



## Flight costs in volant vertebrates: A phylogenetically-controlled meta-analysis of birds and bats

Mélanie F. Guigueno<sup>a,\*</sup>, Akiko Shoji<sup>b</sup>, Kyle H. Elliott<sup>c</sup>, Stéphane Aris-Brosou<sup>d</sup>

<sup>a</sup> Department of Biology, McGill University, Montréal, Québec, Canada

<sup>b</sup> Faculty of Life and Environmental Sciences, University of Tsukuba, Tsukuba, Ibaraki, Japan

<sup>c</sup> Department of Natural Resource Sciences, McGill University, Sainte Anne-de-Bellevue, Québec, Canada

<sup>d</sup> Departments of Biology and of Mathematics & Statistics, University of Ottawa, Ottawa, Ontario, Canada

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### ABSTRACT

Flight costs play an important role in determining the behavior, ecology, and physiology of birds and bats. Mechanical flight costs can be estimated from aerodynamics. However, measured metabolic flight costs (oxygen consumption rate) are less accurately predicted by flight theory, either because of (1) variation in flight efficiency across species, (2) variation in how basal costs interact with flight costs or (3) methodological biases. To tease apart these three hypotheses, we conducted a phylogenetically-controlled meta-analysis based on data from birds and bats. Birds doing short flights in a lab had higher metabolic rates than those with sustained flapping flight. In turn, species that used sustained flapping flight had a higher metabolic rate than those that flew primarily via gliding. Models accounting for relatedness (phylogeny) explained the data better than those that did not, which is congruent with the idea that several different flight *Bauplans* have evolved within birds and bats. Focusing on species with sustained flapping flight, for which more data are currently available, we found that flight cost estimates were not affected by measurement methods in both birds and bats. However, efficiency increased with body mass and decreased with flight speed in both birds and bats. Basal metabolic rate was additive to flight metabolic rate in bats but not birds. We use these results to derive an equation for estimating metabolic flight costs of birds and bats that includes variation in whole animal efficiency with flight speed and body mass.

### 1. Introduction

Flight is the costliest form of locomotion, and the demands of flight have shaped the evolution of birds and bats (Schmidt-Nielsen, 1972; Videler, 2006; Pennycuick, 2008). Indeed, flight costs constrain several important behaviors related to the conservation and ecology of those vertebrates (Shepard et al., 2011; Maggini et al., 2017; Voigt et al., 2017). Many studies have attempted to quantify those costs, and there are several models that purport to predict average flight costs given only the forward speed, body mass, wing span and wing area of a species (Rayner, 1999; Videler, 2006; Pennycuick, 2008). However, most quantifications of flight costs are restricted to a few lineages of birds and bats (Videler, 2006). Because phylogeny can play an important role in the evolution of physiological systems, it is important to account for potential phylogenetic effects when interpreting patterns of physiological costs (Felsenstein, 1985; Garland et al., 2005).

Accurate predictions of flight costs are needed to provide insight

into questions associated with the behavior, conservation and ecology of both birds and bats (Videler, 2006; Pennycuick, 2008). The power curve, the relationship between airspeed and power (energy used per unit time also called metabolic rate), represents the dominant paradigm in vertebrate flight mechanics (Rayner, 1999, 2001; Pennycuick, 2008). Under this paradigm, mechanical flight costs can be separated into three components: (1) induced power, which is the power needed to overcome gravity and keep the animal aloft, (2) parasite power, the power needed to overcome body drag, and (3) profile power, the power needed to overcome drag associated with the wings (Rayner, 1999; Pennycuick, 2008). Based on aerodynamic theory, induced power should decline with forward speed, while parasite power should increase, leading to an U-shaped curve with the existence of an optimum speed. Measurements of mechanical power curves (mechanical work generated by the pectoralis muscles) in vertebrates support the existence of U-shaped curves in virtually all species examined to date (Tobalske et al., 2003; Askew and Ellerby, 2007). However, the

\* Corresponding author.

E-mail address: [melanie.guigueno@mcgill.ca](mailto:melanie.guigueno@mcgill.ca) (M.F. Guigueno).

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biomechanical force required to satisfy aerodynamics must be generated by metabolic power, and measurements of metabolic power curves (oxygen consumption rate vs. speed) in vertebrates have been more variable in shape (Rayner, 1999; Chernetsov, 2010; see debate between Hedenström, 2012 and Chernetsov, 2012).

The metabolic power curve (oxygen consumption rate of the animal) is arguably more important than the mechanical power curve in terms of an animal's behavior and ecological costs (Rayner, 1999; Pennycuik, 2008). Given that animals are only 10–30% efficient in converting food and oxygen into mechanical work, variation in whole animal efficiency can have a larger impact on metabolic power costs than mechanical costs, as calculated flying metabolic rate is proportional to efficiency (Rayner, 1999; Pennycuik, 2008). Currently, the most commonly used value for efficiency is 0.23, based on an estimate made from pigeons flying in a tilted wind tunnel (Pennycuik, 1975). More recently, Ward et al. (1999, 2001) estimated efficiency in starlings using a combination of techniques, and found that the value varied with speed, but was approximately 0.13. Finally, Videler (2006) estimated the value as ~0.1 for small birds and ~0.23 for large birds. The focus of the current study is to determine variation in efficiency among species of homeotherms (birds and bats) after accounting for phylogeny.

Metabolic power is non-zero even when an animal is at rest and mechanical power is zero. The minimal costs of an adult, post-assimilative, thermo-neutral, non-reproductive animal at rest is termed the basal metabolic rate. Basal metabolic rate is often closely associated with energy costs of maintaining the brain, kidney and guts—which must continue to function even at rest. Those tissues must also function when the animal is flying, and one possibility is that basal metabolic rate is additive with metabolic flight costs (Pennycuik, 2008). However, it is also possible that tissues become more active during flight (*i.e.* increased need of brain activity, increased creation of metabolic by-products to be filtered by the kidney), and so perhaps basal metabolic rate is simply subsumed into metabolic flight costs (Pennycuik, 2008). We test those two possibilities within this study.

