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RESEARCH ARTICLE

Bat flight with bad wings: is flight metabolism affected by damaged wings?

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SUMMARY

Infection of North American bats with the keratin-digesting fungus *Geomyces destructans* often results in holes and ruptures of wing membranes, yet it is unknown whether flight performance and metabolism of bats are altered by such injuries. I conducted flight experiments in a circular flight arena with *Myotis albescens* and *M. nigricans* individuals with an intact or ruptured trailing edge of one of the plagiopatagial membranes. In both species, individuals with damaged wings were lighter, had a higher aspect ratio (squared wing span divided by wing area) and an increased wing loading (weight divided by wing area) than conspecifics with intact wings. Bats with an asymmetric reduction of the wing area flew at similar speeds to conspecifics with intact wings but performed fewer flight manoeuvres. Individuals with damaged wings showed lower metabolic rates during flight than conspecifics with intact wings, even when controlling for body mass differences; the difference in mass-specific metabolic rate may be attributable to the lower number of flight manoeuvres (U-turns) by bats with damaged wings compared with conspecifics with intact wings. Possibly, bats compensated for an asymmetric reduction in wing area by lowering their body mass and avoiding flight manoeuvres. In conclusion, it may be that bats suffer from moderate wing damage not directly, by experiencing increased metabolic rate, but indirectly, by a reduced manoeuvrability and foraging success. This could impede a bat's ability to gain sufficient body mass before hibernation.

Key words: energetics, chiroptera, white-nose syndrome, wing damage.

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INTRODUCTION

Since the emergence of the keratinophilic fungus *Geomyces destructans*, bats with damaged wing membranes have been increasingly observed in North American bat populations. This fungus is the major cause of death in hibernating Vespertilionidae in the USA and Canada, resulting in significant declines in bat populations, most importantly in those of *Myotis lucifugus* (Blehert et al., 2009; Frick et al., 2010; Dzal et al., 2011). The fungal infection causes epidermal erosions and ulcers on the wing membrane that may lead to local necrotic areas (Meteyer et al., 2009). Although wing membranes seem to have a large potential to recover from fungal infections (Fuller et al., 2011), necrotic tissues may eventually result in holes or ruptures (Meteyer et al., 2009; Reichard and Kunz, 2009). This may constrain the flight ability and foraging success of infected bats when emerging from their hibernacula with partly necrotic wing membranes (Reichard and Kunz, 2009). Ruptures of wing membranes occur often at the trailing edge of the plagiopatagum – the wing area between the fifth digit, the arm and the body – possibly because the plagiopatagium is the weakest and most extensible part of the wing area (Swartz et al., 1996), and because the continuous mechanical stress imposed by flapping flight on the trailing edge prevents a complete recovery. In contrast to birds, bats are not able to regenerate their wing area during transitional periods of moult. Instead, bats with damaged wings are able to heal the injury (Davis and Doster, 1972; Worthington-Wilmer and Barratt, 1996; Faure et al., 2009; Weaver et al., 2009; Fuller et al., 2011), carry on with a permanently damaged wing membrane (Davis, 1968) or are at risk of dying.

To shed light on the energetic constraints that are possibly inflicted by damaged wing membranes on bats, I investigated how bats with natural asymmetric reductions of the plagiopatagium perform during flight. Specifically, I asked whether a permanent and asymmetric reduction in wing area increases the metabolic rate during flight and lowers the flight performance of bats. I studied this question in two tropical species of the genus *Myotis* (*M. albescens* É. Geoffroy Saint-Hilaire 1806 and *M. nigricans* Schinz 1821). Tropical and subtropical bats are not infected by *G. destructans* because this fungus is adapted to the cold temperatures of cave hibernacula in the temperate zone of the Northern Hemisphere. Consequently, the use of tropical *Myotis* enabled me to look at the effect of ruptured wing membranes on flight performance in the absence of other damage to the wing membrane, e.g. ulcers and necrotic tissues as described for North American *Myotis* after infection with *G. destructans* (Meteyer et al., 2009; Reichard and Kunz, 2009), and also in the absence of possible immunological responses to an infection with *G. destructans*. In populations of the two study species, I observed individuals with ruptured trailing edges of the plagiopatagium that caused a significant decline in wing area. This damage was similar to that previously described for North American *Myotis* suffering from a *G. destructans* infection (Reichard and Kunz, 2009). I hypothesized that a disrupted trailing edge of the plagiopatagium would alter the metabolic requirements and performance of flying bats, because the plagiopatagium is important for generating lift and thrust producing vortices (Muijres et al., 2008; Song et al., 2008; Hubel and Tropea, 2010). Accordingly, I expected that bats with an asymmetric

