

RESEARCH ARTICLE

Terrestrial locomotion imposes high metabolic requirements on bats

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SUMMARY

The evolution of powered flight involved major morphological changes in Chiroptera. Nevertheless, all bats are also capable of crawling on the ground and some are even skilled sprinters. We asked if a highly derived morphology adapted for flapping flight imposes high metabolic requirements on bats when moving on the ground. We measured the metabolic rate during terrestrial locomotion in mastiff bats, *Molossus currentium*, a species that is both a fast-flying aerial-hawking bat and an agile crawler on the ground. Metabolic rates of bats averaged 8.0 ± 4.0 ml CO₂ min⁻¹ during a 1-min period of sprinting at 1.3 ± 0.6 km h⁻¹. With rising average speed, mean metabolic rates increased, reaching peak values that were similar to those of flying conspecifics. Metabolic rates of *M. currentium* were higher than those of similar-sized rodents that sprinted at similar velocities under steady-state conditions. When *M. currentium* sprinted at peak velocities, its aerobic metabolic rate was 3–5 times higher than those of rodent species running continuously in steady-state conditions. Costs of transport (J kg⁻¹ m⁻¹) were more than 10 times higher for running than for flying bats. We conclude that at the same speed bats experience higher metabolic rates during short sprints than quadruped mammals during steady-state terrestrial locomotion, yet running bats achieve higher maximal mass-specific aerobic metabolic rates than non-volant mammals such as rodents.

Key words: Chiroptera, energetics, flight costs, running costs, vertebrate flight.

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INTRODUCTION

Bat morphology is highly adapted for flapping flight (Norberg and Rayner, 1987), an ability that Chiroptera do not share with any other group of the class Mammalia. In response to the aerodynamic requirements of powered flight, bats have elongated forelimbs, relatively more muscle mass associated with the forelimbs than with the hindlimbs, and a flexible wing membrane supported by elongated digits. Despite this highly modified limb and muscle morphology, most bats can also move on the ground, yet most do so poorly (Lawrence, 1969). In contrast to birds, which use forelimbs for flying and hindlimbs for walking, bats use all four limbs for flying and walking. Interestingly, the thinness of hindlimb bones does not constrain a bat's ability to crawl (Riskin et al., 2005), suggesting that other morphological structures, such as hind limb length or metatarsus/femur ratio, may limit the non-aerial locomotion of bats (Christiansen, 2002). Even so, some species such as molossid bats and vampire bats are efficient runners capable of quick sprints (Dietz, 1973; Riskin and Hermanson, 2005; Schutt and Simmons, 2001), and the lesser short-tailed bat (*Mystacina tuberculata*) in New Zealand even forages during extended periods on the ground using quadrupedal locomotion (Daniel, 1979). Riskin and coauthors also documented that common vampire bats (*Desmodus rotundus*) and *M. tuberculata* use a symmetrical lateral-sequence gait similar to that of a broad range of tetrapods (Riskin et al., 2006). In contrast to the bounding gait of small terrestrial mammals, running vampires use their forelimbs instead of their hindlimbs to produce force; probably because the forelimbs have more and stronger muscles

than the hindlimbs (Riskin et al., 2006). The majority of bats rarely make use of quadrupedal locomotion, for example only when moving within roosts or when gleaning food items such as insects from the ground.

Here, we ask how energetically costly quadrupedal locomotion is for bats when sprinting at varying speeds on a horizontal surface and if the highly derived morphological adaptations to aerial locomotion impose higher metabolic costs for terrestrial locomotion on bats than on similar-sized mammals that only use quadrupedal locomotion. We studied these questions in a bat species that belongs to the family Molossidae, a group known for its highly derived wing morphology and energetically expensive manoeuvring flights (Voigt and Holderied, 2012). We used rodents for comparison, because many rodents are similar in size to bats and because of the extensive literature on locomotion energetics for this taxon.