Apart from uncertainty associated with quantifying parameters essential to the underlying theory, uncertainty in estimates of flight costs may be due to variation in methodology. Measurement of flight costs in the wild are often made on animals that glide, and clearly gliding is less expensive than flapping flight (Videler, 2006). Similarly, some measurements in the laboratory have focused on short flights in cages or constrained environments rather than sustained flights, and such short flights have high costs due to the high proportion of each flight associated with takeoff and acceleration (Nudds and Bryant, 2002). Finally, a number of different methods, such as body mass loss, doubly labeled water, heart rate telemetry and open-flow respirometry have been used to measure flight costs, and some authors have criticized particular methodologies as being biased (Wilson & Culik, 1993; Videler, 2006). Indeed, previous studies have suggested that estimates of flight cost may depend on methodology, with measurements in wind tunnels averaging higher than measurements outside of wind tunnels (Masman and Klaassen, 1987; Pennycuik, 2008; Rayner, 1990). Ward et al. (2004) showed that similar results were obtained in a single experiment on European starlings (*Sturnus vulgaris*) that were measured *via* the doubly labeled water, heat loss and respirometry techniques. We extend that study by examining whether flight cost estimates across a variety of studies are influenced by measurement technique.

Although gliding or propulsive flight occurs in some reptiles, amphibians, fish and non-chiropteran mammals, birds and bats are the only two groups of vertebrates that make substantial use of flapping flight. Thus, metabolic flight cost models, such as the Pennycuik model, have primarily been used to answer questions about the ecology and behavior of birds and bats. Early work assumed that the cost of flapping flight is the same for small birds and bats (Rayner 1990; Norberg 1990; Speakman and Racey, 1991). However, more recent work has shown that flight power in small birds is about ~20% higher than bats (Winter and Von Helversen, 1998). A potential energetic

advantage for small bats may result from the lower wingloading, wingbeat frequency and minimum power speed of bats as compared to birds (Norberg and Rayner 1987; Norberg 1990; Rayner 1990; Winter and Von Helversen, 1998). However, it is unclear whether such differences lead to lower mechanical flight costs in bats, or higher efficiency. One might further expect greater variability in efficiency in birds, which have greater phylogenetic diversity (dozens of orders compared to one order for bats), leading to a greater variety of Bauplans and flight styles. Our study examines variation in metabolic rate between birds and bats, and especially examines whether there is variation in how efficiency varies with mass and speed between the two taxa, to resolve what parameters may contribute to higher flight costs in small birds than bats.

Here, we conduct a meta-analysis of all measurements of flying metabolic rate in homeotherms (birds and bats). Earlier work showed that ‘aerial specialists’ (*i.e.* swifts and swallows) had low flight costs while other bird species, such as hummingbirds, had high flights, and so we separated gliding from flapping flight (Masman and Klaassen, 1987; Rayner 1990). We apply modern phylogenetic analyses to account for among-species relatedness. We examine the effect of flight type (short flights, gliding, flapping flight) and measurement technique on estimates of flight costs. We test the hypotheses that variation in flight costs are explained by: (1) variation in flight efficiency with body mass and flight speed; (2) variation in how basal costs interact with flight costs; or (3) measurement technique. Our central objective is to provide robust estimates for whole body efficiency in both bats and birds, thereby presenting a general mathematical framework for estimating the flight costs of birds and bats.

## 2. Materials and methods

### 2.1. Metabolic data

We compiled all measurements of flying metabolic rate in homeotherms (birds and bats) based on previous reviews (Rayner, 1999; McWilliams et al., 2004; Videler, 2006; Elliott et al., 2013), and on searching Web of Science (search string: “flight AND metabo\*”). We also examined studies that cited those studies. Because short flights can be more energetically-costly than long flights (Nudds and Bryant, 2002), and because flapping flight is more energetically-costly than gliding flight (Videler, 2006; Pennycuik, 2008), we separated flight measurements into three categories: short flights (each flight < 5 min), sustained gliding flights (birds that typically flap < 95% of flight time), and sustained flapping flights (birds that typically flap > 95% of flight time), although those categories occur on a continuum. For all analyses, except those demonstrating that phylogenetically-corrected analyses also show differences among flight modes, we focused exclusively on the latter, sustained flapping flight being of most relevance to metabolic flight curves. Furthermore, as measurements of metabolic rate can be affected by the method used (mass loss, hydrogen bicarbonate, doubly labeled water, open flow respirometry, or heart rate telemetry), we also recorded which method was used to measure flying metabolic rate. Although variation of gravity ( $\pm 1\%$  at sea level at the latitudes covered in Pennycuik, 2008) can affect flight, and hence, metabolic rate, we do not account for such variation. Likewise, air density and gravity can vary similarly with altitude, but we minimize such variation by using only data collected within a few hundred meters of sea level. For each species, we also collected basic statistics such as average adult body weight ( $m$ ), wingspan ( $B$ ), and wing area ( $S_w$ ), as recorded alongside the publication of each estimate of metabolic rate. Where those parameters are not described alongside the published metabolic rate measurements, we obtained the values from del Hoyo et al. (2014) for the closest population of the same species.

Following Videler (2006), we excluded some early power estimates thought to be inaccurate, which were based on the rate of average mass loss through the night of birds killed at a lighthouse (Graber and

**Table 1**

Summary of species, body masses and study characteristics in birds and bats included in the analyses with flapping flight. Table also includes studies that were not incorporated into our meta-analysis. Blanks represent cases in which flight speeds were not reported and not used in our study.

