Does the metabolic rate–flight speed relationship vary among geometrically similar birds of different mass?

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Summary

Based on aerodynamic considerations, the energy use–flight speed relationship of all airborne animals and aircraft should be U-shaped. However, measures of the metabolic rate–flight speed relationship in birds have been available since Tucker's pioneering experiments with budgerigars nearly forty years ago, but this classic work remains the only study to have found a clearly U-shaped metabolic power curve. The available data suggests that the energetic requirements for flight within this species are unique, yet the metabolic power curve of the budgerigar is widely considered representative of birds in general. Given these conflicting results and the observation that the budgerigar's mass is less than 50% of the next smallest species to have been studied, we asked whether large and small birds have metabolic power curves of different shapes. To address this question we measured the rates of oxygen uptake and wingbeat kinematics in budgerigars and cockatiels flying within a variable-speed wind tunnel.

These species are close phylogenetic relatives, have similar flight styles, wingbeat kinematics, and are geometrically similar but have body masses that differ by a factor of two. In contrast to our expectations, we found the metabolic rate–flight speed relationship of both species to be acutely U-shaped. We also found that neither budgerigars nor cockatiels used their normal intermittent flight style while wearing a respirometric mask. We conclude that species size differences alone do not explain the previously unique metabolic power curve of the budgerigar; however, due to the absence of comparable data we cannot evaluate whether the mask-related kinematic response we document influences the metabolic rate–flight speed relationship of these parrots, or whether the energetics of flight differ between this and other avian clades.

Key words: bird flight, power curve, metabolic rate.

Introduction

The rates of metabolic energy release required to support vertebrate flapping flight are far greater than those of other modes of locomotion. The high metabolic cost of flight is especially significant to avian species since many birds spend large portions of their lives in the air. For instance, some species feed only while in flight (Cleere, 1999; Chantler, 1999), other must fly to attract a mate (Weidensaul, 1996), and many species fly over 6000 km twice a year during their annual migrations (Elphick, 1995; Klassen et al., 2000). Supplying and presumably minimizing the metabolic requirements of flight have long been considered to be among the primary selective forces in shaping the morphology of volant birds (Savile, 1957; Brown, 1961).

Although the design of the avian respiratory system is consistent with the need to support sustained high metabolic rates, it is unclear what the metabolic energy demands are for birds flying at different speeds (Rayner, 1999). Rates of oxygen uptake measured from birds in flight are known to be at least an order of magnitude greater than those at rest (Ellington,

1991; Norberg, 1996), but considerable uncertainty surrounds the qualitative shape of the metabolic rate–flight speed relationship (Ellington, 1991; Alexander, 1997). Measured values of metabolic energy release from birds flying across a range of speeds have produced relationships that are essentially flat (Tucker, 1972; Bernstein et al., 1973; Torre-Bueno and Larochelle, 1978; Hudson and Bernstein, 1983; Ward et al., 2001), slightly curvilinear (Rothe et al., 1987; Ward et al., 2002), and in a single study, acutely concave (Tucker, 1968). Indeed, if compared on the basis of the difference between the peak and minimum measured rates of oxygen uptake, expressed as a multiple of the resting rate (Lasiewski and Dawson, 1967), only the budgerigars (*Melopsittacus undulatus*) studied by Tucker (Tucker, 1968) appreciably alter their metabolic rate ($\Delta=7.1\times$RMR) during flights across the measured speed range. In contrast, all other published reports indicate that birds require little change in metabolic power in order to fly across a wide range of speeds [mean $\Delta=1.7\pm0.4\times$RMR ($\pm$ s.e.m.; $N=8$ species)]. Thus, the available data indicate that the U-shaped power curve of the budgerigar

is unique; however, the metabolic rate–flight speed relationship of this species is widely considered representative of birds in general (Schmidt-Nielsen, 1997; Blem, 2000; Harrison and Roberts, 2000).

Based on classical aerodynamic theory the mechanical power–flight speed relationship of an airborne animal should be U-shaped. Empirical tests of these predictions obtained from measures of muscle mechanical power across a wide range of speeds (Dial et al., 1997; Tobalske et al., 2003a), provide reasonable agreement between theory and *in vivo* measurement (Rayner, 1999). However, since the relationship between metabolic and mechanical power has not been determined for bird flight, it is not currently possible to calculate the metabolic requirements for flight from measures of mechanical power. Although many investigators justify metabolic–mechanical comparisons through the assumption that the relationship between these quantities is invariant during flight, in other modes of locomotion this relationship is known to vary. For example, the metabolic cost of terrestrial running is not related to the mechanical work performed during this gait (Heglund et al., 1982; Heglund, 2004). Therefore, for flying vertebrates in general, and birds in particular, it is unknown whether an individual animal's metabolic and mechanical power curves are congruent.

Several hypotheses have been offered to account for the apparent discrepancy between metabolic measurement and aerodynamic predictions. These explanations have generally focused on the possible effects of flying within a wind tunnel (Rayner, 1994) or the expectation that the power requirements should vary only slightly across the intermediate range of speeds investigated *via* metabolic measurement (Rayner, 1999). However, it is difficult to reconcile these explanations with the observations of Tucker, who found that laughing gulls (*Larus atricilla*) (Tucker, 1972) produced an essentially flat metabolic curve while flying over a wider range of speeds compared with the budgerigar (Tucker, 1968). An alternative and biological explanation for the metabolic–aerodynamic discrepancy may be the size-specific use of an energy-saving strategy to lower the metabolic power requirements. Accordingly, the 'flat' metabolic power curves may result from a mechanism that either reduces the requirements for muscle mechanical power at certain flight speeds (e.g. Thomas, 1996; Lighthill, 1977) or permits muscle to generate power more economically (e.g. Rome et al., 1988; Biewener et al., 1998).