In rodents, the energetic costs of terrestrial locomotion have mostly been measured using respirometry in animals running under sustainable steady-state conditions on treadmills or in running wheels. These experiments indicate that the energy requirements for transporting 1 g of body mass over the same distance increase linearly with the -0.3 power of body mass (Heglund et al., 1982), i.e. the energy required for running decreases as body mass increases on the per gram scale. Comparative work also suggests that quadrupedal and bipedal running involves similar energy requirements for running rodents (MacMillan and Hinds, 1992). Also, aerobic metabolic rates increase linearly with speed up to a plateau level, after which anaerobic processes are additionally

involved in force production. Anaerobic conditions during running are only sustainable for short periods, and therefore the plateau value of aerobic metabolic rate has been defined as the maximal exercise-induced metabolic rate for running rodents (e.g. MacMillan and Hinds, 1992). Running performance of rodents is likely limited by the inability to increase metabolic rates beyond this plateau (Jones and Lindstedt, 1993).

We tested the hypothesis that running involves higher metabolic rates in bats than in similar-sized rodents because bat morphology is more adapted for flapping flight than for quadrupedal locomotion. In contrast to bats, most rodents are agile, fast runners that spend their entire life on the ground. We predicted that sprinting *M. currentium* encounter higher metabolic rates than similar-sized rodents when running under steady-state conditions at a similar speed. Also, we expected this bat to reach higher peak metabolic rates when sprinting than similar-sized rodents because bats are capable of a higher exercise-induced metabolic rate than non-volant mammals (Schmidt-Nielsen, 1997). Finally, we compared metabolic rates of sprinting *M. currentium* with those of flying conspecifics (Voigt and Holderied, 2012). We predicted that metabolic rates of sprinting *M. currentium* increase with speed and that peak metabolic rates of sprinting bats are similar to those of flying conspecifics because sprinting bats should make use of the same metabolic potential for force production when using their limbs for sprinting or flying.

MATERIALS AND METHODS

Study site, animals and experimental protocol

In October and November 2011, we captured eight *Molossus currentium* (Thomas 1901) when they emerged from daytime roosts in buildings of La Selva Biological Station in Costa Rica (10°25'N, 84°00'W). Bats were transferred singly into linen bags and kept at 30°C until the onset of experiments. We used the ¹³C-labelled Na-bicarbonate technique as initially described in Speakman and Thomson (Speakman and Thomson, 1997), adapted to bolus injections according to Hambly et al. (Hambly et al., 2002; Hambly et al., 2004) and further refined for combined, instantaneous measurements of ¹³C enrichments in animal breath and CO₂ production rates (Voigt and Lewanzik, 2011; Voigt and Lewanzik, 2012; Voigt et al., 2011; Voigt and Holderied, 2012). During experiments, bats sprinted on a racetrack. We preferred this approach over wheel running or treadmills because we were unsure about the importance of echolocation for running bats. Bats are known to refrain from echolocation when resting or moving in a chamber (Speakman et al., 1989), and echolocation could potentially add energetic costs to terrestrial locomotion in bats. Experiments were performed separately on each bat. After administering 200 mg isotonic ¹³C-labelled Na-bicarbonate solution (0.29 mol l⁻¹; Euriso-Top GmbH, Saarbrücken, Germany) intra-peritoneally, we transferred bats into a 1.3 litre chamber in which temperature was kept constant at 30°C (see Voigt and Holderied, 2012). We used a field-deployable cavity ring down spectrometer (G1101 CO₂ isotope analyzer; Picarro, Sunnyvale, CA, USA) to measure the total and relative enrichment of ¹³CO₂ (p.p.m.) and ¹²CO₂ (p.p.m.) in the outlet air of the respirometry chamber. At approximately time (*t*)=23.5±3.9 min post-injection, we transferred bats to a 10-m-long racetrack, which consisted of two 5-m wooden beams (20 cm breadth). To ensure that bats sprinted straight ahead, both beams had wooden walls (each 20 cm height) so that the racetrack formed a U in cross-section. The racetrack was illuminated by dim light. In the following, we use the term 'sprinting bats' to describe rapid horizontal movements using all four limbs, i.e. we do not imply that bats use a distinct 'running' gait as opposed to a 'walking' gait

defined by specific kinematics and kinetics (e.g. Cavagna et al., 1976). We use this term because quadrupedal locomotion, particularly the presence of gaits, has not yet been described for members of the family Molossidae. At the beginning of experiments, bats were carefully placed at the starting line of the racetrack. All bats immediately began to sprint when they were released on the ground. Once a bat finished the 10-m distance of the track, we turned it around by 180° and allowed the bat to continue its sprint. During all experiments, we monitored the presence of ultrasonic calls using an Ultrasound Gate (Avisoft Bioacoustics, Berlin, Germany). In five out of eight bats, we had to manually motivate bats to keep moving over the 1-min period. When bats had run for an average of 63.3±8.4 s, we picked them up from the racetrack and returned them to the respirometry chamber, in which they stayed for at least 10 min during the post-run period. After experiments, bats were weighed to the nearest 0.01 g using a precision electronic balance (PM-100, Mettler, Switzerland) and released at the site of capture.

