 3. The proportion of each wind tunnel flight during which two starlings flew with consistent flapping flight in a steady position in the flight chamber, rather than alternating flapping and gliding flight (bird 15, ●, bird 19, ▲). The lines show the back-transformed relationships between arcsine(proportion of time spent in steady flight) (p) and flight speed (V) for each bird: bird 15, arcsine$p$=(1.86±0.34)−(0.148±0.034)V, r^2=0.46, P<0.001; bird 19, arcsine$p$=(4.67±1.54)−(0.690±0.278)V+(0.032±0.012)V^2, r^2=0.39, P=0.015 (means ± S.E.M., N=24 for bird 15 and 21 for bird 19).

in steady flight, flight speed, $F_{1,43}$=60.4, P<0.001; proportion of steady flight, $F_{1,43}$=2.8, P=0.1).

Analysis of the high-speed ciné film taken during periods of steady flight showed that wingbeat frequency (10.2–11.4 Hz), wingbeat amplitude (43.5–65.6 °) and stroke plane angle (55.6–83.5 °) increased with flight speed, whilst the downstroke ratio (0.47–0.55) was lower during faster flights (Table 1). Wingspan (mean 0.36±0.01 m, N=8) did not vary consistently with flight speed. A more detailed analysis of wingbeat kinematics will be published elsewhere (U. Möller, D. Bilo, S. Ward, J. M. V. Rayner, J. R. Speakman and W. Nachtigall, in preparation).

Mechanical power

The drag on the model starling caused by the respirometry mask and tube increased with air speed (Fig. 4). Additional P_{mech} to carry the respirometry mask and tube was equivalent to 14–19 % of P_{mech} predicted by the lifting line model for unencumbered flight under the same conditions, and was made up of increased induced power (2–3 %), profile power (7–10 %) and power to overcome mask and tube drag (3–10 %). Predictions for drag increments with the vortex ring model were similar, but the birds adjusted their wingbeat kinematics to compensate compared with unmasked flight (Möller et al., 1997; Möller, 1998), so the increase in P_{mech} was not as great. Compensation for mask drag by alteration of wingbeat kinematics cannot be quantified with the lifting line model. No allowance was made for the possible effect of moments induced by the mass of the mask and tube or by the point of action of mask and tube drag.

Wingbeat kinematics (Table 1) were used in computation of P_{mech} by the vortex ring model for bird 15. P_{mech} was relatively

Table 1. *Wingbeat kinematics of bird 15 measured by high-speed cinematography during wind tunnel flight carrying a respirometry mask*

Flight speed (m s^{-1})	Frequency (Hz)	Wingbeat amplitude (degrees)	Downstroke ratio	Stroke plane angle (degrees)	Wingspan (m)
6.5	10.3	57.5	0.546	55.6	0.354
7.6	10.2	43.5	0.480	65.7	0.399
8.4	10.5	53.9	0.475	64.3	0.348
9.2	10.7	62.0	0.465	72.8	0.348
10.2	10.7	50.3	0.494	71.1	0.377
11.2	11.4	65.6	0.482	78.3	0.353
12.1	11.3	64.1	0.478	83.5	0.358
13.3	11.0	63.0	0.484	80.8	0.380

These values were used to predict vortex ring geometry to determine induced power from the vortex ring aerodynamic model (Rayner, 1979).

Wingspan is the maximum measured lateral projection of the wingtip-to-wingtip spacing during the mid downstroke.

Wingbeat amplitude is calculated from maximum upstroke and downstroke positions.

Downstroke ratio is the proportion of time for which the wings moved down.