The qualitative differences between the metabolic power curves of the budgerigar and the other species studied suggest that the determinants of the metabolic rate–flight speed relationship differ among species. Given the preponderance of existing metabolic data we reasoned that the budgerigar's unique metabolic power curve may be related to the budgerigar's lesser body mass; the budgerigar's mass is less than half of the next smallest species to have been studied (Torre-Bueno and Larrochelle, 1978). To test this idea we trained budgerigars and cockatiels (*Nymphicus hollandicus*) to fly within a variable speed wind tunnel and measured both the rates of oxygen uptake and wingbeat kinematics as the birds flew across a wide range of speeds. These species are close phylogenetic relatives (family Psittaciformes), have similar flight styles and wingbeat kinematics, and are geometrically similar (Tobalske et al., 2003b), but have body masses that differ by a factor of two. This difference allowed us to evaluate whether these parrots have metabolic rate–flight speed relationships that are conserved or whether the budgerigar's smaller body mass might account for this bird's outlier status among the species studied.

Materials and methods
Animals and training

Four budgerigars (*Melopsittacus undulatus* Shaw, mass 36.7±2.1 g; mean ± s.e.m.) and three cockatiels (*Nymphicus hollandicus* Kerr, mass=80.5±5.6 g) were purchased from a local pet store and housed at the University of Montana's laboratory animal holding facility and at the Fort Missoula Research Station. The birds were fed a commercially available diet (Kaytee Forti-Diet, Chilton, WI, USA and Mazuri Feed, Purina Mills, St Louis, MO, USA) *ad libitum*. All training and experimental procedures were approved by the University of Montana Institutional Animal Care and Use Committee.

The birds were trained to fly within a variable speed wind tunnel for at least 3 months. Training consisted of 3–5 20 min sessions per week and was continued until the birds could sustain uninterrupted flights of 20 min, or more, at their preferred speed. Once the birds were accustomed to unencumbered wind tunnel flights, they were trained to fly while wearing clear plastic masks. The masks were connected by tubing (i.d.:o.d. 0.8:2.4 mm for budgerigars and 1.6:3.2 mm for cockatiels; Tygon Saint-Gobain Performance Plastics, Akron, OH, USA) to a vacuum source that removed air at metered flow rates. When the birds could maintain uninterrupted flights for a period of 4 min with their masks on, we began to collect pilot metabolic data to determine the minimum flight durations required to reach a metabolic steady state. After three consecutive wind tunnel sessions without an appreciable change in the steady-state metabolic rate at the preferred flight speed, the birds were considered fully trained.

Wind tunnel and air speed

Prior to the initiation of this study, the University of Montana wind tunnel as described by Tobalske and Dial (Tobalske and Dial, 1994) underwent renovations to improve the flow characteristics within the test section. A detailed description of the alterations and subsequent flow testing is presented in the Appendix. Briefly, the mean turbulence of the wind tunnel following the renovation was 1.19±0.02%, and at a mean wind speed of 10 m s^{-1} the coefficient of variation (CV) of 168 measures of air speed from different locations within the test section was 2.7%.

We measured wind speed from the pressure difference across two static pressure tips (Dwyer A-303, Michigan City, IN, USA) upstream of the test section, with one tip on each side of the contraction (Hedrick et al., 2002). The pressure difference

experienced by the static tips was measured by a differential pressure transducer (Datum 2000, Setra, Boxborough, MA, USA; sensitivity 0.2 Pa) and was converted to dynamic pressure by a linear calibration based on dynamic pressure measurements obtained at four locations along the midline (width dimension) of the wind tunnel.

For consistency with earlier metabolic studies we measured true, rather than equivalent, wind speed. True and equivalent, wind speeds are the same only under the conditions of the International Standard Atmosphere. The mean atmospheric pressure in Missoula (elevation 975 m) and the ambient temperature within our laboratory accounted for a reduction in air density (ρ=1.075 *vs* 1.225 kg m^{-3}) that resulted in the true wind speed being 6.3% greater than calculated values of equivalent wind speed. Similarly, the birds flying within the Flight Laboratory wind tunnel experienced equivalent dynamic pressures at true wind speeds that were 5.1% greater than those of the Duke University tunnel (elevation 120 m) (Tucker, 1968).

Metabolic measurements

To capture the respiratory gases of the subject animals in flight the birds wore lightweight custom-designed masks. The masks were made from heat-malleable plastic (PET-G, TAP plastics, Dublin, CA, USA) and vacuum-formed around a species-specific mold (Walsh, 1998). The masks were held in place on the bird by two horizontal strands of elasticized thread that permitted the bird's head to enter the mask but prevented the animal from removing the mask during a flight session. During data collection the length of tubing between the mask and the exit point of the wind tunnel test section was fixed at 63 and 43 cm for the budgerigars and cockatiels, respectively. The mass of the mask and standardized length of tubing was 5.8 g for the budgerigars and 8.9 g for the cockatiels. The tubing was connected to a flow meter (R-6-15-A, Brooks Instrument, Hatfield, PA, USA) and vacuum source (DOA/V191/AA, Gast Manufacturing Inc., Benton Harbor, MI, USA), which ensured a constant flow rate through the mask (Fedak et al., 1981).