Data analysis

As stated above, the cavity ring down laser spectrometer provided data on the enrichment of outlet air with ¹³C- or ¹²C-labelled CO₂ (p.p.m.) and the enrichment of ¹³C in relation to ¹²C in CO₂. For data analysis, we focused on a 20-min period about 4 min after peak enrichment in ¹³C. This interval consisted of a pre-running period (~5 min), the running period (~5 min, including transfers) and the post-running period (~10 min). To calculate the fractional turnover of ¹³C (*k_c*; min⁻¹) in flying bats, we converted delta values into atom% according to Slater et al. (Slater et al., 2001) and computed linear regressions after the least-squares methods for the ln-transformed isotopic data against time for the pre- and post-running period separately. Based on these regressions, we extrapolated the ¹³C enrichment in the exhaled breath of animals at the onset and end of the running period. We calculated *k_c* for running bats according to $k_c = [x^E(^{13}C)_{\text{stop}} - x^E(^{13}C)_{\text{start}}] / t$, where $x^E(^{13}C)$ was the ¹³C excess enrichment (in atom%) at the start and stop of the sprint and *t* was the sprinting duration (min). *k_c* (min⁻¹) was multiplied by the total body bicarbonate pool, *N_c* (mol), as calculated by the plateau method (Voigt and Lewanzik, 2011), and converted to CO₂ production rate (\dot{V}_{CO_2} ; ml min⁻¹) by multiplication with 22.4 l mol⁻¹. We applied correction factors as outlined previously (Hambly et al., 2002; Hambly et al., 2004; Voigt and Lewanzik, 2011; Voigt and Lewanzik, 2012), based on pre-running \dot{V}_{CO_2} , as measured by the isotopic and respirometric methods, and based on isotopic estimates of \dot{V}_{CO_2} during the running period. A bivariate plot of pre-running resting \dot{V}_{CO_2} obtained from both measurements confirmed the high precision (*r*²=0.91) of the method.

We expected that metabolic rates of *M. currentium* would increase linearly with sprinting speed. Therefore, we calculated a linear regression after the least squares method for the data set obtained from *M. currentium* and then compared the slope and the y-axis intercept with data of six selected rodent species (MacMillan and Hinds, 1992) using one-sample Student's *t*-tests. These rodent species were: *Dipodomys ordii*, *Dipodomys panamintinus*, *Heteromys desmarestianus*, *Liomys salvini*, *Microdipodops megacephalus* and *Perognathus fallax*. *Dipodomys ordii*, *D. panamintinus* and *M. megacephalus* were bipedal runners, and the others were quadrupedal runners. As previous studies measured the rate of oxygen consumption in rodents, we converted oxygen consumption rate to carbon dioxide production rate by assuming that rodents oxidized mostly carbohydrates (respiratory quotient=1). Furthermore, we tested whether peak metabolic rates of running *M. currentium* are higher than maximum metabolic rates of running

rodents using a one-sample Student's *t*-test. For all statistical tests, we assumed an alpha value of 5% and used Systat (Version 11). Data are presented as means \pm one standard deviation.

