

## ORIGINAL PAPER

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**Flight of the honey bee VII: metabolic power versus flight speed relation**

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**Abstract** The existing experimental data on metabolic power  $P_m$  of honey bees are critically discussed, partly corrected for real flight conditions and plotted as a function of flight speed  $v$ . New wind tunnel measurements of tethered flight under near-natural conditions are added in the range  $3.3 < v < 5.1 \text{ m} \cdot \text{s}^{-1}$ , derived from exhaustion flight measurements. Within this small sector the latter measurements can be characterised by a linear correlation:  $P_m(\text{mW}) = 6.72v (\text{m} \cdot \text{s}^{-1}) + 13.83$ , the slope of which is significantly different from zero. The over-all  $P_m(v)$  curve is significantly not a straight line of zero slope but a U-shaped minimum curve and may be approximated by a second-order polynomial:  $P_m = 49.2 - 8.9v + 1.5v^2$ . The same is true for relative metabolic power,  $P_{m\text{rel}(e)}$  related to “empty” body mass of 76.5 mg:  $P_{m\text{rel}(e)} = 630.0 - 114.0v + 19.2v^2$  ( $P_m$  in mW;  $P_{m\text{rel}}$  in  $\text{mW} \cdot \text{g}^{-1}$ ;  $v$  in  $\text{m} \cdot \text{s}^{-1}$ ). The data support the existence of a U-shaped power-versus-speed curve in bees.

**Key words** Insect flight · Power-versus-speed relation · Honey bee flight – Bee, *Apis mellifera*

**Abbreviations** *bm* body mass (mg) · *f* full · *e* empty · *mu* muscles ·  $P_m$  ( $\text{mJ} \cdot \text{s}^{-1} = \text{mW}$ ) metabolic power (input) ·  $P_{m\text{rel}}$  ( $\text{mW} \cdot \text{g}^{-1}$ ) relative metabolic power ·  $P_{\text{mec}}$  (mW) mechanical power (output) ·  $\eta$  efficiency (of the flight musculature) ·  $t(s)$  flight time ·  $v$  ( $\text{m} \cdot \text{s}^{-1}$ ) relative speed between bee and air

**Introduction**

Metabolic power  $P_m$  and relative metabolic power  $P_{m\text{rel}(e)} = P_m/bm_e$  ( $bm_e$  “empty” body mass) are basic

energetic parameters of animal movement. They are analogous to engine power input in aircraft. These – as well as output – are functions of flight speed. Technical aerodynamic theories (e.g. Schütt 1934) have shown that the power-versus-speed curve in technical aircraft is a minimum curve. This results from the speed dependency of at least three aerodynamical components of power. This approach was adapted, modified and supplemented in biological flight theories by Pennycuik (1968), Tucker (1973), Rayner (1979) and Norberg (1990). Some birds and bats produce a U-shaped  $P_m(v)$  curve in free (wind tunnel) flight, while other birds and bumblebees do not seem to show such a dependency, at least not very pronounced (Ellington et al. 1990).

$P_m$  and  $P_{m\text{rel}}$  in honey bees have been measured at different flight speeds in several studies, but a  $P_m(v)$  relation curve combining all available data has not yet been derived. This is difficult because relevant boundary conditions are often not given and/or flight conditions are not precisely defined. A comparison of apparently reliable literature data up to 1980 (Rothe and Nachtigall 1989) revealed  $P_{m\text{rel}}$  values of  $360 \pm 80 \text{ mW} \cdot \text{g}^{-1}$  for slow tethered flight and  $500 \pm 70 \text{ mW} \cdot \text{g}^{-1}$  for free hovering animals. Feller and Nachtigall (1989) and Nachtigall et al. (1989), using three different methods (gas analysis, thermoregulation, fuel consumption), obtained an average  $P_{m\text{rel}}$  value of  $350 \pm 130 \text{ mW} \cdot \text{g}^{-1}$  for tethered bees flying at  $0.72 < v < 4.3 \text{ m} \cdot \text{s}^{-1}$ . Since then several methodically different studies have been published, some of which come close to natural conditions.