An aliquot of the evacuated air was dried (W. A. Hammond Drierite Co., Xenia, OH, USA) and analyzed for carbon dioxide fractions (CD3A, AEI technologies, Naperville, IL, USA), scrubbed of CO_2 (Ascarite II, Mallinckrodt Baker, Philipsburg, NJ, USA) and then analyzed for oxygen content (AEI technologies, S-3A). The analog outputs from the analyzers were recorded by strip-chart (Miniservo, Esterline-Angus, Bellevue, WA, USA), to provide a continuous record of the oxygen consumption and carbon dioxide production throughout a flight. The oxygen and carbon dioxide analyzers were calibrated daily with measured flow rates (Brooks, 1054A3A) of nitrogen and carbon dioxide, and the volumes of oxygen consumption and carbon dioxide production were calculated in accordance with Fedak et al. (Fedak et al., 1981). All volumes were converted to STPD with daily measurements from a digital barometer and thermometer.

Only flights with steady-state values of oxygen consumption were included in the subsequent analysis. Flight trial durations at a given speed were at least 4 min and generally greater than 6 min. For birds that were exceptionally strong fliers it was occasionally possible to obtain up to three steady state measurements during the same data collection session; despite the longer trial durations required to obtain the additional measurements the birds did not remain in the mask for more than 20 min. Mass-specific metabolic rates were determined by dividing the measured rate of oxygen consumption by the bird's mass.

High-speed video

To determine the possible influence of wearing a mask on flight kinematics, we used either two internally synchronized digital high-speed video cameras or a single high-speed analog camera (250 and 500 f.p.s., 1/2500 and 1/5000 s shutter speed, PCI 500 and Motionscope S series, Redlake MASD Inc., Tucson, AZ, USA). The whole-body kinematic variables most representative of the duration of pectoralis muscle force production, and thus metabolic energy liberation (Huxley, 1969; Kram and Taylor, 1990) are the frequency and duration of wing downstroke. Accordingly, we measured wingbeat frequency (Hz; budgerigar, *N*=351 wingbeat cycles, cockatiel *N*=306 wingbeat cycles), duty factor (%; budgerigar, *N*=328 wingbeat cycles; cockatiel *N*=297 wingbeat cycles), and the proportion of time spent in flapping flight (%; budgerigar, *N*=564 wingbeat cycles; cockatiel, *N*=788 wingbeat cycles) from two budgerigars and two cockatiels while they flew with and without their masks.

The wingbeat frequency of each bird was calculated as the inverse of the period (s) between the start of one downstroke and the beginning of the subsequent downstroke. Wingbeats that preceded or followed a glide or a bound were not included in the analysis. We calculated the duty factor as the fraction of the downstroke duration compared to the duration of the entire wingbeat cycle. The downstroke and upstroke transitions were determined based on the movements of the bird's wrist.

The proportion of time spent in intermittent flight was determined by comparing the expected number of wingbeats based on the measured wingbeat frequency for a given individual bird and flight speed to the number of wingbeats executed during a recording. We reasoned that the ratio of the tallied number of wingbeats to the expected number was representative of the time spent in flapping flight. For example, a value of 50% would correspond to a measurement of half the expected number of wingbeats for a given flight duration, and was interpreted to represent equal periods of intermittent (e.g. flap-gliding, flap-bounding) and flapping flight.

Statistics

To determine whether the mean rates of oxygen uptake varied across flight speed we performed species-specific one-way ANOVAs, with a Bonferroni test of *post hoc* means. In addition, effect sizes (ES) were calculated for pairwise comparisons using Hedges' *g*-statistic (Hedges, 1981). The effect size is a measure of the strength of the relationship

between two variables; here we use this statistic to assess the effect of changes in flight speed on metabolic rate.

We measured flight kinematics from two budgerigars and two cockatiels and used these data to investigate the influence of wearing the mask on the within-wingbeat kinematics by conducting a 2×6 (budgerigar) and a 2×8 (cockatiel) mixed ANOVA with repeated measures on the flight speed factor. Because the speed protocols between masked and unmasked flights were different for the budgerigars, we compared kinematic measures at adjacent rather than equivalent flight speeds, as was done for the cockatiels. A critical alpha level of $P<0.05$ was adopted for all significance tests. Throughout the manuscript means are reported ± s.e.m.