reduction of the plagiopatagial area would experience a higher metabolic rate compared with conspecifics with intact wings because of the lower wing area and because asymmetric wings may reduce the efficiency of converting muscular work into mechanical power. Further, I predicted that bats with damaged wings would perform fewer aerial manoeuvres compared with conspecifics with intact wings. In my experiment, I refrained from altering the plagiopatagial area of bats experimentally for ethical reasons, but used instead bats with naturally damaged plagiopatagiums caused by a ruptured trailing edge. I measured flight speed and counted the number of flight manoeuvres in a circular flight arena using acoustical tracking (Voigt and Lewanzik, 2012), and I quantified metabolic rates of flying bats using the ^{13}C-labelled sodium bicarbonate (NaB) method (Hambly et al., 2002; Hambly et al., 2004; Voigt et al., 2010; Voigt and Lewanzik, 2011; Voigt and Lewanzik, 2012; Voigt et al., 2012). To the best of my knowledge, this is the first study in bats to investigate whether flight performance and metabolic rate are affected by damaged wing membranes. The results of this study contribute to a better understanding of the direct and indirect health consequences of *G. destructans* infections in bats.

MATERIALS AND METHODS

Experiments complied with current laws in Costa Rica. Field work was carried out at La Selva Biological Station in Costa Rica (10°25′N, 84°00′W) in November and December 2010. Bats with damaged wing membranes, probably caused by a predator, were encountered during routine mist-netting at daytime roosts of *M. albescens* and *M. nigricans*. Both species are common aerial-hawking insectivorous bats in lowland regions of the subtropical and tropical region of the New World, where they forage in the open space of rainforest gaps (Siemers et al., 2001; Rex et al., 2008). Bats were captured between 17:00 h and 19:00 h in front of buildings, using 6 and 9 m mist nets (2.5 m height, Ecotone, Gdynia, Poland). I used one individual each of *M. albescens* and *M. nigricans* that showed a ruptured trailing edge of the left plagiopatagial membrane, and used 10 conspecifics of each species with intact wing membranes for comparison. Bats were transferred to a large box where they were kept at ambient temperature for a maximum of 3 h until the onset of experiments.

I used the NaB technique as originally described (Hambly et al., 2002; Hambly et al., 2004) and further refined (Voigt et al., 2011; Voigt and Lewanzik, 2011; Voigt and Lewanzik, 2012) for instantaneous measurement of ^{13}C enrichment in exhaled breath of animals. Experiments in the doughnut-shaped flight cage (diameter 3.6 m) were performed with one bat at a time. The experimental setup and protocol were as described previously (Voigt and Lewanzik, 2012; Voigt et al., 2012). After experiments, I measured the body mass of the bats (accuracy 0.01 g; PM-100, Mettler, Columbus, OH, USA). Also, I calculated aspect ratio (squared wing span divided by total wing area) and wing loading (body mass × gravitational force divided by wing area) based on digital pictures of the stretched wings (Voigt et al., 2010). Bats were released at the site of capture after experiments.

Acquisition and analysis of respirometric and isotopic data

While the bats tested in the respirometry chamber, I measured the concentration of $^{13}CO_2$ and $^{12}CO_2$ in the outlet air using a cavity ringdown spectrometer (Picarro, Sunnyvale, CA, USA). This instrument provides data on total CO_2 enrichment (p.p.m.) and the enrichment of ^{13}C in relation to ^{12}C in CO_2 expressed in the delta-notation as parts per mil.

