The tail plays a major role in the differing manoeuvrability

of two sibling species of mouse-eared bats

(*Myotis myotis* and *Myotis blythii*)

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ABSTRACT

Two sympatrically occurring bat species, *Myotis myotis,* Borkhausen 1797, and *Myotis blythii,* Tomes 1857 (Chiroptera, Vespertillionidae), share numerous similarities in morphology, roosting behaviour and echolocation and are often difficult to distinguish. However, despite these similarities, their foraging behaviour is noticeably different. Our aim was to examine the extent to which these different foraging strategies reflect morphological adaptation. We assessed whether the morphology of the wing, body and tail differed between *M. myotis* and *M. blythii*. In addition, in a laboratory experiment involving an obstacle course, we compared differences in manoeuvrability by relating them to our morphological measurements.

The two species differed in their overall size, wingtip shape and tail-to-body length ratio. The generally smaller-sized *M. blythii* performed better in the obstacle course and was therefore considered to be more manoeuvrable. Although differences in wingtip shape were observed, we found the most important characteristic affecting manoeuvrability in both species to be the tail-to-body length ratio. Additionally, when we compared two bats with injured wing membranes with unharmed bats of the same species, we found no difference in manoeuvrability, even when the wing shape was asymmetric. We therefore postulate that morphometric differences between the two species in their overall size and, more importantly, in their tail-to-body length ratio are the main physical characteristics providing proof of adaptation to different foraging and feeding strategies.

Key words: *Myotis myotis*, greater mouse-eared bat, *Myotis blythii*, lesser mouse-eared bat, manoeuvrability, obstacle course, bat, sister species, flight behaviour, niche differentiation, sympatric, morphology, performance

INTRODUCTION

In the wild, populations of closely related and similar species can often be seen foraging in the same habitats. Famous examples include the Darwin finches (Darwin 1859) and East African cichlid fishes (Meyer et al. 1990). At first glimpse, these closely related species might appear to be in strong competition with each other, but specialisations can usually be detected in their feeding niches (Schluter 2001). For flying animals, such as bats or birds, the ability to perform manoeuvres is crucial in avoiding obstacles and approaching prey in dense vegetation (Findley et al. 1972; Norberg and Rayner 1987; Norberg 1994). Differences in manoeuvrability have generally been considered to be an important factor in niche differentiation and, ultimately, to represent a fundamental process underlying the adaptive radiation of bats, which are the second most species-rich mammalian order (Aldridge 1985; Aldridge and Rautenbach 1987; Norberg and Rayner 1987; Voigt and Holderied, 2012). In the context of flight, manoeuvrability is usually defined as the minimum radius of a turn an animal can achieve without reducing its speed. Another term related to aerial manoeuvres is agility, which is defined as the maximum roll acceleration during the initiation of a turn and is therefore measured based on the rapidity with which a flight path can be altered (Norberg and Rayner 1987; Norberg 1994). In anecological context, the term manoeuvrability refers to the ability to fly through limited space while avoiding vegetation or other obstacles. Thus, our definition of manoeuvrability includes agility.

Chiroptera encompasses over 1230 species distributed worldwide (Schipper et al. 2008; Kunz et al. 2011) exhibiting diverse wing morphologies and, in the case of species using echolocation for orientation, differentiation in echo-acoustic characteristics (Neuweiler 1984; Schnitzler and Kalko 2001). While we can predict that morphologically and echo-acoustically different species will use and perceive the world in different ways, there are examples of species that co-exist in the same environment despite showing little or no measurable morphological or echo-acoustical difference. It is not obvious how these species can coexist without strong competition (Saunders and Barclay 1992; Arlettaz 1999; Jacobs and Barclay 2009; Salsamendi et al. 2012). Investigating how these morphologically similar and closely related species adapt to different feeding and foraging niches should lead to a better understanding of the mechanisms that encourage coexistence and foraging niche specialisation.