Species	Mass (kg)	Measurement method	Study setting	Speed (m/s)	Study
<b>Birds</b>					
<b>Flapping</b>					
<i>Selasphorus sasin</i> (male)	0.003	Respirometry	Wind tunnel	2.1–13.0	Clark and Dudley, 2010
<i>Calypte anna</i> (female)	0.004	Respirometry	Wind tunnel	2.2–13.2	Clark and Dudley, 2010
<i>Calypte anna</i> (male)	0.005	Respirometry	Wind tunnel	2.0–14.0	Clark and Dudley, 2010
<i>Colibri thalassinus</i>	0.006	Respirometry	Wind tunnel	3.2–11.3	Berger, 1985 (digitized in Clark and Dudley, 2010)
<i>Colibri coruscans</i>	0.009	Respirometry	Wind tunnel	3.2–10.8	Berger, 1985 (digitized in Clark and Dudley, 2010)
<i>Turdus guttatus</i>	0.030	Doubly labeled water	Wild	13	Wikelski et al., 2003
<i>Melospittacus undulates</i>	0.037	Respirometry	Wind tunnel	5.0–14.0	Bundle et al., 2007
<i>Melospittacus undulates</i>	0.037	Respirometry	Wind tunnel	5.2–13.3	Tucker, 1968 (digitized from Rayner, 1999)
<i>Sturnus roseus</i>	0.072	Doubly labeled water	Wind tunnel	8.9–13.9	Engel et al., 2006
<i>Nymphicus hollandicus</i>	0.081	Respirometry	Wind tunnel	5.0–15.0	Bundle et al., 2007
<i>Sturnus vulgaris</i>	0.085	Doubly labeled water, respirometry	Wind tunnel	8.0–18.0	Torre-Bueno and LaRochelle, 1978 (digitized from Rayner, 1999)
<i>Sturnus vulgaris</i>	0.085	Doubly labeled water, respirometry	Wind tunnel	2.0–14.1	Ward et al., 2004
<i>Falco sparverius</i>	0.120	Heart rate	Wind tunnel	9	Gessaman, 1980
<i>Calidris canutus</i>	0.128	Doubly labeled water	Wind tunnel	15	Kvist et al., 2001
<i>Falco tinnunculus</i>	0.197	Doubly labeled water	Flight cage	9	Masman and Klaassen, 1987
<i>Corvus ossifragus</i>	0.275	Respirometry	Wind tunnel	6.0–11.0	Bernstein et al., 1973 (digitized from Rayner, 1999)
<i>Columbia livia</i>	0.296	Respirometry	Wind tunnel	8.0–14.0	Rothe et al., 1987 (digitized from Rayner, 1999)
<i>Larus atricilla</i>	0.332	Respirometry	Wind tunnel	6.0–13.0	Tucker, 1972 (digitized from Rayner, 1999)
<i>Corvus cryptoleucos</i>	0.480	Respirometry	Wind tunnel	8.0–11.0	Hudson and Bernstein, 1983 (digitized from Rayner, 1999)
<i>Uria lomvia</i>	1.000	Doubly labeled water	Wild	19	Elliott et al., 2013
<i>Somateria mollissima</i>	1.752	Heart rate	Wild	17.9	Pelletier et al., 2008
<i>Phalacrocorax pelagicus</i>	1.804	Respirometry	Wild	15.2	Elliott et al., 2013
<i>Branta leucopsis</i>	1.990	Heart rate	Wind tunnel	15.0–17.0	Ward et al., 2002
<i>Anser indicus</i>	2.560	Heart rate	Wind tunnel	18.0–21.0	Ward et al., 2002
<i>Sula bassana</i>	3.200	Doubly labeled water	Wild	16.2	Birt-Friesen et al., 1989
<b>Gliding</b>					
<i>Riparia riparia</i>	0.014	Doubly labeled water	Wild		Westerterp and Bryant, 1984
<i>Delichon urbicum</i> (mean across 4 studies)	0.019	Doubly labeled water, mass loss	Wild		Hails, 1979, Lyuleeva, 1970, Westerterp and Bryant 1984, Kespaik, 1968
<i>Apus apus</i>	0.039	Mass loss	Wild		Lyuleeva, 1970
<i>Oceanites oceanicus</i>	0.042	Doubly labeled water	Wild	7.4	Obst et al., 1987
<i>Onychoprion fuscatus</i>	0.187	Doubly labeled water	Wild		Flint and Nagy, 1984
<i>Rissa tridactyla</i>	0.404	Doubly labeled water	Wild	9.17	Jodice et al., 2003
<i>Fulmarus glacialis</i>	0.754	Doubly labeled water	Wild	10.8	Furness and Bryant, 1996
<i>Larus argentatus</i>	0.912	Respirometry	Wind tunnel	10.8	Baudinette & Schmidt-Nielsen 1974
<i>Sula sula</i>	1.001	Doubly labeled water	Wild		Ballance, 1995
<i>Phoebastria immutabilis</i>	3.064	Doubly labeled water	Wild		Pettit et al., 1988
<i>Thalassarche melanophris</i>	3.580	Heart rate	Wild	8	Bevan et al., 1995
<i>Thalassarche chrysostoma</i>	3.707	Doubly labeled water	Wild	13.2	Costa and Prince, 1987
<i>Macronectes giganteus</i>	3.885	Doubly labeled water	Wild	14.5	Obst and Nagy, 1992
<i>Diomedea exulans</i> (female; mean across 2 studies)	8.330	Doubly labeled water	Wild	5	Adams et al., 1986, Arnould et al., 1996
<i>Diomedea exulans</i> (male; mean across 2 studies)	10.025	Doubly labeled water	Wild	5	Adams et al., 1986, Arnould et al., 1996
<b>Short flights</b>					
<i>Cinnyris osea</i>	0.006	Heavy carbon	Flight cage		Hambly et al., 2004
<i>Poecile montanus</i>	0.012	Doubly labeled water	Flight cage		Carlson and Moreno, 1992
<i>Taeniopygia guttata</i>	0.013	Doubly labeled water	Flight cage		Nudds and Bryant 2000
<i>Erithacus rubecula</i>	0.019	Doubly labeled water	Flight cage		Tatner and Bryant, 1986
<i>Euplectes orix</i>	0.019	Respirometry	Flight cage		Teal, 1969
<i>Passerina caerulea</i>	0.022	Respirometry	Flight cage		Teal, 1969
<i>Spizella pusilla</i>	0.022	Respirometry	Flight cage		Teal, 1969
<i>Zonotrichia albicollis</i>	0.028	Respirometry	Flight cage		Teal, 1969
<i>Passer domesticus</i>	0.029	Respirometry	Flight cage		Teal, 1969
<i>Heterophasia capistrata</i>	0.038	Respirometry	Flight cage		Teal, 1969
<i>Ramphocelus flammigerus</i>	0.045	Respirometry	Flight cage		Teal, 1969
<i>Columbina squammata</i>	0.051	Respirometry	Flight cage		Teal, 1969
<i>Lamprolaima superbus</i>	0.054	Respirometry	Flight cage		Teal, 1969
<i>Coccothraustes vespertinus</i>	0.059	Respirometry	Flight cage		Berger et al., 1970
<i>Turdus iliacus</i>	0.069	Respirometry	Flight cage		Teal, 1969
<i>Cyanocitta cristata</i>	0.089	Respirometry	Flight cage		Teal, 1969
<i>Colaptes auratus</i>	0.147	Respirometry	Flight cage		Teal, 1969
<i>Icterus galbula</i>	0.380	Respirometry	Flight cage		Teal, 1969
<i>Larus delawarensis</i>	0.427	Respirometry	Flight cage		Berger et al., 1970
<i>Larus marinus</i>	0.800	Mass loss	Flight cage		Dolnik and Gavrilov, 1973
<i>Anas rubripes</i>	1.026	Respirometry	Flight cage		Berger et al., 1970
Data not used					