For data analysis, I focused on a 20 min period about 3 min after peak enrichment in ^{13}C. This interval consisted of a pre-flight period (~5 min), the flight period (~5 min, including transfers) and the post-flight period (~10 min). To calculate the fractional turnover of ^{13}C (k_C; min^{-1}) in flying bats, I converted delta values into atom% according to Slater et al. (Slater et al., 2001) and computed linear regressions after the least-squares method for the ln-transformed isotopic data against time for the pre- and post-flight period separately. Based on these regressions, I extrapolated the ^{13}C enrichment in the exhaled breath of animals at the onset and end of the flight period. I calculated k_C for flying bats according to the following equation: $k_C=[x^E(^{13}C)_{end}–x^E(^{13}C)_{start}]/t$, where $x^E(^{13}C)$ is the ^{13}C excess enrichment (in atom %) at the start and end of the flight period and t is the flight duration (min). k_C (min^{-1}) was multiplied by the total body bicarbonate pool N_C (mol) as calculated by the plateau method (Voigt et al., 2010; Voigt and Lewanzik, 2011), and converted to carbon dioxide production rate ($\dot{V}_{CO_2}$; ml min^{-1}) by multiplication with 22.41 mol^{-1}. I applied correction factors as outlined previously (Hambly and Voigt, 2011; Voigt and Lewanzik, 2011; Voigt and Lewanzik, 2012) based on pre-flight $\dot{V}_{CO_2}$ as measured by the isotopic and respirometric method and based on isotopic estimates of $\dot{V}_{CO_2}$ during the flight period. A bivariate plot of resting $\dot{V}_{CO_2}$ (pre-flight period) supported a high precision of this methodological approach (r^2=0.88, P<0.001).

Acquisition and analysis of acoustical data

For estimating the flight speed and the number of U-turns of flying bats, I used the sequence of echolocation calls recorded by eight adjacent microphones (see Voigt and Lewanzik, 2012).

Statistical analysis

Before performing parametric tests, I checked whether the requirements for parametric testing were fulfilled. To test whether morphology (body mass, aspect ratio, wing loading), flight performance (speed and number of U-turns) and metabolic rate differed between individuals with intact and damaged wing membranes, I calculated one-sample Student's t-tests for each species separately. For all tests, I used Systat (Version 11), assuming an alpha value of 5%. Data are presented as means ± 1 s.d., unless otherwise stated.

RESULTS

In both study species, *M. albescens* and *M. nigricans*, I captured one individual with a damaged left plagiopatagial wing membrane. In *M. albescens*, the trailing edge of the left plagiopatagium was ruptured proximally close to the abdomen so that the area was reduced by 21% in relation to the right plagiopatagium (Fig. 1). Consequently, the total left wing area was smaller by 13% than the right wing area (Table 1). In *M. nigricans*, the left plagiopatagum was damaged by a similar rupture of the trailing edge, yet the rupture was more distal, close to the fifth digit. This rupture caused a 20% reduction in the left plagiopatagial area in relation to the right plagiopatagium, and a 13% reduction in left wing area compared with the right wing area (Table 1, Fig. 1). Both individuals with damaged wings weighed less than their conspecifics (Table 2). Wing loading and aspect ratio of bats with damaged wing membranes were significantly higher than those of 10 healthy conspecifics (Table 2).

Resting metabolic rates were not significantly different between pre- and post-flight periods (*M. albescens*: paired Student's t-test, t_9=0.81, P=0.442; *M. nigricans*: paired Student's t-test, t_9=0.28, P=0.785). In *M. albescens*, resting metabolic rate averaged

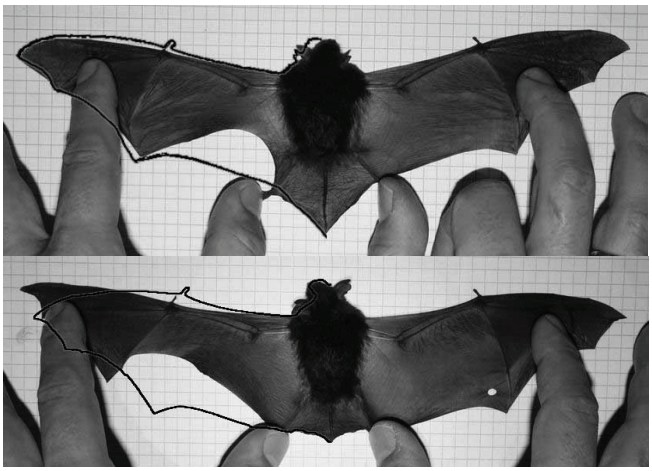

Fig. 1. Pictures of the dorsal view of *Myotis albescens* (top) and *M. nigricans* (bottom) with a ruptured trailing edge of the left plagiopatagial membrane. The counter line of the right wing area was copied over the left wing area to better illustrate the wing damage to the left plagiopatagium. Note that wing punctures were taken with sterile biopsy punches in the right wing after the experiments.