Results
Metabolism during flight

For budgerigars and cockatiels the metabolic cost of flight was greater at fast and slow flight speeds, while at intermediate speeds the birds flew more economically (Fig. 1). The mean rates of oxygen uptake differed across speed (budgerigar, $F_{(5,69)}$=12.44, $P<0.001$; cockatiel, $F_{(6,61)}$=17.54, $P<0.001$), and the peak rates of oxygen consumption were measured at flight speeds of 5 m s^{-1} and 15 m s^{-1} for the budgerigars and cockatiels, respectively. Subsequent *post hoc* tests revealed that the mean rates of oxygen uptake at slower (5 and 6 m s^{-1}) and faster (14 and 15 m s^{-1}) flight speeds were different than those at intermediate flight speeds (8 and 10 m s^{-1}) for the cockatiels, although the 8 *vs* 14 ms^{-1} comparison only approached significance. The budgerigar *post hoc* comparisons revealed that the oxygen uptake elicited at a slow flight speed (6 m s^{-1}) differed from that at intermediate flight speeds (8 and 10 m s^{-1}), and that the effect size comparisons between the minimum power speed (10 m s^{-1}) and slowest (5 m s^{-1}; ES=3.30) and fastest (14 m s^{-1}; ES=1.92) flight speeds indicated a large (ES>0.80) effect of flight speed on metabolic rate. For both species the respiratory exchange ratio (RER: $\dot{V}_{CO_2}/\dot{V}_{O_2}$) was well below 1.0 at all flight speeds, a strong indication that ATP resynthesis was provided entirely by aerobic metabolism (Table 1). The highest measured values of RER for budgerigars, 0.88±0.01, were obtained at the fastest flight speed; in contrast the peak RER values for cockatiels, 0.91±0.02, were measured at the slowest flight speed.

The interpolated minimum power speeds were 9.7±0.1 m s^{-1} for the budgerigars and 9.8±0.2 m s^{-1} for the cockatiels. The energetic requirement of flight at the minimum power speed was estimated to be 9.0±0.4 ml O$_2$ kg^{-1} s^{-1} and 5.3±0.3 ml O$_2$ kg^{-1} s^{-1} for budgerigars and cockatiels, respectively. These values are, respectively, 19.0 and 13.8 times the predicted resting metabolic rate for birds of equal mass (Lasiewski and Dawson, 1967). For the budgerigars and cockatiels, the differences between the peak metabolic rates and those measured at the minimum power speed were 5.9×RMR and 8.4×RMR, respectively,
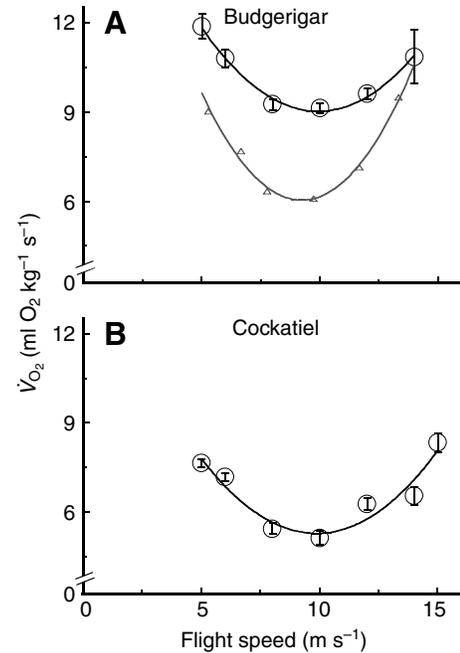

Fig. 1. The metabolic power requirements of flight in budgerigars (A) and cockatiels (B) across a wide range of flight speeds. The gray triangles in A are published values for budgerigars (Tucker, 1968); the curve-fitted gray line was extrapolated to match the current range of flight speeds.

indicating that both species appreciably altered their metabolic rate during flights across the measured speed range.

Wingbeat kinematics

For both budgerigars and cockatiels the values of wingbeat frequency were not statistically different ($P>0.05$) between flights with (budgerigars, N=124 wingbeats; cockatiels, N=186 wingbeats) and without (budgerigars, N=228 wingbeats; cockatiels, N=229 wingbeats) a mask (Fig. 2A,C). Both during free flights and while wearing the mask the wingbeat frequency of the budgerigars varied only slightly across the range of flight speeds, decreasing from 17.3±0.4 Hz at 3 m s^{-1} to 16.2±0.2 Hz at 13 m s^{-1}. In contrast, cockatiels flying with or without the mask increased the duration of their wingbeats by roughly 25% during flights at the slowest compared to the fastest flight speeds. This resulted in cockatiels decreasing their wingbeat frequency from 8.9±0.2 Hz at 2 m s^{-1} to 6.4±0.3 Hz at 14 m s^{-1} (mean of both conditions).

The repeated-measures ANOVA for budgerigar duty factor indicated an effect of wearing the mask ($F_{(1,22)}$=8.60, $P<0.01$). Subsequent pairwise comparisons (Bonferroni method) revealed that for budgerigars wearing the mask (N=118 wingbeats across all speeds) and flying at speeds less than 6 m s^{-1} the duty factor was greater than during free flights (N=210 wingbeats across all speeds) at similar speeds. At speeds greater than 6 m s^{-1} there was no difference in duty factor between the masked and free flight conditions ($P>0.05$).

Table 1. *Rates of oxygen consumption, carbon dioxide production and the respiratory exchange ratio (RER) during flights across a range of speeds*

Flight speed (m s^{-1})	$\dot{V}_{O_2}$ (ml O$_2$ kg^{-1} s^{-1})		$\dot{V}_{CO_2}$ (ml CO$_2$ kg^{-1} s^{-1})		RER ($\dot{V}_{CO_2}/\dot{V}_{O_2}$)	
	Budgerigar	Cockatiel	Budgerigar	Cockatiel	Budgerigar	Cockatiel
5	11.9±0.4	7.7±0.1		6.9±0.2		0.91±0.02
6	10.8±0.3	7.2±0.1	7.8±0.3	5.5±0.2	0.75±0.02	0.76±0.07
8	9.3±0.2	5.4±0.2	7.0±0.1	4.0±0.2	0.77±0.04	0.74±0.05
10	9.1±0.2	5.1±0.2	6.9±0.1	3.8±0.2	0.75±0.04	0.75±0.07
12	9.6±0.2	6.3±0.2	7.7±0.2	4.6±0.2	0.80±0.05	0.72±0.05
14	10.9±0.9	6.6±0.3	9.2±1.3	4.6±0.1	0.88±0.01	0.71±0.04
15		8.3±0.3		6.8±0.9		0.81±0.11

Budgerigars (N=4, body mass=36.7±2.1 g); cockatiels (N=3, body mass=80.5±5.6 g).