(continued on next page)

Table 1 (continued)

Species	Mass (kg)	Measurement method	Study setting	Speed (m/s)	Study
<i>Regulus regulus</i> <sup>a</sup>	0.004	Mass loss	Wild		Nisbet, 1963
<i>Leiothlypis peregrina</i> <sup>a</sup>	0.011	Mass loss	Wild		Raveling and LeFebvre, 1967
<i>Erithacus rubecula</i> <sup>a</sup>	0.016	Mass loss	Wild		Nisbet, 1963
<i>Setophaga striata</i> <sup>a</sup>	0.019	Mass loss	Wild		Nisbet, 1963
<i>Melospiza melodia</i> <sup>a</sup>	0.022	Mass loss	Wild		Nisbet, 1963
<i>Pyrrhula pyrrhula</i> <sup>a</sup>	0.030	Mass loss	Wild		Dolnik and Gavrilov, 1973
<i>Oenanthe oenanthe</i> <sup>a</sup>	0.031	Mass loss	Wild		Nisbet, 1963
<i>Catharus fuscescens</i> <sup>a</sup>	0.032	Mass loss	Wild		Hussell, 1969
<i>Catharus minimus</i> <sup>a</sup>	0.032	Mass loss	Wild		Hussell, 1969
<i>Progne subis</i> <sup>b</sup>	0.050	Doubly labeled water	Wild		Utter and LeFebvre, 1970
<i>Pluvialis fulva</i> <sup>a</sup>	0.140	Mass loss	Wild		Johnstone and McFarlane, 1967
<i>Anas platyrhynchos</i> <sup>c</sup>	1.000	Mass loss	Wild		Dolnik and Gavrilov, 1973
<i>Morus capensis</i> <sup>d</sup>	2.580	Doubly labeled water	Wild		Adams et al., 1991
<b>Bats</b>					
<i>Pipistrellus pipistrellus</i>	0.007	Respirometry, Doubly labeled water	Flight cage	3.5	Speakman and Racey, 1991
<i>Plecotus auritus</i>	0.008	Respirometry, Doubly labeled water	Flight cage	3.5	Speakman and Racey, 1991
<i>Glossophaga commissarisi</i>	0.009	Mass loss	Flight cage	3.6	Winter and Von Helversen, 1998
<i>Hylonycteris underwoodi</i>	0.009	Mass loss	Flight cage	3.6	Winter and Von Helversen, 1998
<i>Glossophaga soricina</i>	0.011	Mass loss	Flight cage	3.7	Winter and Von Helversen, 1998
<i>Glossophaga longirostris</i>	0.016	Mass loss	Flight cage	3.8	Winter and Von Helversen, 1998
<i>Choeronycteris mexicanus</i>	0.020	Mass loss	Flight cage	3.9	Winter and Von Helversen, 1998
<i>Leptonycteris curasoae</i>	0.028	Mass loss	Flight cage	4	Winter Winter and Von Helversen, 1998
<i>Phyllostomus hastatus</i>	0.093	Respirometry	Wind tunnel	6.0–9.0	Thomas, 1975
<i>Hypsignathus monstrosus</i>	0.258	Heart rate, Respirometry	Wind tunnel	4.0–8.0	Carpenter, 1986
<i>Eidolon helvum</i>	0.315	Heart rate, Respirometry	Wind tunnel	6	Carpenter, 1986
<i>Pteropus poliocephalus</i>	0.628	Heart rate, Respirometry	Wind tunnel	4.0–8.6	Carpenter, 1986
<i>Pteropus alecto</i>	0.779	Respirometry	Wind tunnel	7.0–10.0	Thomas, 1975

<sup>a</sup> No accurate initial measure of body mass.

<sup>b</sup> Sample size very small for doubly labeled water multiple regression.

<sup>c</sup> Small sample size for mass loss method.

<sup>d</sup> No accurate measurement of time spent flying.

Graber, 1962; Hussell, 1969; Hussell and Lambert, 1980). Such studies underestimate flight metabolic rate relative to other studies (Videler, 2006), presumably because birds that arrived later at the lighthouse also sometimes started migrating later, so the slope of mass against time killed is not an accurate estimate of mass lost per hour flying.

We then used data from our literature review (Table 1) to estimate mechanical power ( $P_{mech}$ ), measured in watts, according to Pennycuick (2008):

$$P_{mech} = \frac{59.80m^2}{VB^2} + 0.000403m^{0.666}V^3 + \frac{43.65m^{1.667}S_w}{B^{3.5}} \quad (1)$$

where body mass  $m$  is in kg, wingspan  $B$  is in m, airspeed  $V$  is in m/s,  $S_w$  wing area is in  $m^2$ . Here, we have followed Pennycuick (2008) in assuming that air density is  $1.23 \text{ kg/m}^3$ , acceleration due to gravity is  $9.81 \text{ m/s}^2$ , the induced power coefficient is 1.2, the dimensionless profile power constant is 8.2 and the drag coefficient is 0.08. Although several other mechanical flight models have been advocated (Rayner, 1999; Elliott et al., 2004; Pennycuick, 2008), we use the Pennycuick model as that model is easily the most widely-used. Moreover, the power curves estimated from other models are typically quite similar to the Pennycuick model (e.g. Elliott et al., 2004). Next, we consider the conversion of  $P_{mech}$  into metabolic flight costs (in watts),  $P_{met}$ , based on whole body efficiency  $\eta$  and basal metabolic rate  $BMR$  (estimated separately for birds and bats). From this expression of  $P_{mech}$  we can derive  $P_{met}$  as:

$$P_{met} = \frac{P_{mech}}{\eta} + 3.516m^{0.669} \text{ (birds)} \text{ or } P_{met} = \frac{P_{mech}}{\eta} + 2.82m^{0.744} \text{ (bats)} \quad (2)$$

where basal metabolic rate is estimated as:  $\log(BMR \text{ in } W) = -1.461 + 0.669\log_{10}(m \text{ in grams})$  which converts to  $BMR \text{ in } W = 3.516(m \text{ in kg})^{0.669}$  for birds (McKechnie and Wolf, 2004) or  $\log$