In this paper a critical comparison of existing data is given and combined with the results from continuous long-term measurements of all relevant variables in tethered flying bees which were able to choose their own speed. From these data it may now be possible to formulate average  $P_m(v)$  and  $P_{m\text{rel}(e)}(v)$  relations for flying honey bees. These values are prerequisites for comparisons with calculations from mechanical flight power and thus for calculating flight muscle efficiencies.

## Materials and methods

Exhaustion flight measurements within  $3.3 < v < 5.1 \text{ m} \cdot \text{s}^{-1}$

These measurements were made with the experimental setup described in Hanauer-Thieser and Nachtigall (1995) and summarized in the Discussion here. Although the animals were tethered to a two-component aerodynamical balance, the flight conditions came very close to natural free-flight conditions.

### Regression analysis

Polynomial models of increasing order were fitted to the data by a program for polynomial regression analysis (Mörz 1989). The order of the polynomials was successively increased: (1)  $P_m = b_0$ ; (2)  $P_m = b_0 + b_1v$ ; (3)  $P_m = b_0 + b_1v + b_2v^2$ ; (4)  $P_m = b_0 + b_1v + b_2v^2 + b_3v^3$ . Model (1) infers independence of  $P_m$  from  $v$  [e.g. Ellington et al. (1990); *Bombus terrestris*]; model (2) is irrelevant; model (3) infers quadratic dependence of  $P_m$  from  $v$  [U-shaped  $P_m(v)$  curve]; model (4) was only used to test whether model (3) could explain the variance between the data. Model (3) was accepted when the residual variance of model (1) was significantly decreased by the introduction of  $b_1 + b_2$  ( $F$ -test; error level 5%). Similarly (4) was tested against (3).

### Methods described in other studies

Literature data are calculated either from  $\text{O}_2$  consumption,  $\text{CO}_2$  production, fuel consumption, manometry or volumetry or from cooling experiments of bees flying in closed tunnels, in closed vessels, on roundabouts and in front of open tunnels, or from free collecting flights. They are given in Fig. 1A and, where necessary, critically discussed in the text.

## Results

### Flight success

Literature data seldom contain information on flight success. From 151 animals tested at  $3.3 < v < 5.1 \text{ m} \cdot \text{s}^{-1}$ , 21% flew at least twice and finally 44 flights could be used, from which 28 contained all the information required for calculations.

### $P_m(v)$ plot

In Fig. 1A all available results from the literature which seemed to be reliable are presented according to increasing  $P_m$ . In Fig. 1B the  $P_m$  data are plotted as a function of  $v$ , including the four mean values of our  $3.3 < v < 5.1 \text{ m} \cdot \text{s}^{-1}$  measurements made with four different feeding volumes (see Discussion). Each individual value of the latter measurements is represented by a cross. (These single values were not used when calculating the  $P_m(v)$  curve in Fig. 1B; point "ad (7)", extrapolated from these measurements, was not taken into account either.) From literature sources 1, 4

and 8 corrected values (see Discussion) were used. The calculated compensation curve is  $P_m = 49.2 - 8.9v + 1.5v^2$  ( $P_m$  in mW;  $v$  in  $\text{m} \cdot \text{s}^{-1}$ ).

In Fig. 1C the data for our  $3.3 < v < 5.1 \text{ m} \cdot \text{s}^{-1}$  measurements are plotted on a larger scale. Due to the small section of the  $v$  interval they can be characterised by a linear correlation  $P_m = 6.72v + 13.83$  ( $P_m$  in mW;  $v$  in  $\text{m} \cdot \text{s}^{-1}$ ), the slope of which is significantly ( $\alpha = 1\%$ ) different from zero.

### $P_{m\text{rel}}(v)$ relations

Similarly, metabolic power was calculated relative to "empty" body mass averaging 76.5 mg (Hanauer-Thieser and Nachtigall 1995). The equation is  $P_{m\text{rel}(e)} = 630.0 - 114.0v + 19.2v^2$  ( $P_{m\text{rel}}$  in  $\text{mW} \cdot \text{g}^{-1}$ ;  $v$  in  $\text{m} \cdot \text{s}^{-1}$ ).