The overall mean value of 0.49±0.01% suggests that across the entire range of flight speeds the duration of the wingbeat cycle was nearly evenly divided between the downstroke and upstroke phases (Fig. 2B). Cockatiels flying at faster speeds decreased duty factor by roughly 15% compared to values at slower flight speeds (Fig. 2D). Thus at fast flight speeds, cockatiels have a longer upstroke than downstroke. For cockatiels the values of duty factor were similar (P>0.05) for flights with and without the mask (cockatiels; no mask, N=223 wingbeats; with mask, N=177 wingbeats).

Both budgerigars and cockatiels altered their use of intermittent flight during flights with *versus* without the mask (Fig. 3). During unencumbered flights, both the budgerigars (N=17 flights, 422 wingbeat cycles) and cockatiels (N=24 flights, 527 wingbeat cycles) used intermittent flapping flight at intermediate and fast speeds. In contrast, when budgerigars (N=14 flights, 142 wingbeat cycles) and cockatiels (N=26

flights, 261 wingbeat cycles) flew while wearing their masks they relied almost entirely upon continuous flapping flight (Fig. 3B,D).

Discussion

For both the budgerigars and cockatiels the metabolic rate-flight speed relationship was acutely concave. A similar U-shaped power curve has previously been measured for budgerigars (Tucker, 1968), and based on aerodynamic considerations this relationship is predicted for all birds (Pennycuick, 1968; Rayner, 1979), yet the cockatiel is only the second avian species for which clear descending and ascending limbs of a U-shaped metabolic power curve have been obtained. In contrast to our expectations, the qualitatively similar power curve of the larger cockatiel, a close relative of the budgerigar with similar aspect ratio, wing loading and flight styles, indicates that species size differences alone do not explain the previously unique metabolic power curve of the budgerigar. Our kinematic data indicate that both cockatiels and budgerigars eliminate the use of intermittent flight (Fig. 3) while wearing the mask. However, because empirical measures of the potential energetic savings from intermittent flight are unavailable we cannot assess the effect of these kinematic differences. Further, because kinematic data
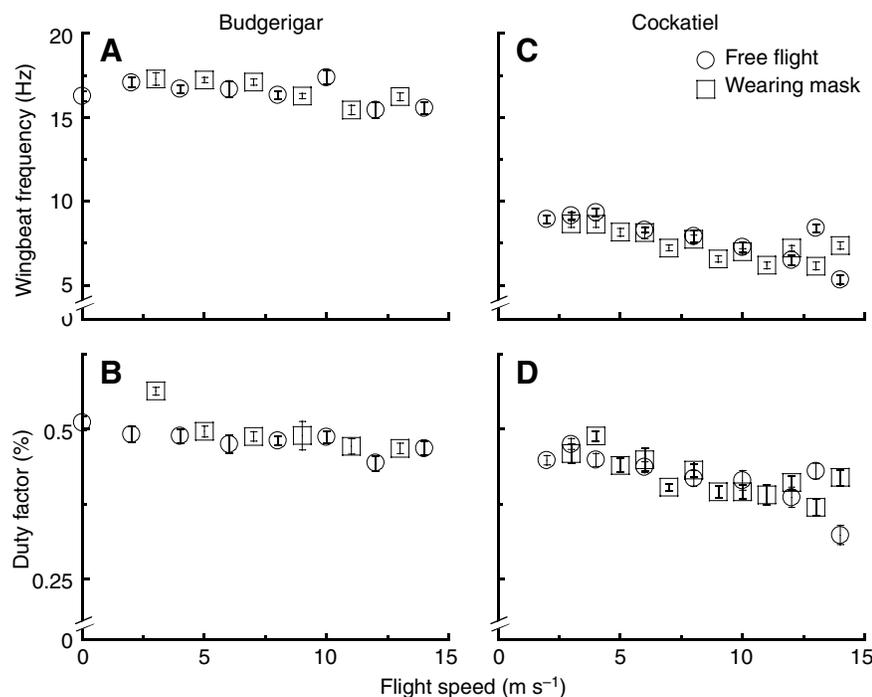