( $BMR \text{ in ml O}_2/h) = 1.0895 + 0.744 \log_e(m \text{ in grams})$  which converts to  $BMR \text{ in } W = 2.83(m \text{ in kg})^{0.744}$  for bats (Speakman et al. 2003). Finally, we considered the possibility that efficiency is a function of the interaction of forward speed and body mass, leading to the following estimators of metabolic power for birds and bats:

$$P_{met} = m^\beta(\alpha + \gamma V)P_{mech} + 3.516m^{0.669} \text{ (Birds)} \quad (3)$$

$$P_{met} = m^\beta(\alpha + \gamma V)P_{mech} + 2.82m^{0.744} \text{ (Bats)} \quad (4)$$

We estimated  $P_{met}$  from 55 studies measuring metabolic flight costs, with separate estimates for birds and bats. Some studies reported only a single average value for flight costs across all speeds, whereas other studies reported values for a range of flight speeds. Data were input into the model together. Thus, those studies with a range of flight speeds weighted more heavily in the model due to their larger sample size. In addition, for a few species there were multiple studies on the same species. In those cases, we considered these studies to be separate datapoints (and were particularly powerful in distinguish the effects of method). As the phylogenetic difference was essentially zero within the same species, our phylogenetic analyses accounted for this pseudoreplication by considering these studies as phylogenetically duplicate points. We used nonlinear least-squares regression to estimate all parameters ( $\alpha$ ,  $\beta$ , and  $\gamma$ ), with data excluded if speed was below 2.0 m/s. Finally, we completed the same analysis with efficiency considered to be the sum of non-interaction body mass and forward speed [ $\eta = (\alpha m^\beta + \delta + \gamma V)^{-1}$ ].

## 2.2. Phylogenetic analyses

To take the phylogeny into account, we retrieved gene sequences of bird and bat species considered here and conducted two separate phylogenetic analyses. We included additional birds (*Rhea americana*,



*Dromaius novaehollandia*, and *Struthio camelus*) and mammals (*Mus tericolor*, *Myrmecobius fasciatus*, and *Tamias sibiricus*) to root the trees. Two mitochondrial genes (*cox1* and *cytB*) are commonly used for bar-coding (Hajibabaei et al., 2007) and are hence available for many species; as such, we primarily focused on these two genes to reconstruct the phylogenies of birds and bats. We used BLASTn searches (Altschul et al., 1990) to identify gene sequences from each individual species (see Table S1 for accession numbers), before aligning them gene-by-gene with the software program Muscle (Edgar, 2004) for each clade independently. Sequences were duplicated in the alignment for those species with > 1  $P_{met}$  sample available. In both clades, AIC-based model selection (Darriba et al., 2012) determined that the data sets should be analyzed with GTR +  $\Gamma$  + I (e.g., Aris-Brosou and Rodrigue, 2012). Phylogenetic trees were reconstructed under maximum likelihood (ML) with PhyML (Guindon et al., 2010), which was also used to generate 1000 bootstrapped trees. The outgroup taxa were used to root the trees, and were then removed from each tree before phylogenetically mapping the metabolic data.

### 2.3. Statistical analyses

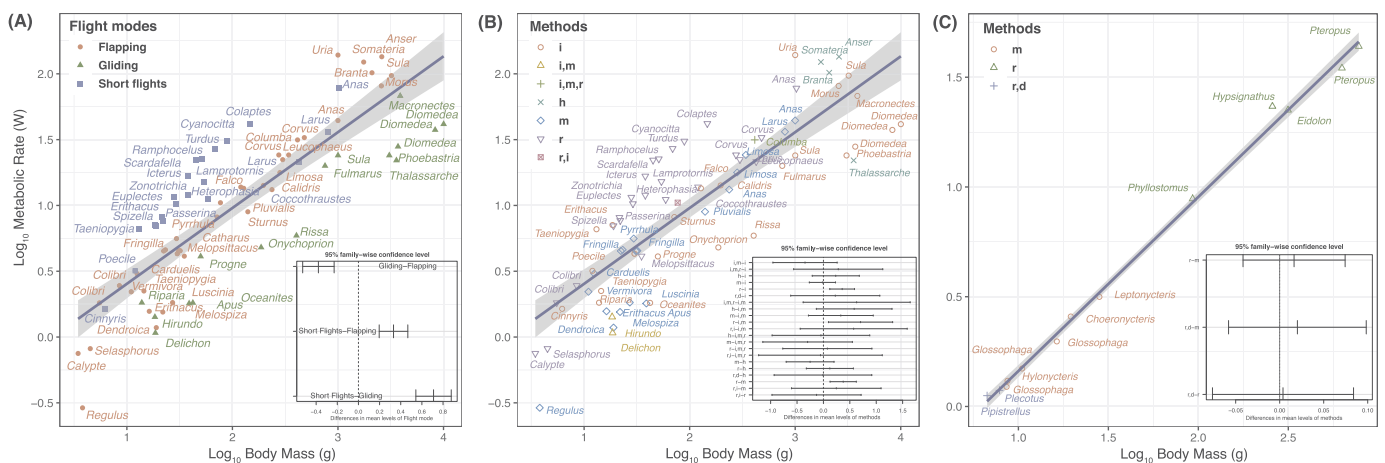
These trees were used to construct all subsequent analyses of metabolic data. All real-valued variables were  $\log_{10}$  transformed, unless otherwise stated. Least-square (LS) regressions were used to compute residuals of mass-corrected metabolic rates (residuals of metabolic rate on body mass), which were then used in the Phylogenetic Independent Contrasts (PIC) analyses. In post-hoc comparisons, Tukey's Honest Significant Differences (HSD) were computed, and pairwise  $t$ -tests were Holm-corrected for multiple comparisons. These were both conducted under regular least-square and robust regressions to reweight outliers. Phylogenetic generalized linear models (PGLS; Freckleton et al., 2002) were employed to test for the predictors of efficiency and the impact of the phylogeny as in Shoji et al. (2016); briefly, this impact can be measured by a parameter called  $\lambda$ : when  $\lambda = 1$ , the regression is driven by the phylogeny, while  $\lambda = 0$  implies a complete phylogenetic independence. In order to test the impact of the phylogeny in driving the regression, we compared a model that assumed complete dependence ( $\lambda = 1$ ) with a model estimating  $\lambda$  by maximum likelihood, and assessed model fit by means of the Akaike Information Criterion, corrected for small sample sizes ( $AIC_c$ ). To take phylogenetic uncertainty into account, each PIC or PGLS analysis was also run on the 1000 bootstrapped trees to generate the sampling distributions of our estimated parameters (see also Shoji et al., 2016). Significance is taken at the 5% level (or 2 units of log-likelihood for differences in AIC, noted