Stroke plane angle is the angle between a line joining the maximum upstroke and downstroke positions, and the horizontal.
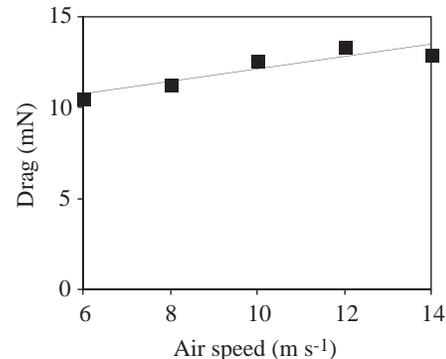

Fig. 4. Respirometry mask and tube drag (D, mN) in relation to air speed (U, m s^{-1}): D=(8.74±0.92)+(0.340±0.089)U (r^2=0.83 %, P=0.032, mean ± S.E.M., N=5). See text for details.

low at 7.6 and 10.2 m s^{-1} because measured wingspan was greater (0.39±0.02 m, mean ± S.D.) during these flights than during those at the other speeds (0.36±0.01 m, mean ± S.D.). P_{mech} varied between 1.2 and 2.6 W, rose more steeply with flight speed when calculated from the vortex ring model than from the lifting line model and was greater for faster flight and for the heavier bird (Fig. 5). The data in Fig. 5 do not show conventional power curves since air density, bird mass and wingbeat kinematics varied slightly between measurements.

Efficiency

Mean E_{FM} was 0.17±0.002 for bird 15 (range 0.15–0.20, N=24) and 0.19±0.004 (range 0.16–0.23, N=21) for bird 19
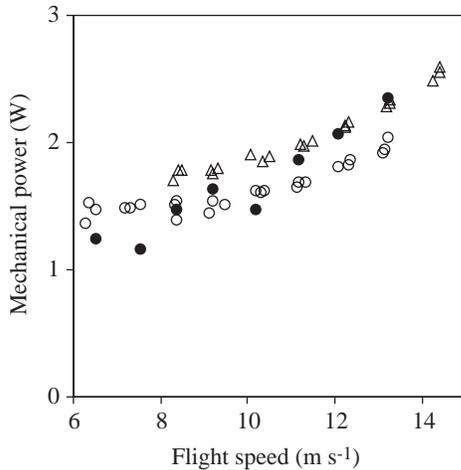
Fig. 5. Mechanical power (P_{mech}) for wind tunnel flight by two starlings carrying a respirometry mask, with P_{mech} estimated by two aerodynamic models (bird 15, vortex ring model ●; bird 15, lifting line model ○; bird 19, lifting line model △).
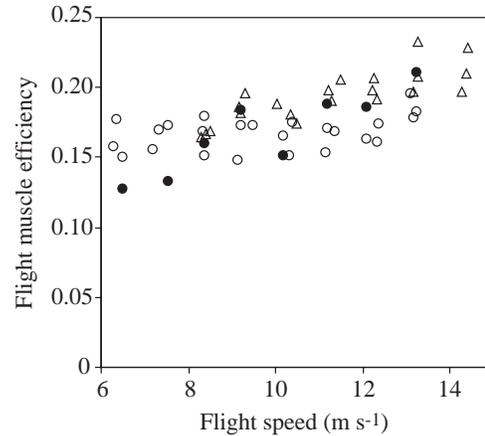

Fig. 6. Flight muscle efficiency (E_{FM}) of two starlings during wind tunnel flight (bird 15, P_{mech} estimated from the vortex ring model ●; bird 15, P_{mech} estimated from the lifting line model ○; bird 19, P_{mech} estimated from the lifting line model △), where P_{mech} is mechanical power.

when P_{mech} was calculated with the lifting line model (Fig. 6). Mean E_{FM} for bird 15 was 0.17±0.003 (range 0.13–0.21, N=8) when P_{mech} was calculated with the vortex ring model. GLM ANCOVA analysis of the influence of the factor aerodynamic model and co-variate flight speed upon E_{FM} of bird 15 showed a difference in gradients ($F_{1,31}$=25.7, P<0.001) and intercepts ($F_{1,31}$=23.8, P<0.001) of the relationship between E_{FM} and flight speed between the two aerodynamic models. E_{FM} increased more steeply with flight speed V for bird 15 if P_{mech} was calculated by the vortex ring model [regression E_{FM}=(0.012±0.002)V+(0.054±0.022), r^2=0.81, P<0.001, N=8] than if P_{mech} was calculated from the lifting line model (regression E_{FM} not related to flight speed, P=0.1, N=24). E_{FM} increased with flight speed for bird 19 when P_{mech} was calculated with the lifting line model [regression E_{FM}=(0.007±0.001)V+(0.112±0.015), r^2=0.64, P<0.001, N=24]. E_{FM} was greater for bird 19 than for bird 15 when P_{mech} was calculated with the lifting line model for both birds, and E_{FM} increased with flight speed for bird 19 whilst it did not for bird 15 [GLM ANCOVA analysis of gradients, $F_{1,44}$=10.8, P=0.002, intercepts, $F_{1,44}$=4.4, P=0.04; regression for bird 19, E_{FM}=(0.007±0.001)V+(0.112±0.015), r^2=0.64, P<0.001].