The European greater mouse-eared bat (*Myotis myotis*, Borkhausen 1797) and the lesser mouse-eared bat (*Myotis blythii*, Tomes 1857) can sometimes be found roosting together and even occasionally hybridising (Berthier et al. 2006). Regarding morphology, *M. myotis* is very similar to *M. blythii* in general, though it is usually slightly larger than *M. blythii* (Arlettaz et al. 1991; Dietz et al. 2009). The echolocation calls of these species are similar, and although differences occur, none of them appear to be consistent among all individuals. Thus, distinguishing these two species in the field is difficult (Russo and Jones 2002; Walters et al. 2012). However, despite their morphological and acoustic similarities, these two species show behavioural divergence in foraging behaviour (Arlettaz 1996, 1999; Berthier et al. 2006; Siemers et al. 2011). *M. myotis* prefers habitats with open accessible ground, in contrast to *M. blythii*, which typically hunts in long grass meadows (Arlettaz 1996; Güttinger et al. 1998; Arlettaz 1999; Rainho et al. 2010; Siemers et al. 2011). Our purpose was first to more closely examine the wing, body and tail morphology of these two species to determine whether they actually differ only in their overall size, or if differences in shape exist as well. We expected that all of the length and area measurements of the wing, body and tail of *M. blythii* would present significantly lower values compared with *M. myotis*. In other words, we expected to find that the main difference between these species is due to their different sizes and that the two species are simply scaled versions of the same model (Norberg and Rayner 1987; Stockwell 2001; Andreas et al. 2013). Then, in a second step we sought to ascertainwhether the differences in the ecology of the two species could be attributed to morphological adaptations, followed by differences in flight performance. Arlettaz (1996) speculated that *M. blythii* gleans insects directly from grass stalks, which would require greater manoeuvrability than *M. myotis*, which lands on the ground to catch prey (Arlettaz 1999). We followed these suggestions and hypothesised that *M. blythii* is morphologically better

adapted than *M. myotis* to slow, manoeuvrable flight, close to or within dense ground vegetation (e.g., long grass meadows, steppe-like areas). We assumed that the smaller wing span of *M. blythii* would play a major role in making the species more manoeuvrable than *M. myotis* (Norberg 1994; Stockwell 2001). However, in cases where the observed morphological differences deviate from the overall size, we assumed that the two species would differ in a way that is consistent with *M. blythii* being more manoeuvrable, for example, presenting a wing shape with more pointed wing tips (Findley et al. 1972; Norberg and Rayner 1987; Norberg 1994). To test our hypotheses, we compared wing, body and tail measurements of the two sibling species as well as size-independent wing shape ratios and indices (Norberg and Rayner 1987; Norberg 1994) (Table 1). Moreover, we evaluated the manoeuvrability of both species in a standardised vegetation-like obstacle course (Aldridge 1985; Rhodes 1995; Stockwell 2001). The results obtained from the obstacle course were first tested for variability between species. Second, we removed the species variable and instead included the morphological variables to assess how these parameters contributed to performance differences.

MATERIALS AND METHODS

Animals

We caught bats using a harp trap (Faunatech, Victoria, Australia) or mist nets (Ecotone, Sopot, Poland) at the entrance of caves in northeastern Bulgaria from the beginning of May until the end of August 2010. The capture and husbandry of the bats and behavioural analyses were carried out under license from the official Bulgarian authorities (MOEWSofia and RIOSV-Ruse, permit numbers 193/01.04.2009 and 205/29.05.2009) in accordance with recommendations of the Canadian Council on Animal Care for bats and the EUROBATS Resolution 6.5.

We identified the two species based on differences in forearm length (*M. myotis*: 5.5 - 6.7 cm and *M. blythii*: 5.1 - 6.2 cm) and upper tooth row length (caninus to the 3rd molar, *M. myotis*: 0.92 to 1.06 cm and *M. blythii*: 0.81 to 0.95 cm) (Dietz et al. 2009). Individuals of intermediate size (forearm length between 6.0 - 6.2 cm) were not used in the experiments because they could not be precisely identified to the species level. All of the bats were sexed and weighed (electronic scale, Kern, EMB 500-1, $d = 0.1$ g, Balingen, Germany), and further standard measurements (body length, wing span, tail length) were obtained with a dial calliper (Measy 2000 calliper, Switzerland, precision 0.1 mm) (Fig. 1 B). Only adult bats were used for the experiments.

The bats were retained for a maximum of 10 days at the Tabachka Bat Research Station (Bulgaria) of the Sensory Ecology Group (Max Planck Institute for Ornithology, Seewiesen, Germany). Up to six bats were housed together in a cage (49 cm length x 37 cm height x 35 cm breadth) at 20 °C ± 3 °C under a 14/10 h light/dark photoperiod. The bats were fed mealworms (*Tenebrio molitor*, Linnaeus, 1758, larvae, Coleoptera) by hand each night. We measured the body mass of the bats every day to ensure that they maintained their body condition. Water was available *ad libitum*. After the experiments, all of the bats were released in good health at the site of capture.