Fig. 2. Wingbeat frequency (A,C) and duty factor (B,D) during budgerigar (A,B) and cockatiel (C,D) flights with and without a respirometric mask. Wearing a mask did not elicit substantial changes in wingbeat frequency or duty factor for either budgerigars or cockatiels. For the budgerigars, wingbeat frequency and duty factor were nearly constant across flight speed. In contrast, cockatiel wingbeats were roughly 25% longer and had downstroke durations that were relatively shorter at the fastest compared to slowest flight speeds.
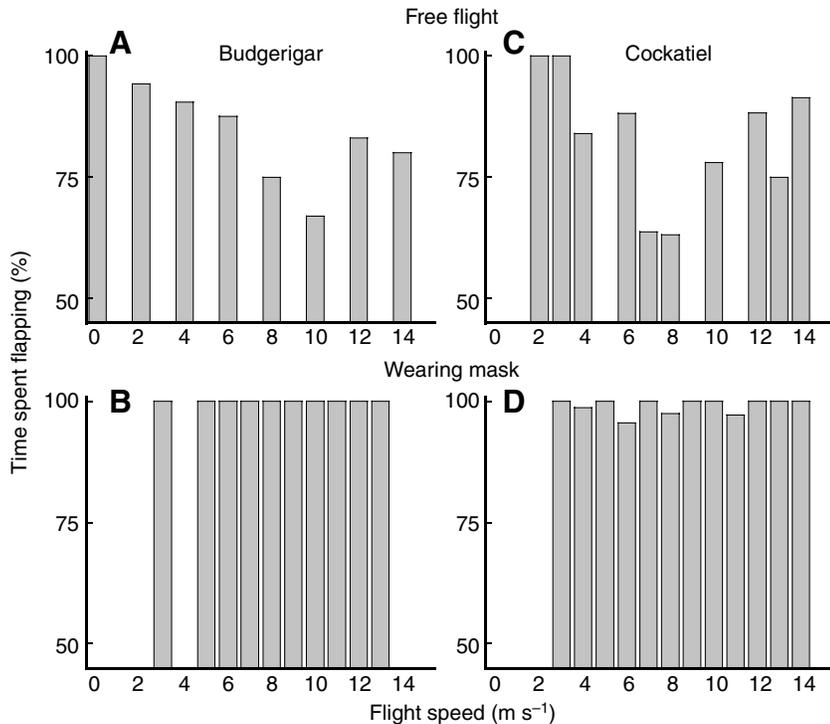
Fig. 3. Use of intermittent flight during wind tunnel flights with (A,C) and without (B,D) the respirometric mask for budgerigars (A,B) and cockatiels (C,D). During free flight both species used intermittent flight at intermediate and fast flight speeds; in contrast, while wearing the mask both species relied almost entirely on continuous flapping flight.

from other energetic studies are also unavailable we cannot determine whether similar kinematic responses are ubiquitous among birds flying with a mask or whether the results we report here are specific to Psittacids. Therefore, although the metabolic rate–flight speed relationship is conserved across geometrically similar birds of different body mass, we cannot exclude the possibility that these U-shaped power curves may have been influenced by the elimination of intermittent flight during the metabolic recordings.

High rates of aerobic metabolism in birds

The rates of oxygen consumption measured from the budgerigars were greater than those traditionally attributed to this species at equivalent flight speeds (Tucker, 1968). At the slowest, minimum power, and fastest flight speeds, the means we report here were 19, 33 and 2% higher, respectively, than existing data at similar flight speeds (Fig. 1). A possible explanation for these differences may be the greater masses of both our birds and the respiratory mask, due to the longer length of tubing required by the greater dimensions of our wind tunnel test section. The apparent convergence of the two budgerigar power curves (Fig. 1) at faster flight speeds is consistent with this explanation, since the fraction of mechanical power required to overcome weight support is reduced during fast flight (Pennycuick, 1989). Although the rates of oxygen consumption we report here are greater than those normally

attributed to budgerigars (Tucker, 1968), they should not be considered species maximums since they are less than earlier published values (Tucker, 1966).

Measurements of oxygen uptake during bird flight have identified the highest known mass-specific metabolic rates in the vertebrate world (Suarez et al., 1991). It has been unclear, however, whether the metabolic rates measured at the limits of flight performance are caused by, coincident with, or independent of the functional limit of the respiratory system. The available data and our results suggest that the upper performance limits of bird flight are probably not set by metabolic limitations. The failure of hummingbirds (*Archilochus colubris*) to remain aloft in a hypo-dense gas mixture (Chai and Dudley, 1995) was not caused by metabolic factors but was unambiguously caused by the mechanical inability of increasing wingbeat amplitude beyond 180° (Dudley and Chai, 1996). Further, Epting (Epting, 1980) found that hummingbirds who had lost wing feathers due to molt, had rates of oxygen uptake while hovering that were 50% greater than those previously measured for similar flights. Despite being generally cooperative and well-trained the budgerigars and cockatiels studied here could not, or would not, fly at speeds beyond those reported, and the highest measures of RER were considerably less than 1.0, indicating the intensity was likely below the aerobic limit (Seeherman et al., 1981; Bundle et al., 1999). Finally, the results we present here and the rates of oxygen uptake measured during the continuous ascending flights of budgerigars (Tucker, 1968) were less than similar measures obtained from this species flying in a highly turbulent fluid (Tucker, 1966). The apparent absence of a consistent relationship between performance limitation and metabolic rate strongly suggests that non-metabolic factors influence the maximum flight speeds and hovering performances in birds.