$\Delta AIC$  below; Edwards, 1992; Burnham and Anderson, 2002).

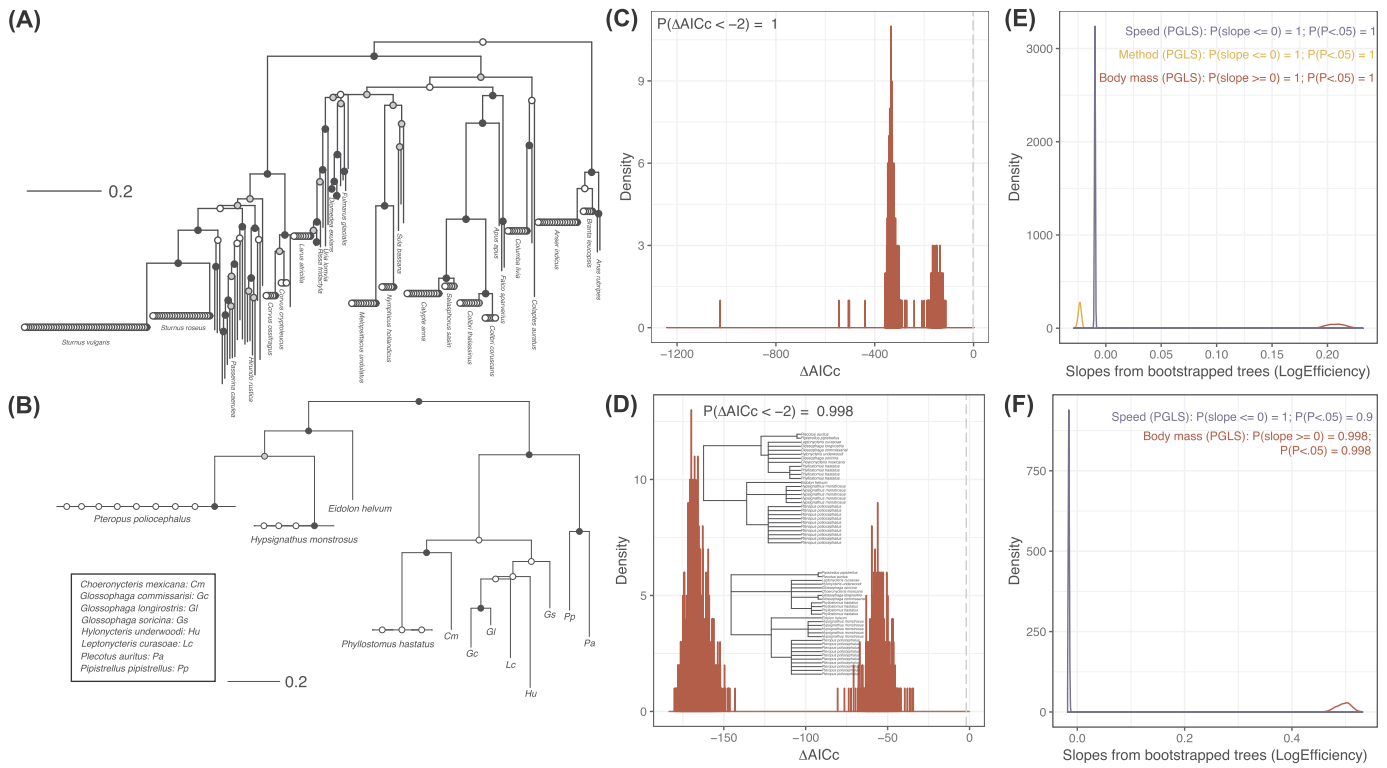
### 3. Results

Short flight had a higher metabolic rate than sustained flapping flight ( $P = 1.2 \times 10^{-7}$ , Holm-corrected pairwise  $t$ -tests), while sustained gliding flight had a lower metabolic rate than sustained flapping flight ( $P = 9.0 \times 10^{-8}$ ; Fig. 1A). We further investigated the relationship between metabolic rate and body mass in birds (Fig. 1B), and in bats (Fig. 1C), and tried to tease apart the role of shared history (phylogeny) or methodological biases. A regular LS regression was statistically significant (birds:  $t = 25.99$ ;  $P < 2.0 \times 10^{-16}$ ; bats:  $t = 61.75$ ;  $P = 2.5 \times 10^{-15}$ ), and the robust regressions of PICs of metabolic rate on methods were not significant (birds:  $t = 1.40$ ;  $P = .169$ ; bats:  $t = 1.01$ ;  $P = .344$ ), while the robust regressions of PICs of metabolic rate on body mass were statistically significant (birds:  $t = 16.47$ ;  $P < 2.0 \times 10^{-16}$ ; bats:  $t = 123.20$ ;  $P = 2.1 \times 10^{-14}$ ), even after accounting for phylogenetic uncertainty.