RESULTS

Molossus currentium used in the experiment weighed, on average, 19.3 ± 1.6 g ($N=8$; Table 1). After injecting the ^{13}C -labelled Na-bicarbonate solution, the label rapidly equilibrated in the body bicarbonate pool, as indicated by the early peak enrichments in ^{13}C in exhaled breath at $t=17.8 \pm 4.3$ min post-injection (Fig. 1). Mean carbon dioxide production rate (\dot{V}_{CO_2}) was 0.519 ± 0.246 ml min^{-1} , and the fractional turnover (k_c) was 0.038 ± 0.019 min^{-1} before animals started to sprint (Table 1, Fig. 1). After introducing bats to the racetrack, they sprinted a mean distance of 21.9 ± 11.6 m (range, 7.4–37.9 m) during the 1-min period. Bats never emitted echolocation calls while engaged in terrestrial locomotion. While sprinting at a speed (v) of 1.3 ± 0.6 km h^{-1} , mean k_c 0.44 ± 0.18 min^{-1} and mean \dot{V}_{CO_2} was 8.03 ± 4.01 ml CO_2 min^{-1} . During sprints, \dot{V}_{CO_2} of *M. currentium* was ~ 15 times higher than during rest (Wilcoxon matched-pairs test; $n=8$ pairs, $W=-36$, $T+=0$, $T=-36$, $P=0.0078$). Mass-specific \dot{V}_{CO_2} increased with increasing v ($r^2=0.76$, $P=0.0051$; Fig. 2). The parameters (\pm one standard error) of a least-squares regression calculated for the bivariate relationship between mass-specific \dot{V}_{CO_2} (ml CO_2 g^{-1} h^{-1}) and v (km h^{-1}) are: mass-specific $\dot{V}_{\text{CO}_2}=5.7(\pm 6.2)+15.5(\pm 4.4)v$. The slope of this regression was steeper than those established for the relationship between mass-specific \dot{V}_{CO_2} and v in rodents running under steady-state conditions (one-sample Student's *t*-test; $t_5=109$, $P<0.001$; Fig. 2). Maximal mass-specific \dot{V}_{CO_2} of running rodents was always lower than that of *M. currentium* running at maximum speed (Fig. 2). We converted the metabolic rate of running bats to energy turnover by assuming that bats oxidized exclusively glycogen (respiratory quotient=1; caloric equivalent 21.1 J ml^{-1} CO_2 produced). Accordingly, metabolic costs of running equalled 2.8 ± 1.4 W, which was not different from the metabolic costs of manoeuvring flight in *M. currentium* [3.6 ± 1.1 W; Mann–Whitney *U*-test: $n_1=11$, $n_2=8$, $U=28$, $U'=60$, $P=0.21$; data for flying *M. currentium* (Voigt and Holderied, 2012)]. However, costs of transport were 13 times higher for running (454.8 ± 180.7 J kg^{-1} m^{-1}) than for conspecifics flying at ~ 20 km h^{-1} (35.6 ± 7.9 J kg^{-1} m^{-1}) (Voigt and Holderied, 2012) (Fig. 3).

DISCUSSION

Metabolic rates of sprinting *Molossus currentium*

Our study provides the first data on the energetic requirements of terrestrial locomotion in a bat species. During the experiments, *M. currentium* were agile sprinters that reached considerable speed even though their limb morphology is more adapted for flapping flight than for quadrupedal locomotion on the ground (Vaughan, 1966; Voigt and Holderied, 2012). Sprinting in *M. currentium* was almost as fast as in the common vampire bat (Riskin and Hermanson, 2005), which is specialized in approaching resting prey at night by quadrupedal locomotion. A high agility on the ground is probably essential for *M. currentium* when moving quickly through the small and complex crevices of their daytime roosts. Furthermore, and in contrast to most other bat species, most molossid bats are unable to launch themselves into flight from the ground because of their long and slender wings. Instead, molossids try to reach vertical substrates, such as a tree trunk, as quickly as possible to climb upwards for a few metres to facilitate take-off for flight (Vaughan, 1959).

Metabolic rates of running *M. currentium* increased with speed and reached values that were similar to those of flying conspecifics (Voigt and Holderied, 2012). Indeed, the metabolic scope for the