A mechanical or aerodynamic limit to the maximum levels of lift and thrust that can be developed by birds may explain why clear maximum rates of oxygen uptake have only been obtained from flightless birds running on a treadmill (Bundle et al., 1999; Ellerby et al., 2003). It may be that volant birds are not able to generate the levels of muscle mechanical power that would be required to fully engage their metabolic capacity. Due to the absence of flight-elicited maximal values, a number of investigators (Schmidt-Neilsen, 1984; Bishop, 1997) have inferred that the peak measures from certain studies are maximal. The data from five flight studies (Gessamen, 1980; Tucker, 1968; Torre-Bueno and Larochelle, 1978; Wells, 1993; Chai and Dudley, 1995) were used to evaluate the accuracy of a predictive physiological model that estimates the aerobic capacity of birds (Bishop, 1997). Based

on the quantitative agreement of this approach, the model has subsequently been used to generate detailed quantitative predictions that address the dynamics of muscle function, the flight performance of birds, and a proposed functional equivalency between the mammalian and avian respiratory systems (Bishop, 1997; Bishop, 1999; Bishop, 2005). However, the data from hummingbirds (Wells, 1993; Chai and Dudley, 1995) were from mechanical but not metabolic maximums and published values exist for budgerigars (Tucker, 1968) and starlings (*Sturnus vulgaris*) (Torre-Bueno and Larochelle, 1978) that are 50% (Tucker, 1966) and nearly 100% (Ward et al., 2004) greater, respectively, than those that were considered maximal in the accuracy test (Bishop, 1997). Thus the estimated error of this model (±20%) (Bishop, 2005) has been considerably under-reported and the extent to which the subsequent predictions reflect physiological reality is unknown.

Flight mechanics

The U-shaped power curves measured here suggest that the increments in the metabolic cost of flight that occur with departures from the minimum power speed are greater for budgerigars and cockatiels than for the other species from whom similar metabolic measurements are available. The metabolic power curves that are nearly independent of flight speed may have been caused by only obtaining measurements from intermediate flight speeds, where power requirements are not expected to vary appreciably with flight speed (Pennycuick, 1989; Rayner, 1999). However, this explanation is not supported by our results, since both budgerigars and cockatiels experience large differences in metabolic rate, 30% and 60%, respectively (Fig. 1), within an absolute range of flight speeds that is less than the range obtained from laughing gulls, which have a power curve that varies by a maximum of 6% (Tucker, 1972). Moreover, theoretically based predictions of the power requirements of laughing gulls and larger birds in general (Pennycuick, 1989), generate steeper not shallower U-shaped curves due to the greater than geometric scaling of avian wing dimensions [dimensional scaling data from Rayner (Rayner, 1988)].

Some species of smaller birds may reduce their mechanical power requirements for flight and potentially flatten their power curves by altering their flight styles. For example, budgerigars and cockatiels normally utilize intermittent flight at intermediate and fast flight speeds (Fig. 3A,C). The use of flap-gliding flight may achieve a metabolic energy saving by lowering muscle mechanical power requirements and allowing the pectoralis to use more economical isometric muscle contractions rather than relying solely on concentric contractions (Lighthill, 1977; Tobalske and Dial, 1994). However, the potential metabolic energy savings from flap-gliding flight were not available to the budgerigars and cockatiels in this study because they rarely if ever used intermittent flight while wearing the mask (Fig. 3B,D). From our data alone we cannot evaluate whether the speed-dependent 2–19% increase in metabolic power that has been predicted for

flight with a mask (Tucker, 1972) is equal to the energy savings that would have been available from intermittent flight.

The cockatiel metabolic data we report here and existing measures of *in vivo* muscle power output for this species (Tobalske et al., 2003a) permit a preliminary inspection of the relationship between metabolic and mechanical power during bird flight. Notwithstanding the potentially substantial influence of the different experimental conditions and protocols, the mechanical power estimates of Tobalske and colleagues (Tobalske et al., 2003a) suggest the mechanical minimums (5 m s^{-1}) occur at slower flight speeds than those identified by our metabolic measures (10 m s^{-1}). Although both the metabolic and mechanical measures produce qualitatively similar power curves, the greater metabolic minimum power speeds account for the positive relationship between estimates of flight efficiency ($\dot{P}_{mech}/\dot{P}_{metab}$) and flight speed. When evaluated at the metabolic minimum power speed this preliminary comparison generates an estimate of flight efficiency of roughly 20%; considerably greater than estimates obtained during the hovering flight of hummingbirds [i.e. 10% (Chai and Dudley, 1995)].

Conclusions

The metabolic rate–flight speed relationships of budgerigars and cockatiels are unique among the species studied in their complete qualitative agreement with theoretical aerodynamic predictions. Although without a compelling reason to dismiss the energetic studies that have used similar methodology and found metabolic power curves that are nearly independent of speed, we urge caution in extending these results to birds in general. It remains unclear whether the kinematic differences we report or other unidentified factors influence the metabolic power curves of budgerigars and cockatiels to a greater extent than in birds of other clades. Given the evolutionary, ecological and biomechanical significance of power curves of different shape, comparative attempts to investigate this issue and to more quantitatively link the energetics and mechanics of flight will address considerable voids in the understanding of avian flight biology.