To assess if  $\eta$  (as reformulated in Eqs. (3) and (4)) depends on body mass, speed, measurement method or phylogeny, during sustained flapping flight, PGLS analyses were conducted in birds and bats based on the estimated phylogenetic trees (Fig. 2, A-B; see Fig. S1-S2 for full trees). We included 22 species of birds and 13 species of bats ranging from 0.003–3.2 kg and 0.007–0.779 kg in body mass, respectively (Table 1). A model estimating the impact of the phylogeny ( $\lambda$ ) fitted the data better than a complete dependence model ( $\lambda = 1$ ) in both clades (birds:  $\Delta AIC_c = -312.79$ ; bats:  $\Delta AIC_c = -173.61$ ; values shown for models with BMR; similar results without BMR term). For models that estimated  $\lambda$  as a free parameter, models with a BMR term fit slightly better for bats ( $\Delta AIC_c = 1.73$ ) and models without a BMR term fit slightly better for birds ( $\Delta AIC_c = 13.84$ ). In bats, in the model that included BMR,  $\lambda$  was estimated to be 0.808 (95% CI: [0.512, 0.939]) while in birds, in the model that did not include BMR,  $\lambda$  was estimated to be 0.857 (95% CI: [0.741, 0.931]). Under these models, body mass positively impacted efficiency in both birds ( $\beta = 0.208$ ,  $t_{179} = 3.97$ ,  $P = .0001$ ; Fig. 2C-E), and bats ( $\beta = 0.505$ ,  $t_{25} = 8.31$ ,  $P = 1.12 \times 10^{-8}$ ). Speed negatively impacted efficiency in both birds ( $\gamma = -0.010$ ,  $t_{179} = -5.43$ ,  $P = 1.77 \times 10^{-7}$ ) and bats ( $\gamma = -0.016$ ,  $t_{25} = -2.26$ ,  $P = .0331$ ). Measurement methods, which only varied among birds, had no impact on efficiency ( $t_{179} = -1.50$ ,  $P = .1345$ ), but here phylogenetic uncertainty affected the results, suggesting a significant negative impact (Fig. 2E). In bats, the greater phylogenetic uncertainty leading to two trees and a bimodal  $\Delta AIC_c$  distribution has little impact on parameter estimates that remain mostly of the same



**Fig. 1.** Variation in flying metabolic rate among flight types after correcting for body mass in birds and bats. Both panels (A) and (B) show the same least-square regression on  $\log_{10}$ -transformed data in birds, with data color-coded for: (A) flight mode; (B) measurement method (i: isotopic dilution [bicarbonate or doubly labeled water]; m: mass-loss; r: respirometry; h: heart rate). (C) same as (B), in bats (m: mass-loss; r: respirometry; d: doubly labeled water). Insets: Tukey's HSD at the 95% threshold.



**Fig. 2.** Impact of phylogeny, speed, body mass and methods on efficiency (without BMR). Maximum likelihood phylogenetic trees estimated for birds (A) and bats (B) are shown with their SH-like approximate likelihood ratio tests support values (*S*; white:  $S < 0.70$ ; gray:  $0.70 \leq S < 0.90$ ; black:  $S \geq 0.90$ ); only select species names are shown, see Fig. S1 and S2 for full names. Based on the 1000 bootstrapped trees, PGLS models were fitted with  $\lambda$  constrained to 1 or not, and the corresponding distribution of  $\Delta AIC_c$  scores are shown for birds (C) and bats (D); the distribution is bimodal in this case due to phylogenetic uncertainty. In each case, the probability of observing a  $\Delta AIC_c$  score more extreme than  $-2$  was computed over the bootstrapped trees. Under the unconstrained models ( $\lambda$  estimated by ML), the distributions of the parameter estimates obtained under the bootstrapped trees are shown for birds (E) and bats (F), along with the probability that these estimates are  $> 0$ , and significant.

sign and significant for both body mass and speed.

To provide inputs into our model for flight costs, we considered a nonlinear regression for efficiency. Based on the results above, we considered a model without BMR for birds and with BMR for bats. For birds, an additive model had better fit than an interactive model ( $\Delta AIC_c = 4.11$ ). For bats, an interactive model fit better than an additive model ( $\Delta AIC_c = 2.11$ ). For birds, the intercept ( $t_{189} = 12.77$ ,  $P < 2.0 \times 10^{-16}$ ), mass exponent ( $t_{189} = 6.82$ ,  $P < 1.21 \times 10^{-10}$ ), mass coefficient ( $t_{189} = 7.14$ ,  $P < 1.92 \times 10^{-11}$ ) and speed coefficient ( $t_{189} = -1.98$ ,  $P = .0497$ ) were significant. For bats, only the mass exponent was significant ( $t_{24} = 9.21$ ,  $P = 2.41 \times 10^{-9}$ ). The final models were:

$$P_{met} = \frac{1}{(0.057m^{0.77} + 0.074 - 0.001V)} \times \left( \frac{59.80m^2}{VB^2} + 0.000403m^{0.666}V^3 + \frac{43.65m^{1.667}S_w}{B^{3.5}} \right) \text{ (Birds)} \quad (5)$$

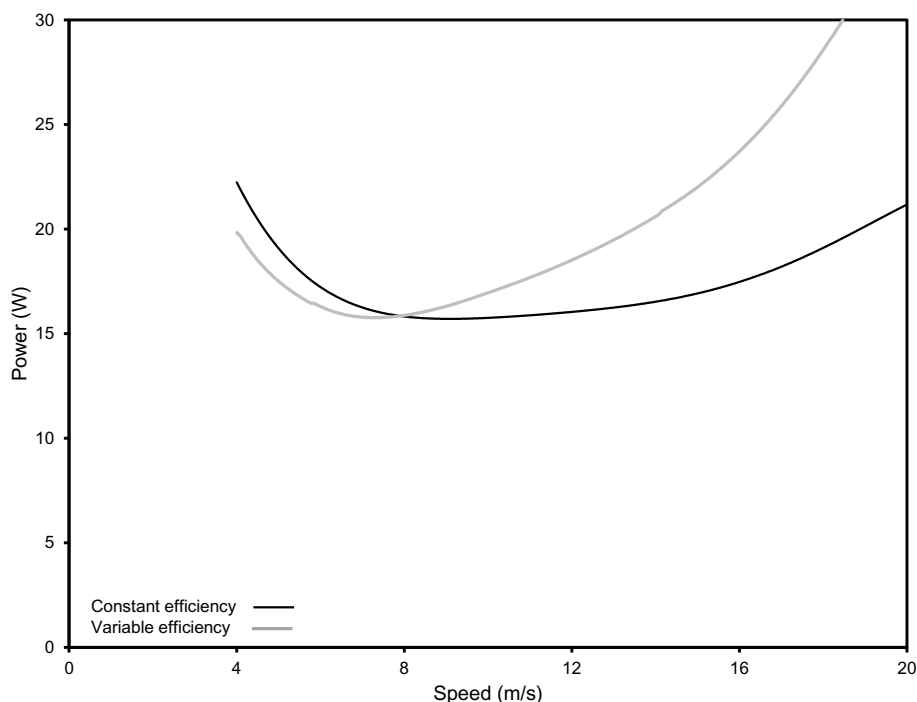
$$P_{met} = \frac{m^{-0.34}}{(0.30 - 0.008V)} \times \left( \frac{59.80m^2}{VB^2} + 0.000403m^{0.666}V^3 + \frac{43.65m^{1.667}S_w}{B^{3.5}} \right) + 2.82m^{0.744} \text{ (Bats)} \quad (6)$$