Predicted metabolic power

We predicted P_{met} from P_{mech} by using equation 1, assuming E_{FM}=0.23 and P_{BMR}=0.9 W (allometric prediction of resting-phase basal metabolic rate, BMR; Aschoff and Pohl, 1970) and compared the results with our measured P_{met}. This is a test of the values of P_{mech} calculated from mechanical models and the assumed values for E_{FM}, P_{BMR} and the costs of respiration and circulation from which P_{met} is typically estimated when direct measurements are not available (e.g. Pennycuick, 1975; Pennycuick, 1989). Predicted P_{met} was 2.9±0.4 W (24.7±4.1 %) lower than measured P_{met} for bird 15 if P_{mech} was calculated from the lifting line model and 2.9±0.1 W (24.8±1.0 %) lower if P_{mech} was predicted from the vortex ring

model (Fig. 7A). This showed that the increased detail from the measured wingbeat kinematics used to calculate P_{mech} from the vortex ring model did not improve the match between predicted and measured P_{met}. Predicted P_{met} was 1.8±0.2 W (14.5±1.6 %) lower than measured P_{met} for bird 19 when P_{mech} was calculated by the lifting line model (Fig. 7B).

Predicted P_{met} was substantially lower than measured P_{met} for both birds when it was predicted from equation 1 using the lifting line model and a constant value of E_{FM} of 0.23. This discrepancy could be due to too high an assumed value for E_{FM} or inaccurate predictions of P_{mech} from the aerodynamic models. We therefore also compared measured P_{met} with predicted P_{met} from P_{mech} calculated with the lifting line model and the mean E_{FM} determined for each bird (0.17 for bird 15 and 0.19 for bird 19) from equation 1. This tests whether reducing the assumed value of E_{FM} from 0.23 to a lower, constant value removes the discrepancy between measured P_{met} and predicted P_{met}. The difference between measured and predicted P_{met} was much less: 0.2±0.2 W (1.3±1.3 %) for bird 15 and 0.2±0.2 W (1.9±1.9 %) for bird 19, and was of the order of only one-tenth of the estimated mechanical power. The mean discrepancy between measured and predicted P_{met} was 0.1±0.7 W (equivalent to 1.2±5.6 %) for bird 15 when the vortex ring model was used to calculate P_{mech} when E_{FM} was 0.17. Use of the mean E_{FM} across both birds (0.18) to predict the P_{met} of both birds led to an overall discrepancy of 0.03±0.2 W (0.1±1.5 %) when P_{mech} was calculated from the lifting line model. The excellent overall average match between predictions and measurements of P_{met} includes errors in estimates from individual flights of −16.3 to +26.9 % (Fig. 7). Predicted P_{met} increased more steeply with flight speed than measured P_{met} when P_{mech} was predicted from the vortex ring model for bird 15, with the predicted values being lower than those measured during slow flight and higher than those measured during fast flight (Fig. 7A). Predicted P_{met} was consistently lower than measured P_{met} when P_{mech} was calculated from the lifting line model for bird 15 (Fig. 7A).
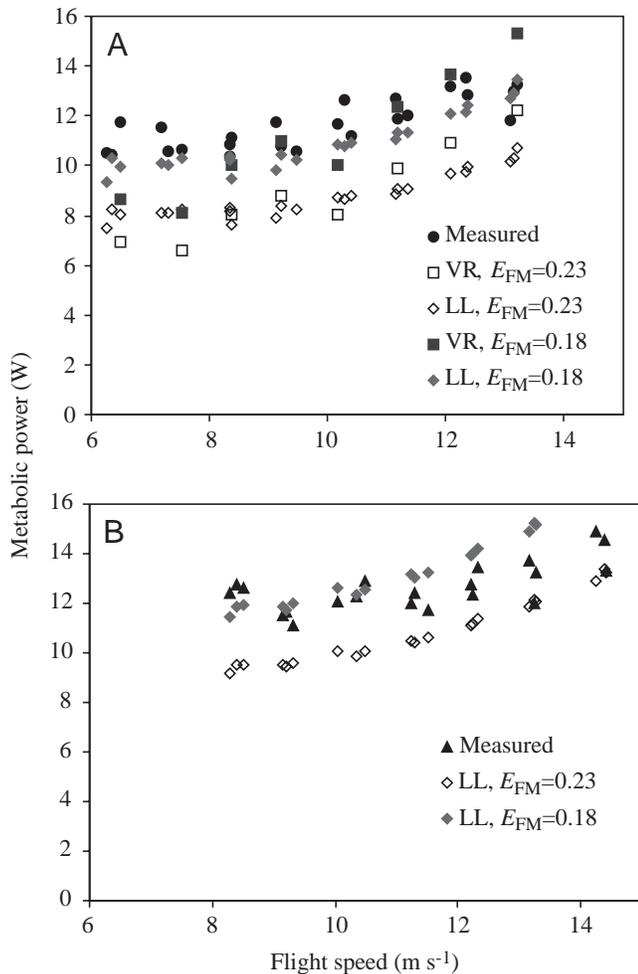
Fig. 7. Comparison of measured and predicted metabolic power (P_{met}) for (A) bird 15 and (B) bird 19. P_{met} was predicted for both birds from the lifting line model assuming a constant efficiency of 0.23 (LL, E_{FM}=0.23) and a constant efficiency of 0.18 (LL, E_{FM}=0.18) and for bird 15 from the vortex ring model assuming a constant efficiency of 0.23 (VR, E_{FM}=0.23) and a constant efficiency of 0.18 (VR, E_{FM}=0.18), where E_{FM} is flight muscle efficiency.