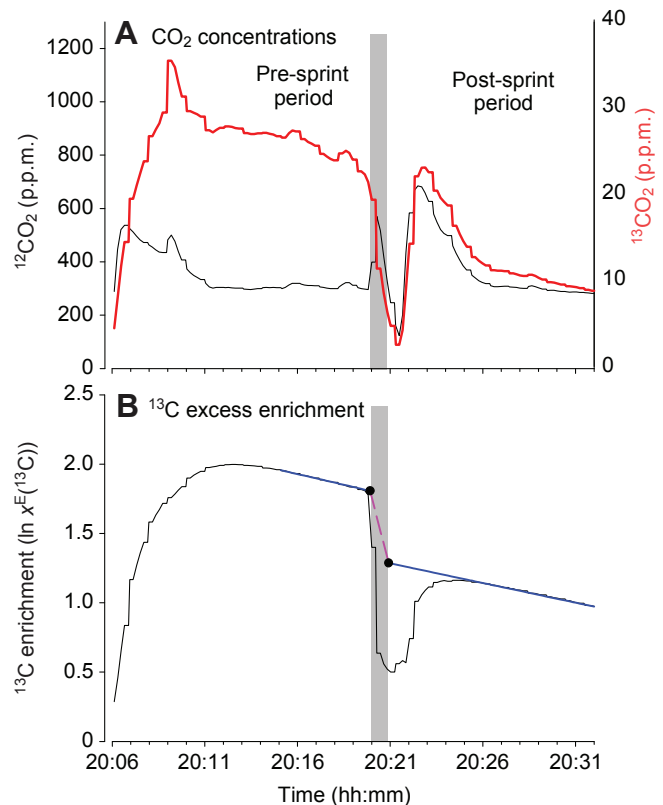


Fig. 1. Example plot of (A) the concentration (p.p.m.) of $^{13}\text{CO}_2$ (red line) and $^{12}\text{CO}_2$ (black line) in the exhaled breath of a *Molossus currentium* during an experiment. The sprinting period is indicated by a grey box. (B) Atom% enrichment of ^{13}C during the course of the experiment (note logarithmic y-scale). ^{13}C enrichment of exhaled breath at the onset and end of the flight period was extrapolated based on two least-squares linear regressions (blue lines calculated over 3 min of the pre-sprint period and 10 min of the post-sprint period). The fractional turnover of the ^{13}C label of the flying bat is indicated by the broken pink line.

transition from resting to running (~ 15) was almost the same as the scope for the transition from resting to flying (~ 17) (Voigt and Holderied, 2012), signifying that running may become as energetically costly as flying when a bat has to move at relatively high speed on the ground. As sprinting *M. currentium* did not emit echolocation calls, metabolic rates did not include any energetic costs for echolocation call production (Speakman et al., 1989) and, as a result, we could not evaluate whether or not echolocation calls increase the metabolic requirements of running in this species. Other bat species, such as *M. tuberculata*, are known to echolocate during non-aerial locomotion, yet limb motion and call production are not coupled – a prerequisite for saving energetic costs for call production (Parsons et al., 2010). Possibly, walking bats may not be able to reduce the cost of non-aerial locomotion by linking call production with limb motion, as suggested for powered flight of bats (Speakman and Racey, 1991).

Although our experimental setup had the advantage of performing metabolic measurements in animals outside of a respirometry chamber, our methodological approach had certain limitations. Firstly, we were not able to measure steady-state running performance because ^{13}C -labelled Na-bicarbonate integrates over relatively short periods (Hambly and Voigt, 2011) and because *M. currentium* was not willing to sprint over an extended period of time. This complicates

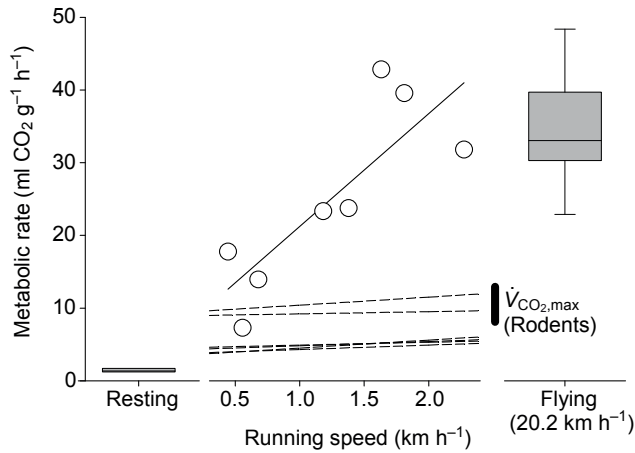


Fig. 2. Mass-specific metabolic rates ($\text{ml CO}_2 \text{ g}^{-1} \text{ h}^{-1}$) for resting, running and flying *Molossus currentium*. Box margins indicate the 25 and 75 percentiles; whiskers indicate the 5 and 95 percentiles; the centre line of the box indicates the median. A linear regression line was calculated after the least-squares method for the relationship between metabolic rates and speed for running *Molossus*. The equation reads: mass-specific $\dot{V}_{\text{CO}_2} = 5.7 \pm 6.2 + 15.5 \pm 4.4 v$ ($r^2 = 0.76$). Broken lines indicate the relationship between mass-specific metabolic rates and running speeds in six rodent species according to MacMillan and Hinds (MacMillan and Hinds, 1992). The vertical solid line indicates the range of maximal mass-specific metabolic rates for the same rodent species.