## Discussion

### Critical interpretation of data

The studies cited in Fig. 1A, but which are not numbered, have not been included in Fig. 1B because they lack relevant data or methodical clarity. If body masses were not given  $P_{m\text{rel}(e)}$  was calculated using  $bm_e = 76.5 \text{ mg}$  as the most probable value (Hanauer-Thieser and Nachtigall 1995);  $bm_f$  ("full" body mass) was recalculated using feeding solution masses.

Under the following sub-headings numbers in parentheses refer to studies indicated in Fig. 1A.

### Tethered flights

(1) Soltavalt (1954) used 50% glucose solutions. Since wingbeat frequency was significantly smaller ( $189 \pm 17 \text{ s}^{-1}$ ) than in free flight, his  $P_m$  must be too small. Recalculation of  $P_m$  for  $225 \text{ s}^{-1}$  gives  $42.7 \pm 9 \text{ mW}$ .

(2) Loh and Heran (1970) used  $0.25 \pm 0.1 \text{ mol} \cdot \text{l}^{-1}$  glucose solutions; their data seem to be at the lower border.

(3) Crailsheim's (1988) data, related to 1 and  $2 \text{ mol} \cdot \text{l}^{-1}$  glucose solutions, do not differ statistically and seem to be reliable.

(4), (5), (6) The data from Nachtigall et al. (1989) related to exhaustion flights with  $1.54 \text{ mol} \cdot \text{l}^{-1}$  glucose monohydrate solution are definitely too low due to the method used: a low wingbeat frequency ( $167.7 \pm 15.1 \text{ s}^{-1}$ ) and possibly too low a solution concentration (real concentration might have been  $1.28 \text{ mol} \cdot \text{l}^{-1}$ ). Data are recalculated for  $220 \text{ s}^{-1}$  as  $39.6 \pm 4.8 \text{ mW}$ . The data related to gas exchange in closed tunnels at 1.8 and  $0.72 \text{ m} \cdot \text{s}^{-1}$  may be slightly