Predicted and measured P_{met} were similar during slow flight for bird 19, although predicted P_{met} increased more rapidly with flight speed (Fig. 7B). These analyses show that the discrepancy between measured and predicted P_{met} can be greatly reduced by assuming a constant value of E_{FM} of 0.18 rather than 0.23. The remaining discrepancy between predicted and measured P_{met} could be due to variation in efficiency between birds and across flight speeds or to variation in P_{mech} that is not reflected in the aerodynamic models.

Discussion
Measured metabolic power

Our values of measured P_{met} for starlings lie in the range 10.4–14.9 W for birds of mass 0.080–0.091 kg. Metabolic power increased significantly with flight speed, but not as steeply as expected from aerodynamic modelling of P_{mech}. To date, there are published measurements of P_{met}/speed curves during wind tunnel flight for eight species of bird and five species of bat (e.g. Rayner, 1994; Butler and Bishop, 2000). Values of P_{met} between 9 and 10 W, which did not vary with flight speed, have previously been reported for starlings (mean bird mass 0.073 kg) (Torre-Bueno and Larochelle, 1978); those values have generally been regarded as anomalous, especially at high flight speeds, since measured power was lower than expected and was independent of flight speed. To our knowledge, the present measurements are the first reported replication of such measurements for any vertebrate.

Our values are higher than those of Torre-Bueno and Larochelle, especially at faster flight speeds (Fig. 2). A number of factors may explain this difference, including a combination of the lower mass of the previous birds (8 g or 10 % lighter than bird 15 and 18 g or 20 % lighter than bird 19), a reduction in flight costs as a result of ground and wall effects (Rayner, 1994), which was likely to be more influential in the smaller wind tunnel used by Torre-Bueno and Larochelle (Torre-Bueno and Larochelle, 1978), the relatively poor aerodynamic performance of that tunnel (S. Vogel, personal communication) and the extra power required to overcome the drag of the respirometry mask and tube in the current experiment (Ward et al., 1998). Of these factors, only wind tunnel performance is an obvious explanation for the difference in shape of the two sets of power curves.