comparisons with data from running rodents because experiments with rodents usually involved continuous runs on a treadmill or a running wheel, with animals being in a steady-state physiological condition (e.g. MacMillan and Hinds, 1992). Secondly, our results were integrated measures from short sprints and brief periods of rest. Only the fastest animals sprinted continuously over the whole 1-min period. From a physiological point of view, a sequence of short sprints interrupted by rest periods is not equivalent to running at a lower but constant speed. Generally, the total metabolic requirements of several brief activity bouts are lower than a single activity bout of corresponding length (Edwards and Gleeson, 2001). Thus, sprinting bats may have reduced the total metabolic costs of running by intermittent periods of rest. Thirdly, the methodological delay between the end of the sprint and the onset of the post-sprint period in the respirometry chamber reduced the accuracy of our measurements because bats possibly expressed excess post-exercise oxygen consumption (and carbon dioxide production) (Baker and Gleeson, 1999) and because any inaccuracy in the calculated regression models

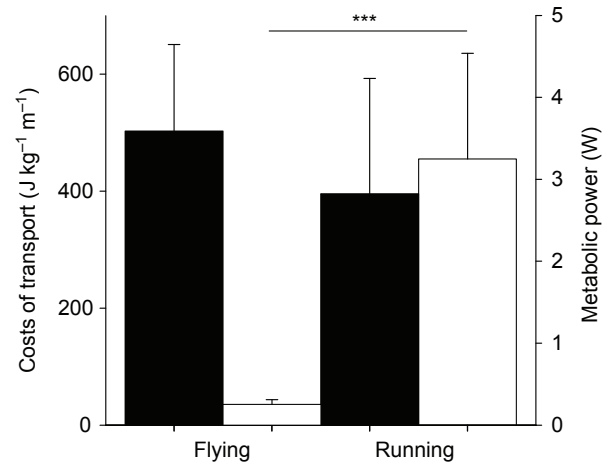


Fig. 3. Metabolic power (Watt; filled column) and costs of transport ($\text{J kg}^{-1} \text{ m}^{-1}$; open column) for running and flying *Molossus currentium*. The horizontal line linking columns indicates a significant difference (***) at $P < 0.001$.

for predicting $x^{\text{E}(^{13}\text{C})_{\text{stop}}}$ may have increased the inaccuracy of extrapolated sprinting metabolic rates. The neglect of excess post-exercise oxygen consumption may have led to an underestimation of the measured sprinting metabolic rate. Thus, our sprinting metabolic rates for *M. currentium* should be considered as conservative, highlighting that metabolic costs of non-aerial locomotion are indeed high for bats. The second methodological issue [inaccuracy of extrapolated $x^{\text{E}(^{13}\text{C})}$ for the onset and end of flight period] should have hampered our ability to find a relationship between sprinting metabolic rates and speed. Yet, our data confirms a strong correlation between these two variables. Therefore, we consider the second issue to be negligible for the present data set.

Metabolic rates of bats and rodents during terrestrial locomotion

A comparison of metabolic rates between *M. currentium* and six rodent species during terrestrial locomotion revealed that metabolic rates of sprinting *M. currentium* increased more with speed than in any of the rodent species used in the analysis (MacMillan and Hinds, 1992). However, it is important to keep in mind that the method we used differed from those typically performed on rodents and that experiments were conducted in unsteady conditions for bats and in steady-state conditions in rodents. Also, metabolic rates of running mammals are known to vary with ambient temperature and distance covered