0.22±0.10 ml CO_2 min^{-1} during pre-flight and 0.20±0.06 ml CO_2 min^{-1} during post-flight periods. Corresponding values for *M. nigricans* are 0.27±0.12 ml CO_2 min^{-1} for the pre-flight and 0.28±0.14 ml CO_2 min^{-1} for the post-flight period.

Injection of ^{13}C-labelled sodium bicarbonate caused a sharp increase in ^{13}C enrichment in the exhaled breath (Fig. 2). Following a plateau a few minutes post-injection, ^{13}C enrichment in the exhaled breath decreased exponentially. The flight interval caused an abrupt decline in ^{13}C enrichment when pre-flight and post-flight enrichment are compared. Fractional turnover rate during flight intervals averaged 0.618±0.139 min^{-1} for *M. albescens* and 0.573±0.124 min^{-1} for *M. nigricans*. Fractional turnover rate was 8.7 times higher during flight than during rest in *M. albescens* and 9.2 times higher in *M. nigricans*.

During flight experiments, bats with damaged wings flew at a similar speed to conspecifics with intact wings (Table 2). However, bats with damaged wings performed fewer U-turns in the circular flight arena than conspecifics with intact wings (Table 2). In both species, flight metabolism (ml CO_2 min^{-1}) was lower in individuals with damaged wings than in individuals with intact wings (Table 2, Fig. 3). When controlling for variation in body mass, differences in metabolic rate were still either marginally (*M. nigricans*) or significantly different (*M. albescens*) between bats with damaged and intact wing membranes (Table 2).

DISCUSSION

Bats have delicate wing membranes that may get permanently damaged by ruptures of the membrane edge or by punctures. This damage may constrain the ability of a bat to fly efficiently and thus may increase the metabolic rate of aerial locomotion. To the best of my knowledge, this study is the first to address the question of whether flight performance and metabolic rate of bats are affected by a permanent and asymmetric reduction in wing area. An asymmetric reduction of wing area could result in increased flight metabolism because of increased aspect ratio and wing loading (Voigt, 2000), and because of the asymmetric force production of the left and right wing.

In partial agreement with the predictions, I found that bats with damaged wing membranes performed fewer U-turns than conspecifics with intact wing membranes when flying in the circular flight arena, yet I cannot rule out the possibility that I selected individuals from the local population that were less agile and therefore became the victim of a predator, causing the rupture of the edge of the plagiopatagium. Thus, it remains unclear whether

Table 1. Morphology, flight performance and metabolic rates of 11 *Myotis nigricans* and 11 *M. albescens*

Ind.	Sex	m_b (g)	AR	WL (N m^{-2})	t (s)	U-turns (n)	v (m s^{-1})	Resting k_C (min^{-1})	Flight k_C (min^{-1})	$\dot{V}_{CO_2}$ (ml min^{-1})	Mass-specific $\dot{V}_{CO_2}$ (ml g^{-1} min^{-1})
Mn1	M	4.7	6.6	4.9	85	44	2.41	0.126	0.508	2.12	0.45
Mn2	M	4.2	6.3	4.8	71	21	1.55	0.083	0.583	2.45	0.58
Mn3	M	4.2	6.5	4.7	93	26	2.02	0.053	0.448	1.82	0.44
Mn4	M	4.6	6.3	4.8	74	13	1.86	0.068	0.410	2.06	0.45
Mn5	M	3.9	6.4	4.9	60	8	2.16	0.048	0.574	1.89	0.49
Mn6	M	3.9	6.2	4.5	72	16	2.05	0.038	0.652	2.10	0.55
Mn7	F	4.0	6.2	4.4	89	27	1.98	0.144	0.591	1.84	0.46
Mn8	M	4.2	n.a.	n.a.	68	12	1.72	0.064	0.570	2.42	0.58
Mn9	M	4.6	6.4	5.2	72	18	1.80	0.028	0.555	2.61	0.57
Mn10	M	4.4	6.2	5.3	71	38	1.73	0.109	0.886	1.52	0.35
*Mn11**	F	3.9	8.6	5.3	55	11	1.86	0.132	0.524	1.71	0.44
Ma1	F	5.4	6.4	6.1	61	49	3.02	0.061	0.703	1.75	0.32
Ma2	M	4.6	n.a.	n.a.	142	14	0.72	0.088	0.313	1.61	0.35
Ma3	F	4.3	6.7	4.4	60	7	1.98	0.103	0.521	1.09	0.26
Ma4	F	4.6	6.1	4.6	77	32	1.35	0.063	0.610	1.46	0.32
Ma5	F	5.7	6.4	6.1	61	5	1.09	0.069	0.807	2.04	0.36
Ma6	F	5.7	6.3	6.4	81	16	2.86	0.075	0.593	1.71	0.30
Ma7	F	5.6	5.9	6.1	115	30	1.71	0.073	0.532	1.41	0.25
Ma8	F	4.6	6.2	5.8	71	27	1.34	0.067	0.688	1.58	0.35
Ma9	F	5.0	n.a.	n.a.	60	15	0.96	0.064	0.725	1.62	0.32
Ma10	F	5.8	5.9	5.8	76	28	1.62	0.077	0.686	1.91	0.33
*Ma11**	M	4.2	6.8	6.3	91	12	1.42	0.069	0.564	1.12	0.27