Our P_{met} values were of the same order of magnitude expected from extrapolation of other wind tunnel oxygen uptake measurements; those by Torre-Bueno and Larochelle (Torre-Bueno and Larochelle, 1978) were markedly lower than expected (Rayner, 1994). Our values of P_{met} were also similar to those predicted from cardiac output (11–12 W; Bishop, 1997) and to those measured in free-flying starlings using the doubly labelled water technique (8.4–12.5 W; Westerterp and Drent, 1985). From this evidence, we suggest that our measurements of P_{met} in starlings are likely to be more realistic than those of Torre-Bueno and Larochelle (Torre-Bueno and Larochelle, 1978).

Comparison with free flight

Measurements of P_{met} by mask respirometry in wind tunnels may not be representative of flight costs in free-living birds for several reasons. Metabolic rate during wind tunnel flight may be raised, relative to free flight by the same birds, as a result of the stress associated with the unnatural environment and abnormal sensory input or because the bird cannot determine its flight speeds or duration. Costs of diving, for example, differ between forced and voluntary diving (for a review, see Butler and Jones, 1997). Metabolic rate could potentially be lower during wind tunnel flight than during free flight if a bird is able to reduce mechanical power by exploiting wind tunnel boundary effects (Rayner, 1994). Physiological changes in our starlings during the 2 year period of captivity prior to data collection could also alter flight costs from those of free-living birds, since digestive morphology, resting metabolic rate and flight muscle mass can change over much shorter periods (e.g. Scott et al., 1996; Dietz et al., 1999; Lindström et al., 2000).

Comparison with free-flight doubly labelled water measurements of starling flight costs (Westerterp and Drent, 1985) suggests that any distortion in power due to wind tunnel flight or the use of captive birds is likely to be relatively small in magnitude. However, we cannot rule out the possibility that the magnitude of such distortion depends on flight speed.

Power curves

The discrepancies between measured P_{met} and P_{met} predicted from P_{mech} by equation 1 suggest either that P_{mech} calculated by aerodynamic models is too small or that E_{FM} is lower than the value of 0.23 that is normally assumed, especially during faster flight. There have been few independent controls on the aerodynamic models; values of body drag are based on limited experimental evidence that is currently being reassessed (see below), while measurements of wing drag, especially in smaller birds, are few; the magnitudes of induced (or vortex) power have been confirmed by flow visualization experiments, but represent a relatively small proportion of mechanical power at normal flight speeds (Rayner, 1999). Direct measurements of force production by the pectoral muscles in magpies (Dial et al., 1997) suggest that P_{mech} may form an L-shaped rather than a U-shaped relationship with flight speed and that aerodynamic models overestimate P_{mech} during faster flight. The difference between these measurements and predictions of the vortex ring model is relatively small, although the model does appear to overestimate power slightly for fast flight (Rayner, 1999; Rayner and Ward, 1999). Our calculated P_{mech} values rise with flight speed, but if they are to be consistent with our measured P_{met}, E_{FM} must increase with flight speed. This result could be caused by systematic overestimation of P_{mech} during faster flights rather than by a change in E_{FM} across flight speeds. Overestimation of P_{mech} by aerodynamic models during faster flight is consistent with the measured mechanical power production by starling pectoralis muscle of 1.1 W during flight at 13.7 m s^{-1} (Biewener et al., 1992), which is lower than P_{mech} predicted by the aerodynamic models at this speed (2.0–2.3 W, depending upon the aerodynamic model and bird), although some of this discrepancy will be accounted for by work performed by other muscles.

The starlings sometimes used intermittent bounding (flap-bounding) or undulating (flap-gliding) flight (Rayner, 1985; Tobalske, 1995; Tobalske and Dial, 1996; Rayner et al., 2001) during our measurements of flight metabolic rate between the bouts of continuous flapping flight upon which the calculations of P_{mech} are based. The use of intermittent flight (Rayner et al., 2001) or wind tunnel boundary interference effects (Rayner, 1994) could each reduce P_{mech} by a maximum of 10%, although it is not known whether birds exploit these mechanisms effectively. The proportion of intermittent flap-gliding compared with steady flapping during flights was not related to P_{met}, so the intermittent flight pattern sometimes adopted by our birds apparently did not have an important influence upon flight metabolic rate. Intermittent flight patterns were used more frequently during fast flight both by one of our starlings and by those studied by Tobalske (Tobalske, 1995),

and this may reduce P_{mech} during fast flight in ways that have not yet been quantified by aerodynamic modelling. This would be consistent with the steeper rise in P_{mech} than in P_{met} as flight speed increased, although the discrepancy may equally arise for other reasons, as discussed below.