Table 1. Experimental data of individual bats

Individual	Sex	M_b (g)	Pre-running period			Running period		
			k_c (min^{-1})	Isotopic \dot{V}_{CO_2} (ml min^{-1})	Respiratory \dot{V}_{CO_2} (ml min^{-1})	Distance covered (m)	k_c (min^{-1})	\dot{V}_{CO_2} (ml min^{-1})
1	F	19.6	0.014	1.11	0.52	9.45	0.21	2.4
2	F	18.6	0.061	0.71	0.37	27.2	0.76	13.3
3	M	18.9	0.027	0.59	0.32	11.5	0.27	4.4
4	M	22.9	0.031	0.64	0.49	37.9	0.52	12.1
5	F	18.2	0.029	0.63	0.42	30.2	0.59	12.0
6	M	19.2	0.039	1.06	0.56	19.7	0.38	7.5
7	M	19.3	0.031	0.71	0.38	7.4	0.36	5.7
8	F	17.4	0.073	1.90	1.09	32.2	0.41	6.9
Mean \pm s.d.		19.3 \pm 1.6	0.038 \pm 0.019	0.92 \pm 0.44	0.52 \pm 0.25	21.9 \pm 11.6	0.44 \pm 0.18	8.0 \pm 4.0

Body mass (M_b), fractional turnover (k_c), metabolic rate (\dot{V}_{CO_2}), and distance covered during the 1-min runs on the racetrack (F=female, M=male)

(Chappell et al., 2004); two variables that could not be controlled for in our comparison. Keeping the different experimental setups and conditions in mind, we will briefly discuss the general differences.

Whereas most rodent species reached higher maximum speeds of 4–6 km h⁻¹ during continuous runs in steady-state conditions (MacMillan and Hinds, 1992), *M. currentium* were able to run briefly at a maximum speed of only ~2 km h⁻¹. Peak metabolic rates of running *M. currentium* were higher than those measured in the rodent species we included in the analysis. Since experimental animals did not echolocate during sprints, additional metabolic costs for emitting echolocation calls cannot explain the discrepancy in running metabolic rates between bats and rodents. One likely reason for a higher energy cost of terrestrial locomotion in Chiroptera might be that limb morphology in bats may not be efficient for terrestrial locomotion, thereby adding metabolic costs to locomotion when bats are crawling on the ground. For example, bats may lack the ability for elastic energy storage during quadrupedal locomotion; a mechanism that helps rodents in reaching a high mechanical efficiency during terrestrial locomotion (Biewener et al., 1981). We are uncertain if bats were exhausted after running for ~1 min at high speed but, considering that bats of the genus *Molossus* are capable of flying continuously for 30–60 min when foraging (Esbérard and Bergallo, 2010), it seems unlikely that physiological exhaustion prevented them from continuing their sprint. Molossid bats performed well during terrestrial locomotion, yet they seem to lack the high efficiency of rodents in converting muscular work into running speed. Nonetheless, it is noteworthy that *M. currentium* reached considerable metabolic rates during fast sprints. These high metabolic rates during running were probably facilitated by the high aerobic capacity of limb muscles that are adapted for energetically costly flapping flight.

Conclusions

In summary, our experiments highlight that fast quadrupedal locomotion is energetically costly for *M. currentium* and probably also for other bats. In our study, sprinting *M. currentium* reached metabolic rates similar to those of flying conspecifics. Additional metabolic costs for echolocation cannot explain the relatively high metabolic requirements for sprinting in bats because experimental animals never emitted echolocation calls. Possibly, Chiroptera may encounter higher metabolic rates than terrestrial mammals during non-aerial locomotion because the morphology of bats is inefficient for crawling, running or sprinting. Lastly, our study demonstrates that costs of transport were more than 10 times lower for flying bats than for running conspecifics, highlighting the immense advantage of powered flight over non-aerial locomotion.

LIST OF ABBREVIATIONS

k_c	fractional turnover of ¹³ C label (min ⁻¹)
M_b	body mass (g)
N_c	total body bicarbonate pool (mol)
t	duration of sprint (min)
v	sprinting speed (km h ⁻¹)
\dot{V}_{CO_2}	carbon dioxide production rate (ml CO ₂ min ⁻¹)
$x(^{13}C)$	¹³ C enrichment (atom%)
$x^{E(^{13}C)}_{start}$	excess ¹³ C enrichment (atom%) at the start of the sprint
$x^{E(^{13}C)}_{stop}$	excess ¹³ C enrichment (atom%) at the end of the sprint

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