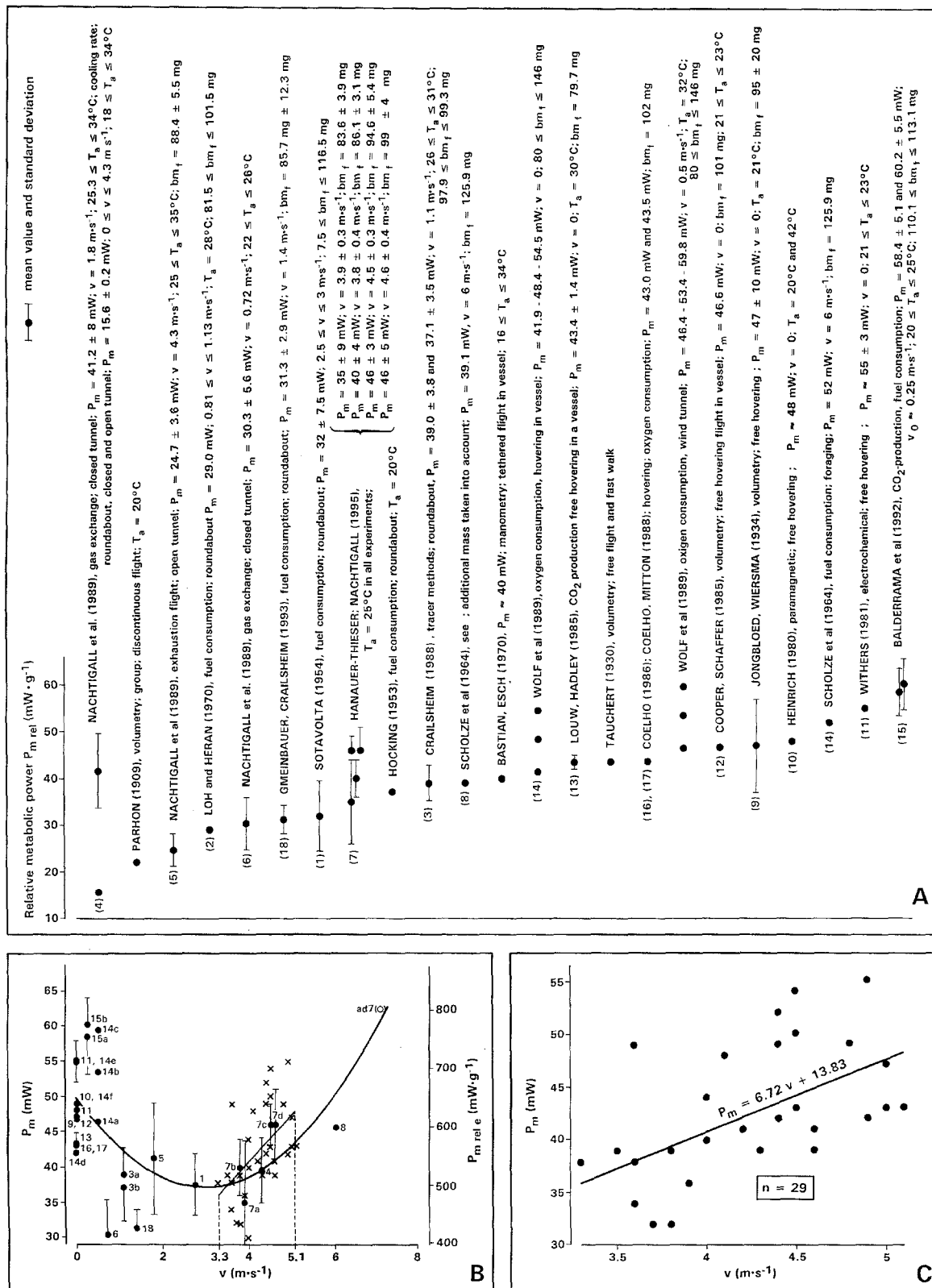


Fig. 1A-C Literature data and  $P_m(v)$  relations: A literature data, arranged from low to high metabolic power. Compare Fig. 1B and Discussion; B metabolic power as a function of flight speed. Data from the authors of 1A (numbers indicated are the same as in A; cf.

text.) Original data from this paper (7) are additionally plotted in the velocity range  $3.3 < v < 5.1 \text{ m} \cdot \text{s}^{-1}$ . For point "ad 7" see text; C original data from this paper (7) in the range  $3.3 < v < 5.1 \text{ m} \cdot \text{s}^{-1}$ , plotted on a broader scale, and linear approximation

too low due to the method of suspension and to relatively low wind temperatures.

(7) Hanauer-Thieser and Nachtigall's (1995) data seem to come as close to natural conditions as possible: free choice of speed and thrust by the bee, continuous registration of lift and thrust, optimum temperature of 25°C, high wing-stroke frequency of  $225 \pm 7 \text{ s}^{-1}$  (at 5  $\mu\text{l}$ ) within the range of stroke frequencies of free flight ( $220 < f < 270 \text{ s}^{-1}$ ), lift usually equal to or even surpassing body weight, long steady flights. We believe that these values are the most reliable for tethered flight so far obtained. The test was carried out by feeding different amounts (5, 10, 15 or 20  $\mu\text{l}$ ) of  $1.28 \text{ mol} \cdot \text{l}^{-1}$  glucose monohydrate solution, the energy content  $W$  of which was 18.5, 37.0, 55.5, 74.0 J, flying the bees to exhaustion and registering (in addition to other parameters) flight time  $t$  and flight speed  $v$ . Metabolic power was calculated from  $P = W \cdot t^{-1}$ . Higher  $W$  usually resulted in higher  $v$  and higher  $P_m$ . The  $P_m(v)$  plot in Fig. 1C was constructed from 28 such triple values. For the calculation of the overall power-versus-speed curve, the four mean values of  $P_m$  for the four energy contents mentioned were used. From these, the mean of the two lower values ( $35 \pm 9 \text{ mW}$  at  $3.9 \pm 0.3 \text{ m} \cdot \text{s}^{-1}$  and  $40 \pm 4 \text{ mW}$  at  $3.8 \pm 0.4 \text{ m} \cdot \text{s}^{-1}$ ) was significantly ( $\alpha = 5\%$ ) different from the mean of the two upper values ( $46 \pm 3 \text{ mW}$  at  $4.5 \pm 0.3 \text{ m} \cdot \text{s}^{-1}$  and  $46 \pm 5 \text{ mW}$  at  $4.6 \pm 0.4 \text{ m} \cdot \text{s}^{-1}$ ), giving a mean incremental factor of 1.23.