Body drag, mechanical power and efficiency

One of the three major drag components in the aerodynamic models is the body parasite drag (equation 4). We used a constant value of parasite drag depending on body mass from a formula from Pennycuick (Pennycuick, 1975) in both models. For a bird of mass 0.08 kg, the equivalent flat plate area is 5.3×10^{-4} m^2. The frontal projected area of a starling is approximately 2.1×10^{-3} m^2 (W. J. Maybury, personal communication), so the body drag coefficient C_{Db} based on frontal projected area is estimated to be approximately 0.26. Tucker (Tucker, 1973) measured a slightly higher value of drag on a starling flying at 11 m s^{-1}, corresponding to $C_{Db}\approx0.31$. Recent measurements on starling bodies in a wind tunnel give C_{Db} in the range 0.35 (at 6 m s^{-1}) to 0.20 (at 15 m s^{-1}) (Maybury, 2000; Maybury and Rayner, 2001), which is comparable with predictions from the Pennycuick formula and Tucker measurement at lower air speeds, but is markedly lower at higher speeds. Gesser et al. (Gesser et al., 1998a; Gesser et al., 1998b) made a preliminary report of C_{Db} of the order of 0.24 on a smooth model starling at 8 m s^{-1} (this is the same model that we used to determine mask and tube drag). Taken together, this experimental evidence suggests that the drag formula of Pennycuick's model is of the correct order of magnitude at the lower range of flight speeds over which we measured power but may not capture a decrease in drag coefficient with flight speed.

Values of body parasite drag close to those predicted (Pennycuick, 1975) have recently been determined for birds of similar size to that of starlings whilst descending rapidly with wings folded at the end of migratory flights (Hedenström and Liechti, 2001). Pennycuick et al. (Pennycuick et al., 1995) have argued, on the basis of a mismatch between power model predictions and observed wind tunnel flight patterns, that the body drag values used in aerodynamic models may be too high by a factor of 5. There is no direct experimental evidence supporting drag values as low as this in small birds, and the available measurements appear to confirm that, in small passeriform birds, the predictions of the Pennycuick (Pennycuick, 1975) formula are of the right order of magnitude, although parasite drag probably decreases with flight speed. Measured drag does appear to be much lower than predicted by equation 4 in larger birds. If drag measurement experiments were in error by as much as suggested by Pennycuick et al. (Pennycuick et al., 1995), the predicted P_{mech} of our starlings would be reduced by 25–40% (in addition, predicted optimum flight speeds would be increased by approximately 50%). A decrease in body parasite drag with flight speed may, however, form a partial explanation of why our estimates of E_{FM} increase with speed.

We have estimated E_{FM} in the range 0.13–0.23, varying between birds and depending on flight speed. These values are

significantly below the constant 0.23–0.25 normally recommended (e.g. Norberg, 1990). The dilemma we face is that, if P_{mech} is overestimated by the aerodynamic models (as is most likely for faster flight), then E_{FM} will be further reduced below the values that we have calculated; Pennycuick's proposal of drag coefficients C_{Db} in the range 0.04–0.07 would be associated with E_{FM} values for starlings in the range 0.10–0.14.