AR, aspect ratio; F, female; Ind., individual; k_c, fractional turnover; M, male; m_b, body mass; n.a., not available; $\dot{V}_{CO_2}$, metabolic rate; t, duration; v, flight speed; WL, wing loading.

*Individual with damaged wing.

Table 2. Comparison of morphological, behavioural and respirometry data of the two study species between individuals with a damaged wing and conspecifics with intact wings

	M. albescens			*M. nigricans*		
	Mean ± s.d.	Ind.	Test	Mean ± s.d.	Ind.	Test
Morphology						
m_b (g)	5.1±0.6	4.2	t_9=5.1, **P=0.001**	4.3±0.3	3.9	t_9=4.1, **P=0.003**
WL (N m^{-2})	5.7±0.7	6.3	t_8=4.3, **P=0.003**	4.8±0.3	5.3	t_8=4.8, **P=0.001**
AR	6.2±0.3	6.9	t_8=5.8, **P=0.001**	6.3±0.1	8.6	t_8=47, **P<0.001**
Flight behaviour						
Speed (m s^{-1})	1.67±0.77	1.42	t_9=1.01, P=0.34	1.93±0.25	1.86	t_9=0.85, P=0.42
U-turns	22.3±13.4	12	t_9=2.43, **P=0.038**	22.3±11.6	11	t_9=3.1, **P=0.013**
Metabolic rate						
$\dot{V}_{CO_2}$ (ml CO$_2$ min^{-1})	1.62±0.27	1.12	t_9=5.9, **P<0.001**	2.08±0.34	1.71	t_9=3.5, **P=0.007**
Mass-specific $\dot{V}_{CO_2}$ (ml CO$_2$ min^{-1})	0.32±0.04	0.27	t_9=4.3, **P=0.021**	0.49±0.08	0.44	t_9=2.1, P=0.0629

AR, aspect ratio; Ind., individual; m_b, body mass; MR, metabolic rate; WL, wing loading.
Test statistics are for one-tailed Student's *t*-tests. Significant differences are highlighted in bold.

the wing damage or a predisposition caused the lower manoeuvrability. The overall flight speed of bats over the 1 min period was similar in individuals with damaged and intact wings. In contrast to my prediction, flight metabolism was lower in bats with a damaged wing membrane than in healthy conspecifics. This difference may have originated from the fact that bats with damaged wings weighed less than conspecifics with intact wings. However, the difference in flight metabolism was still marginal (*M. nigricans*) or significant (*M. albescens*) when taking the variation in body mass into account. Thus, variation in body mass only partly explained differences in flight metabolism between bats with damaged wing membranes and healthy conspecifics. Presumably, bats with damaged wings showed a lower flight metabolism because they performed fewer flight manoeuvres than bats with intact wings. It is noteworthy that the pattern of reduced flight performance, metabolism and body mass was the same in the two species.