Appendix
Wind tunnel

Prior to the initiation of this study, the flow characteristics of the University of Montana wind tunnel were consistent with the description offered by Tobalske and Dial (Tobalske and Dial, 1994). To achieve steady-state measures of oxygen uptake at a given flight speed improvements in the flow characteristics of the wind tunnel were deemed necessary. We undertook the following steps to achieve this goal: first, the wind tunnel was moved to a room at the Fort Missoula Research Station where the inlet and exhaust were at least 4 m from the building walls. Second, we replaced the 5-mm honeycomb baffling (10 cm thick) immediately upstream of the test section with a wire mesh (1 cm^2 openings) that ensured the animals remained within the test section. Third, we inserted
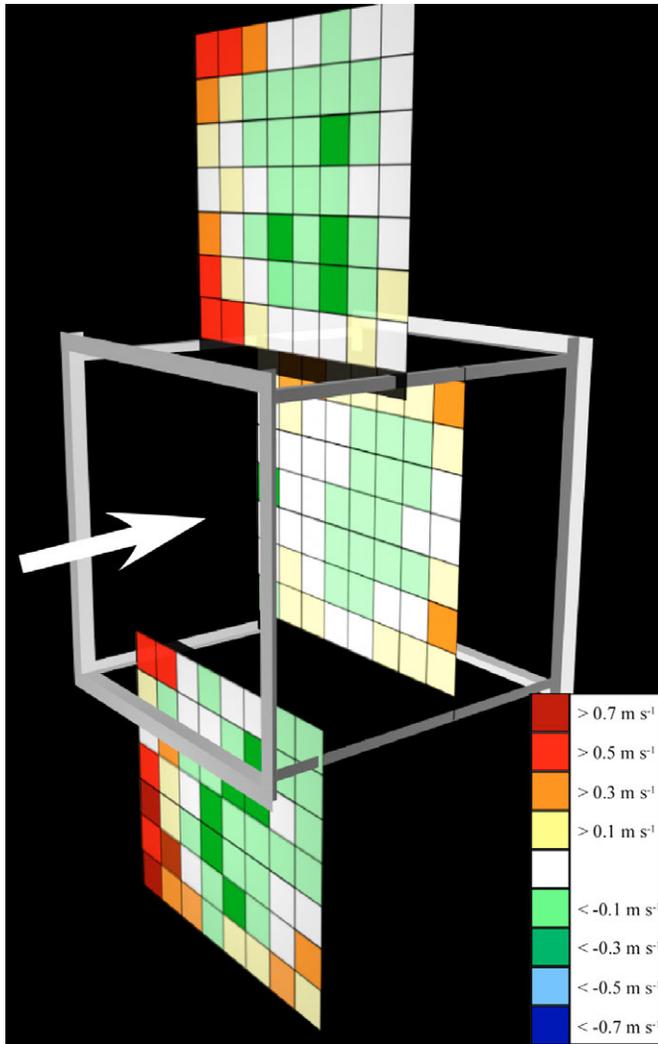
Fig. A1. Measured wind speed deviations (in m s^{-1}), from a mean wind tunnel speed of 10.0 m s^{-1}. Measurements were obtained at the vertices of an 8×7 grid that was sampled along three transects located 15, 35 and 55 cm downstream from the front of the test section. The white arrow indicates direction of wind speed.

four wire mesh screens, separated by a distance of 5 cm, with opening sizes of 10, 7.3, 5.2 and 2.5 mm (McMaster Carr Inc., Los Angeles, CA, USA) and open areas of 62.4, 73.6, 65.9 and 64%, respectively, behind a 10 cm thick honeycomb baffle in a 'settling section' upstream of the contraction (Rae and Pope, 1984). The screens were placed in the order reported with the smallest opening size closest to the test section. Fourth, we designed a port covering with a 2 mm rubber diaphragm that provided a seal around objects inserted into the test section. The port cover allowed access to the subject animals during flight sessions, without the undesirable consequence of air rushing through an open porthole.

To evaluate the effectiveness of these modifications, we sampled the flow velocity at 56 locations on each of three transects that were progressively further from the upstream edge of the test section (15, 35, 55 cm). At each of the 168 positions we used a pitot static tube (Dwyer, Series 160-6) connected to a digital manometer (Dwyer, Series 475 Mark III) to measure the dynamic pressure, while the average wind speed in the test section was held constant at 10.0 m s^{-1}. We converted the measures of dynamic pressure to flow velocity according to:

$$V = \sqrt{2q / \rho}, \qquad (A1)$$

where V is the flow velocity, q is the dynamic pressure, and ρ is the air density, which was calculated using a gas constant of 287.05 J kg^{-1} K^{-1} and measured values of atmospheric pressure and ambient temperature. The 168 measured deviations (in m s^{-1}) from the average wind speed of 10.0 m s^{-1} appear in Fig. A1.

We estimated the percent turbulence within the test section of the wind tunnel using a 30 cm diameter turbulence sphere (Rae and Pope, 1984). We assumed an ideal Reynolds number (Re) of 3.85×10^5 for the sphere, and calculated a turbulence factor by dividing the ideal Re by the measured critical Re. We used the regression of turbulence factor on percent turbulence provided by Rae and Pope (Rae and Pope, 1984) to determine the percent turbulence of the wind tunnel. The critical Re was determined by measuring the speed at which an abrupt pressure change occurred behind the sphere (Rae and Pope, 1984). We placed the sphere at the midpoint of the tunnel in the fore–aft and width axes and measured the critical Re with the base of the sphere at a height of 15 cm and 30 cm. The calculated mean percent turbulence was 1.19±0.02%. This value compares favorably with the mean percent turbulence reported for a wind tunnel designed to study animal flight (Hedrick et al., 2002), but the measured turbulence factor (1.97±0.01) is considerably greater than the value reported for a low-turbulence wind tunnel (1.03) (Pennycuick et al., 1997).

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