Accurate prediction of P_{met} from P_{mech} by equation 1 relies upon four assumptions: (i) that the value of P_{mech} predicted by aerodynamic models is correct, (ii) that an appropriate value of E_{FM} is used, (iii) that P_{BMR} should be added to metabolic rate during flight and (iv) that additional costs of respiration and circulation each contribute 5 % to P_{met}. Predictions of P_{met} from equation 1 are most sensitive to the value of E_{FM}, but there is no direct experimental evidence for the assumptions about basal metabolic rate, respiration and circulation. Taken together, 16–19 % of P_{met} in our starlings originates from P_{BMR} (6–9 %) and the combined cost of additional respiration (5 %) and circulation (5 %). Some metabolism presumably occurs during flight other than in the flight muscles and the organs needed to supply them with oxygenated blood, but the assumed value of P_{BMR} may either be too high or too low to account for this. Metabolism not associated with flight could be lower than P_{BMR} because metabolic rate is reduced in parts of the body not required during exercise (Butler et al., 1988) and the heat produced in the flight muscles substitutes for thermoregulatory heat production. Alternatively, metabolism not associated with flight could be higher than nocturnal P_{BMR} because our starlings were not post-absorbative and were flown during the day. The birds also flew at air temperatures below the thermal neutral zone, but metabolic rate would not need to be increased to maintain body temperature since the additional heat generated as a by-product of muscular activity more than compensates for the increase in heat loss due to the greater surface area and movement of air past a flying bird (Ward et al., 1999).

The assumptions that respiration and circulation each contribute 5 % to metabolic rate during flight and that P_{BMR} should be added to metabolic rate during flight will not lead to error in P_{met} when P_{met} is calculated from equation 1 if E_{FM} is also calculated using equation 1 from simultaneous estimates of P_{met} and P_{mech}, using the same assumptions about the values of P_{BMR} and the costs of respiration and circulation during both calculation of E_{FM} given P_{met} and P_{mech} and prediction of P_{met} given E_{FM} and P_{mech}. If the combined costs of additional respiration and circulation or P_{BMR} were to increase, the calculated E_{FM} would increase proportionally, so that, if these revised data were used to predict P_{met}, the result would be the same as if the lower E_{FM} and costs of respiration, circulation and basal metabolic rate were used. It might be better to calculate whole-animal efficiency, E_W (where $E_W=P_{mech}/P_{met}$), and to rearrange this equation to predict P_{met}. This would avoid making assumptions that cannot be tested about the contributions of respiration, circulation and P_{BMR} to metabolic rate during flight. However, the value of E_{FM} is insensitive to the values of P_{BMR} and the costs of circulation and respiration: halving or doubling these values changes E_{FM}

by less than 0.02. We have used equation 1 to calculate E_{FM} to make our values consistent with those in previous work and because changing the formula does not increase the accuracy of predicted P_{met}. An E_W of 0.15 is equivalent to an E_{FM} of 0.18 for our starlings; the value 0.23 that has normally been used for E_{FM} in equation 1 is equivalent to an E_W of 0.19.

Estimation of metabolic power

The aerodynamic models that are used to calculate P_{mech} (e.g. Pennycuick, 1975; Pennycuick, 1989) are important because it is difficult to measure P_{met} directly in the field, and measurements under controlled conditions such as during wind tunnel flight cannot necessarily be extrapolated to other flight conditions or to other species. Estimated P_{met} from aerodynamic models is highly sensitive to E_{FM}, mainly because the mechanical work is a small component of the total. A change in E_{FM} of only 0.01 represents a 5 % change in P_{met}.

Uncertainty in the efficiency of flying birds means that it is not possible to predict P_{met} accurately from P_{mech} calculated by aerodynamic modelling and an assumed uniform value of E_{FM}. The discrepancy was reduced, but not removed, in our starlings by the use of a fixed value for E_{FM} of 0.18 rather than 0.23. Calculation of P_{mech} by the more detailed vortex ring model did not improve the accuracy of predicted P_{met} if a constant value of E_{FM} was assumed, even though changes in wingbeat kinematics due to flying in a wind tunnel carrying a respirometry mask were taken into account by this model. If P_{met} for birds of the size range of starlings (0.075–0.1 kg) is to be extrapolated from P_{mech} calculated by the most popular method (the lifting line model, Pennycuick, 1989, program 1A), we suggest the use of an E_{FM} of 0.18. This value of E_{FM} is not appropriate for substantially larger or smaller birds because efficiency is expected to vary with size (Rayner, 1990; Rayner, 1995). Muscle efficiency increases with body size in running mammals and birds (Heglund et al., 1982; Heglund and Cavagna, 1985) and in flying insects (Casey, 1988; Casey and Ellington, 1989), and E_{FM} may equally be expected to increase with size in flying birds. An approximate estimate of the size-scaling of whole-body efficiency (E_W) may be determined from the scaling with body mass of the measured metabolic power (P_{met}, W) for flight in birds and bats:

$$P_{met} = 64.64M^{0.782} \qquad (5)$$

(Rayner, 1990), where M is body mass in kg, and calculated mechanical power (P_{mech}, W):

$$P_{mech} = 14.95M^{1.161} \qquad (6)$$

(Rayner, 1988), as:

$$E_W = P_{mech}/P_{met} = 0.23M^{0.379}. \qquad (7)$$

E_W increases with size because P_{met}, like other physiological variables, scales approximately as mass$^{0.75}$; e.g. Tucker, 1973), while P_{mech} scales approximately as mass$^{7/6}$, as expected on aerodynamic grounds (e.g. Pennycuick, 1975; Rayner, 1988; Rayner, 1990; Rayner, 1995; Speakman and Racey, 1991). For a bird of mass 0.08 kg comparable with our starlings, equation

7 predicts a rather low E_W of 0.088. Whole-body efficiency (E_W, W) and flight muscle efficiency (E_{FM}, W) are related by:

$$E_{FM} = E_W/[0.91 - (P_{BMR}/P_{met})] \qquad (8)$$

(derived from equations 1 and 7). With $P_{BMR}=0.9\,\text{W}$ and $P_{met}=9\,\text{W}$ (representative values for starlings), equation 8 gives $E_{FM} \approx 0.10$. These values for efficiency are somewhat lower than we have measured (Fig. 6), but they confirm our argument that efficiency increases with size across the range of birds and bats and, in smaller species, is much lower than a uniform value of 0.23. If necessary, these allometric equations could be used to estimate E_{FM} in birds; however, it must be noted that equations 5 and 6 are derived from analysis of independent and diverse observations, and the experiments we report here on starlings remain the only measurements to date in which metabolic and mechanical power have been determined simultaneously in flying vertebrates during forward flight.

The physiological or mechanical mechanisms responsible for variation in efficiency with size are not known, and we cannot be certain that equation 7 should apply to all avian taxa. Our arguments take no account of the anticipated and theoretical maximum efficiency of 0.25, which might be attained in larger birds. A possible explanation for the difference between the values of E_{FM} determined directly in bats and hummingbirds and the values of E_P measured in tilting wind tunnels is therefore that the larger birds, which give rise to the E_P measurements, have higher efficiencies.

Lower values of efficiency are appropriate for smaller bats and hummingbirds (0.0035–0.01 kg): a value of 0.12±0.01 is the mean of the average efficiencies calculated from simultaneous estimates of P_{met} and P_{mech} determined during hovering by the nectar-feeding bat *Glossophaga soricina* (0.15; Norberg et al., 1993) and ruby-throated hummingbirds hovering in heliox (0.10; Chai and Dudley, 1995) and in air (0.12; Chai et al., 1998). The lower E_{FM} during hovering flight is also consistent with increases in efficiency with flight speed and bird mass, although further studies are required to confirm this pattern. Studies of larger birds during which P_{met} is measured simultaneously with wingbeat kinematics that allow calculation of P_{mech} from aerodynamic models would be particularly valuable.

Further measurements of efficiency during flight may reveal patterns in variation across individuals and species with different flight morphology, and above all with different mass, that will allow P_{met} to be predicted from P_{mech} with greater accuracy. It is also important to determine the mechanisms that cause efficiency to vary. Given that further measurement of efficiency requires simultaneous measurement of P_{met} and P_{mech}, it might be as accurate, as well as less technically demanding, to concentrate on measurement of P_{met} in more species of flying animal, so that P_{met} can be predicted from body mass with confidence by using allometric equations such as those presented by Masman and Klaassen (Masman and Klaassen, 1987), Rayner (Rayner, 1991), Speakman and Racey (Speakman and Racey, 1991), Bishop (Bishop, 1997), Winter and von Helversen (Winter and von Helversen, 1998) and Butler and Bishop (Butler and Bishop, 2000).

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