#### *Free horizontal flight*

(8) The bees in the study by Scholtze et al. (1964) wore an additional weight of 45 mg; the corrected value for normal body weight is 39.1 mW.

#### *Hovering and very slow flight*

Studies by (9) Jongbloed and Wiersma (1934), (10) Heinrich (1980), (11) Withers (1981) and (12) Cooper, Schaffer (1985) are very similar, but lack information on feeding solution and (10, 11) on body masses.

(13) Louw and Hadley's (1985) solution concentration in feeding volume is not known; their relatively low  $P_m$  for hovering could be related to an insufficient energy content of the solution and a rather low  $bm_f$  of 79.7 mg.

(14) Wolf et al. (1989) used different volumes of a 50% saccharose solution at a high temperature of 32°C; their data seem to be reliable and there was no statistical difference between hovering in a vessel and very slow ( $0.5 \text{ m} \cdot \text{s}^{-1}$ ) flight in a tunnel.

(15) The data from Balderrama et al. (1992) are based on foraging flights in an artificial foraging field, in which 50% saccharose was presented at a rate of  $6.5 \text{ mg} \cdot \text{min}^{-1}$ . The bees' flying speed when flying be-

tween artificial flowers standing close together is not known, but may have been between  $0.1$  and  $0.5 \text{ m} \cdot \text{s}^{-1}$ . The  $P_m$  values are the highest found in the literature; a systematic source of error was not discernible.

(16) Coelho (1986) and (17) Coelho and Mitton (1988) compared worker bees and drones and found a somewhat higher (12%) metabolic power for hovering in workers. They do not give detailed information on ambient conditions but the measurements seem to be correct.

(18) Gmeinbauer and Crailsheim (1993) compared workers, queens and drones by glucose consumption in roundabout flights at  $1.4$ – $1.8 \text{ m} \cdot \text{s}^{-1}$ .  $P_m$  values are relatively low possibly due to the relatively low speed but the method seems to be correct.

#### *Most probable curve*

Hovering at or near  $v = 0$ . Many measurements are available. From (12), (13), (14) some values seem to be slightly too low, (15) slightly too high, but the extremes cancel one another out.

Low speed. Due to the uncertainty in (1) we take the mean value of 37.35 mW between the corrected and the uncorrected value.

Medium to fast speed. (4) is clearly too low; we take the corrected value of  $39.6 \pm 48 \text{ mW}$ ; (7) seems to be very reliable.

High speed. (8) must be too high due to the additional weight, but could be – per se – relatively low due to the measuring procedure. We take the mean value of 45.55 mW between the given and the corrected value as the most probable value.

Very high speed. There are no  $P_m$  measurements available. From Nachtigall and Hanauer-Thieser (1992) a speed relative to the surrounding air substantially higher than  $7.5 \text{ m} \cdot \text{s}^{-1}$  is not probable as a constant long-distance flight speed. Taking this as the “mean highest speed”, we extrapolated our  $3.3 < v < 5.1 \text{ m} \cdot \text{s}^{-1}$  curve to this speed and corrected it for “lift = body weight”. The resulting point (“ad 7”) was not used for calculating the  $P_m(v)$  curve, but lies well within its extrapolated range. No direct metabolic measurements at very high speed are available.

#### *U-shaped versus straight $P_m(v)$ graph*

Our method was to combine critically selected literature data, in which obvious errors were corrected, with our own measurements which were made within the sector “medium to fast speed” of the velocity range. Only the latter measurements were evidential for a

significant increase of  $P_m$  with  $v$  and only within this range. These data, together with data from literature, clearly support the existence of a U-shaped  $P_m(v)$  curve. There is no statistical tendency for velocity independence of  $P_m$  as Ellington et al. (1990) found in the bumblebee (*Bombus terrestris*) within the velocity range  $0 < v < 4 \text{ m} \cdot \text{s}^{-1}$  in animals flying free in a wind tunnel. These authors do not give information on their original data and their boundary conditions, so that a critical recalculation or discussion of their data is not possible. In birds there are pronounced U-shaped curves for example in budgerigars (Tucker 1966) and pigeons (Rothe et al. 1987), and very flat curves in starlings (Torre-Bueno and La Rochelle 1987) and hummingbirds (Berger 1985). Some of the latter seem to be more or less straight lines, but to our knowledge, no significance tests to show the existence of a minimum power speed have been applied to them.