Two scenarios may explain the lower body mass of bats with damaged wings. Body mass reduction might be a compensatory mechanism, enabling bats to avoid an increased metabolic rate when the wing area is permanently reduced. Alternatively, bats with damaged wing membranes may have had a lower body mass because they were less efficient during foraging, leading to a decline in body reserves. As I captured free-ranging bats with naturally occurring wing damage, I cannot reject or accept either of the two hypotheses. However, bats with damaged wing membranes performed fewer U-turns in the flight arena, and this may indicate that the flight ability of bats is indeed constrained by a damaged trailing edge of the plagiopatagium. Recent experiments in another vespertilionid flying in the same circular flight arena confirmed that the number of aerial manoeuvres decreased with increasing wing loading (Voigt and Lewanzik, 2012). Unfortunately, the cause and effect regarding the relationship between wing area reduction and change in body mass remains uncertain in the current study. Interestingly, severe wing damage caused by *G. destructans* infections were also associated with a lowered body mass (Reichard et al., 2009), suggesting that foraging success of temperate zone *Myotis* species may also suffer from damaged wings or that bats may use a strategy of body mass loss. Wing membranes are important not only for producing lift and

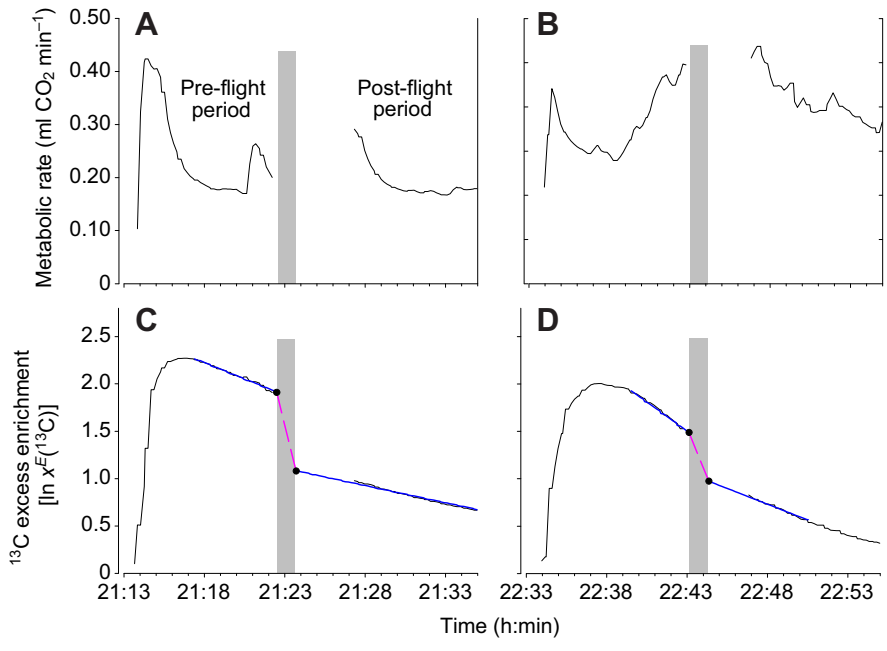

Fig. 2. Two examples of respirometric and isotopic measurements: *M. albescens* (A,C) and *M. nigricans* (B,D). (A,B) The metabolic rate of resting animals during the course of the experiment. (C,D) The excess enrichment of ^{13}C (ln scale) in the breath of animals. Because of the contamination of chamber air with ambient CO_2 when animals are transferred back to the chamber after the flight trial, metabolic rate and ^{13}C excess enrichment could not be monitored for about 3 min after the flight trial. The excess ^{13}C enrichment of exhaled breath was extrapolated for the onset and end of the flight period (indicated by a grey box) based on two least-squares linear regressions (blue lines calculated over 3 min periods of the pre-flight period and 10 min of the post-flight period). The fractional turnover of the ^{13}C label of the flying bat is indicated by the pink dashed line.