The influence of our Eq. (6), as compared to classic models with constant efficiency, is shown in Fig. 3. For an average-sized bat (*Phyllostomus hastatus*), the decreasing efficiency with forward speed causes a substantial shift in the shape of the U-shaped power curve.

#### 4. Discussion

Sustained flapping flight costs were  $\sim 1.8$  times lower than costs during short flights, presumably due to the acceleration costs associated with taking off (Nudds and Bryant, 2000). Meanwhile, sustained flapping flight costs averaged  $\sim 2.5$  times higher than costs for sustained gliding flight, illustrating the high costs associated with sustained flapping flight. Moreover, gliding flight costs appeared much more variable than flapping flight costs after accounting for body mass (Videler, 2006; Elliott et al., 2013). Considering only flapping flight, there was no significant variation in flight costs measured with different methods, implying that doubly labeled water (or bicarbonate), heart rate, direct respirometry and mass loss are all equivalent methods for measuring flight costs. Our comparative results are like those reported by Ward et al. (2004), who also noted no difference in metabolic flight costs among three methods (respirometry, doubly labeled water and heat loss) within the context of a single study. As noted earlier, however, and following Videler (2006), we excluded estimates from mass loss where initial mass was not known (Table 1). Those studies provide estimates for flight costs that are substantially lower than those reported here.

Efficiency increased with body mass for both birds and bats. A previous study found that small bats flew more cheaply than small birds (Winter and Von Helversen, 1998), which is not consistent with the higher exponent (0.34) for bats than birds (0.19). However, overall, birds had lower efficiency than bats, presumably reflecting their higher overall metabolic rate than mammals. Efficiency decreases with increasing flight speed in birds and bats. In contrast, Ward et al. (2004) found that flight efficiency increased with flight speed in starlings *Sturnus vulgaris*. However, Ward et al. (2004) likely overestimated  $P_{mech}$



**Fig. 3.** Impact efficiency variability on power curves. Variation in U-shaped metabolic power curve ( $P_{met}$ ) are shown for an average-sized bat, *Phyllostomus hastatus*, with constant efficiency of 0.15 (black line) and our variable efficiency model (gray line).

at high flight speeds because they used earlier, high values for the parasite drag coefficient. Their data is included within our own, and with a revised version of the drag coefficient, their data, like the larger comparative dataset, shows a stable or decreasing trend in efficiency with flight speed. As such, our results concur with the main conclusion of Ward et al. (2004) that efficiency varies with flight speed and should not be considered constant.

Some ‘basal’ processes, such as brain neural activity and metabolic activity, may increase during flight, while others, such as digestive maintenance and thermoregulation (due to heat increment from activity) may decrease. Thus, it is not immediately obvious that BMR would be additive to mechanical flight costs rather than subsumed within the efficiency term. Indeed, in birds, models without BMR were more parsimonious than models with BMR. In contrast, in bats, models with BMR as an additive factor to flight costs were more parsimonious than models without BMR, supporting previous models where BMR was added to flight models (Pennycuick, 2008). Perhaps one way that bats maintain higher overall efficiency is by separating BMR from costs directly associated with flight.

Much of the research into flight costs occurred prior to 2000, with relatively few experiments in the following two decades. We argue that more data are needed to confirm both mechanical and metabolic costs. For instance, many of the parameters in the Pennycuick model are only approximately known. A good example is the parasite drag coefficient whose value was estimated based on assuming that the wingbeat frequency minimum corresponded with the minimum power speed (Pennycuick et al., 1996), yet that assumption has since been refuted (Tobalske et al., 2003; Askew and Ellerby, 2007). Confirmation of estimates for the induced power coefficient, the parasite drag coefficient and the profile power coefficient across a variety of *Bauplans* and a wider range of body masses would allow us to estimate mechanical costs with increasing accuracy, and should be simpler today than in the past due the possibility of numerically simulating many of those costs.

The Pennycuick model has been the basis for a large subfield of behavioral ecology focusing on optimal migration and flight speed that

have qualitatively verified many of the behavioral predictions arising from that model (e.g., Welham and Ydenberg, 1993; Hedenström and Ålerstam, 1995; Ålerstam and Hedenström, 1998). Our proposed equations (Eqs. (5) and (6)), which consider variation in efficiency with body mass and forward speed, could be the basis for more accurate predictions. As shown in Fig. 3, with as an example for an average-sized bat (*Phyllostomus hastatus*), the decreasing efficiency with forward speed can cause a substantial shift in the shape of the U-shaped power curve. Such a shift can lead to alterations in predicted optimal speeds and estimates of energy expended during flight. Given that the miniaturization of heart-rate loggers and accelerometers (the ‘golden age’ of biologging) allows for the measurement of mechanical and metabolic flight costs in the field (Bishop et al., 2015; Elliott, 2016), we are entering a golden age for flight research, where flight curves can be measured on wild birds moving at different speeds (Shepard et al., 2008, 2016; Portugal et al., 2014).

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#### Declarations of interest

None.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cbpa.2019.06.003>.

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