The study presented here shows that a minimum curve  $P_m(v)$  results for honey bees. From the tests indicated, it follows that the model (1)  $P_m = b_0 = \text{const}$  is not sufficient to describe the variance in the data. The residual variance of the model  $P_m = b_0 + b_1v + b_2v^2$  is significantly lower than the residual variance calculated for the model  $P_m = b_0 = \text{const}$ . The introduction of a cubic term (model 4) did not decrease the residual variance significantly, so that model (3) best fits the data. Minimum metabolic power was approximately 37.5 mW for medium-weight bees. Minimum power speed was approximately  $3 \text{ m} \cdot \text{s}^{-1}$ . Compared to this value of the curve there is a factor of increase of 1.3 relative to  $v = 0$ , of 1.17 relative to our fastest measured speed of  $5.1 \text{ m} \cdot \text{s}^{-1}$ , of 1.39 relative to fastest speed analysed in free flight (Scholze et al. 1964) and – extrapolated – of 1.63 relative to the “mean maximum” flight speed of  $7.5 \text{ m} \cdot \text{s}^{-1}$  (Nachtigall and Hanauer-Thieser 1992).

Therefore, in approximation the bees may nearly double their metabolic power during the fastest possible, steady collecting flights, compared to a minimum value at medium flight speeds. Hovering power lies inbetween and seems to be clearly lower than maximum possible power output in straight flight.

Casey and Ellington's (1989) curves for euglossine bees indicate size-independent muscular-specific power output  $P_{\text{mech mu}}$  of  $100 \text{ mW} \cdot \text{g}_{\text{mu}}^{-1}$  for total elastic energy storage (inertial power then being zero), and  $200 \text{ mW} \cdot \text{g}_{\text{mu}}^{-1}$  for no storage. Flight muscle efficiencies for a 0.087-g bee (resembling the weight of a honey bee) were 6.4% for total storage and 9.3% for no storage. Heinrich (1980) found that 75% of the 37.5 mg thorax mass of a honey bee, i.e. 24.4 mg are due to the flight muscle mass. Our minimum power input of  $P_{\text{m min}} = 37.5 \text{ mW}$  then means a muscle-specific minimum power input of  $P_{\text{m min(mu)}} = 37.5 \text{ mW}/24.4 \text{ mg} = 1537 \text{ mW} \cdot \text{g}_{\text{mu}}^{-1}$ . Combining this and Casey and Ellington's (1989) data, muscular efficiencies at minimum power input are  $\eta = P_{\text{mech min(mu)}}/P_{\text{m min(mu)}} =$

$100 \text{ mW} \cdot \text{g}_{\text{mu}}^{-1}/1537 \text{ mW} \cdot \text{g}_{\text{mu}}^{-1} = 6.5\%$  for total storage and 13.0% for no storage. At hovering, at  $5.1 \text{ m} \cdot \text{s}^{-1}$  and at “mean maximum speed” of  $7.5 \text{ m} \cdot \text{s}^{-1}$   $\eta$ -values would be 4.9 and 9.6%, 4.2 and 8.4%, and 4 and 8%, respectively. Real efficiencies should be somewhere inbetween, but certainly not much higher than 10% at the optimum speed and lower than this at very low and at very high speeds.

Power measurements during real free flights within the full speed range  $0 < v < 9 \text{ m} \cdot \text{s}^{-1}$ , and especially at high and very high speeds, are required to check the results and to test the conclusions presented here. As long as they are not available, the most probable equations  $P_m(v)$  and  $P_{\text{m rel(e)}}(v)$  given in this paper may be used for calculations.

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