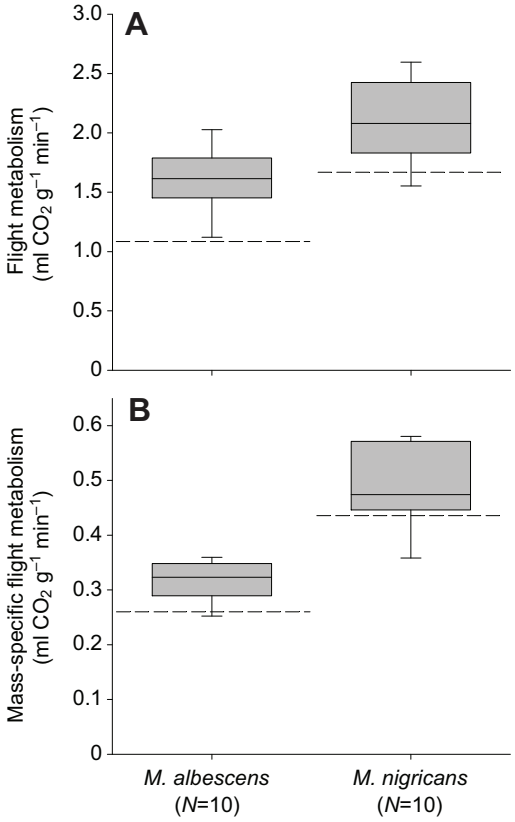

Fig. 3. Flight metabolism (A) and mass-specific flight metabolism (B) for flying *M. albescens* and *M. nigricans* with intact wing membranes. Corresponding values for conspecifics with a damaged wing membrane are indicated by a dashed line.

thrust in flying bats but also for other physiological processes, such as evaporative water loss (Speakman and Racey, 1989; Thomas and Cloutier, 1992), thermoregulation (Speakman and Hays, 1992; Reichard and Kunz, 2009) and possibly also respiration (Herreid et al., 1968; Makanya and Mortola, 2007). Recently, it was also shown that wing membranes carry important sensory hairs that most likely help bats to perceive and control air flow around wing membranes (Chadha et al., 2011). Yet, it is unclear whether a reduction of the wing area of about 10% would significantly influence any of the aforementioned processes in bats of the current study.

Thus far, questions related to performance and metabolic rate of vertebrates flying with damaged wings have only been looked at in birds suffering from a partial loss of feathers during seasonal moult. Bird feathers usually wear down according to their intrinsic robustness and the mechanical stress they are exposed to during flight. During moult, wing areas of birds often get smaller when lost feathers cause so-called moult gaps. For birds with moult gaps, aerodynamic theory predicts an increase in metabolic requirements for continuous horizontal flight (Hedenström and Sunada, 1999; Hedenström, 2003). Yet, past studies produced controversial results with respect to flight performance and metabolic rate of moulting birds. For example, studies in hummingbirds have shown that moulting individuals are able to tolerate a 30% loss in wing area without any changes in flight metabolism, but this was mainly achieved by a reduction in body mass (Chai, 1997), a pattern that is also apparent in the experiments with *Myotis*. In addition, moulting hummingbirds experienced a reduction in flight efficiency and performance (Chai, 1997; Chai and Dudley, 1999). Another study supported the finding that moulting hummingbirds reduced their body mass and experienced a lower aerodynamic force production and flight speed when they lost primary flight feathers (Chai et al., 1999). However, high-speed video recordings of take-off flights in birds suggested that European starlings did not experience a lowered flight performance during moult (Williams and Swaddle, 2003).

In summary, individuals of two species of *Myotis* that had a damaged trailing edge of the plagiopatagium showed a decrease in flight metabolism, probably resulting from a lower number of energetically costly flight manoeuvres. Presumably, bats lowered their body mass to compensate for the higher aspect ratio and wing loading when parts of the plagiopatagial wing area were lost. Alternatively, bats may suffer from reduced foraging success when their wing area is reduced, leading to a lower body mass and flight metabolism. As I did not reduce the wing area of individual bats experimentally because of ethical considerations, it is not possible to distinguish between these two scenarios. Also, it is important to keep in mind that *Geomyces*-inflicted damage to the wing membrane differs greatly and that infected bats may encounter varying problems of limited manoeuvrability depending on the specific location and extent of the damage. A lowered body mass associated with a reduced wing area could have drastic consequences for the survival of vespertilionid bats when facing adverse environmental conditions. Presumably, these bats may lack sufficient body reserves to survive extended periods of torpor. This may exacerbate the effect of fungal infections in North American bats when they depend on crucial body reserves for hibernation.

LIST OF SYMBOLS AND ABBREVIATIONS

k_C	fractional turnover of ^{13}C label (min^{-1})
m_b	body mass
t	duration of flight (s)
V	flight speed ($m\ s^{-1}$)
$\dot{V}_{CO_2}$	carbon dioxide production rate ($ml\ min^{-1}$)
$x(^{13}C)$	^{13}C enrichment (atom%)
$x^E(^{13}C)_{start}$	^{13}C excess enrichment (atom%) at the start of the flight period
$x^E(^{13}C)_{end}$	^{13}C excess enrichment (atom%) at the end of the flight period

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COMPETING INTERESTS

No competing interests declared.

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