Morphology

In addition to the standard morphological measurements, we took pictures of the wings of 17 male *M. myotis* and 15 male *M. blythii*. We held each bat on a sheet of graph paper and carefully stretched the wings until they were fully extended. We took several digital pictures of each bat from a distance of approximately 1 m. To reduce measurement errors, we analysed three pictures per individual and noted the average values. In each picture, we measured either the left or the right wing depending on which was more stretched based on an estimate of the wing area (wing length x wing width). Using these pictures, we measured the handwing length, armwing length, handwing area (chiropatagium) and armwing area (propatagium and plagiopatagium: Fig. 1 A)

according to Norberg and Rayner (1987). Additionally we measured the tail membrane area (uropatagium), body width and body area. To obtain these measurements, we used the image processing program Image J (version 1.44) (Rasband 1997-2012).

Using the wing and body measurements and the standard morphological measures, we calculated the aspect ratio, relative wing loading, tip length ratio, tip area ratio, wingtip shape index (Norberg and Rayner 1987; Norberg 1994), tail-to-body length ratio and tail-to-wing area ratio (Fig. 1 and table S 1[1]). In the next step, we compared each parameter between the two *Myotis* species with non-parametric Kruskal-Wallis tests in R(version: 3.0.0, 13.04.03) (RcoreTeam 2013), adjusting the *p*-values for multiple testing with a Bonferroni correction. We employed the nonparametric Kruskal-Wallis tests because the data were not normally distributed among the species populations. The 95 % confidence intervals of the median values for the differing parameters were calculated using the bootstrapping method (type: percentile) (Canty and Ripley 2013). To reveal the relationships between the obtained parameters, all of the morphological measures, ratios and indices were compared to determine their degree of correlation using a cluster dendrogram in R, in the R package pvclust (Suzuki and Shimodaira 2006).

Manoeuvrability

From the bats that were used to obtain wing measurements, we randomly chose seven individuals of each species and conducted a manoeuvrability test for each of them in a flight tunnel (8.0 m length x 1.5 m breadth x 2.4 m height). Performance was assessed using an obstacle course consisting of three rows of plastic tubes (grey PVC, length approx. 2.3 m). The obstacles all had a diameter of 6 mm and were detectable using echolocation (Sumer et al. 2009). The surface of the obstacles was roughened to enhance detection. Upon ensonification of the obstacles using a frequency-modulated signal ranging from 120 kHz to 20 kHz, they produced a distinct echo (Fig. S 1[2]). For ensonification, we positioned a microphone (Gras microphone 1/8-inch Type 40DP, Holte, Denmark) above a loudspeaker (Ultrasonic Dynamic Speaker ScanSpeak, Avisoft, Berlin, Germany) at a height of 110 cm and placed an obstacle 50 cm in front of the loudspeaker.

The obstacles were suspended from the ceiling on hooks mounted on a wooden plate and fixed on the ground in sand that covered the floor of the experimental room. A wooden plate attached to a frame was placed 4 m away from the entrance to the flight tunnel (Fig. 2), and the obstacles were spaced equidistantly within and between the three rows.

The trials took place at night, and before the actual trials began, each bat had a chance to fly through the tunnel once without obstacles to become familiar with the flight tunnel and the procedure. Then, at the beginning of each individual trial, a single bat was hung on a perch. After a period of 3 min, during which the bat could start flying on its own, the perch was gently turned to prompt the bat to fly. After the bat started flying, it was given 3 min to fly through the obstacle course to the end of the flight tunnel. In cases where a bat stopped and perched, it was prompted to continue flying by finger snapping, or it was removed and re-released on the perch at the beginning of the tunnel. The first arrangement tested for *M. myotis* employed spacing of 41 cm between obstacles, while that for *M. blythii* employed 38 cm spacing, corresponding to their average respective wing spans. For all other trials, arrangements with 9 different spacings (19 cm, 21 cm, 29cm, 31 cm, 38 cm, 41 cm, 44 cm, 48 cm and 52 cm) were presented to the individuals three times each in a pseudo-randomised order. The same spacing was never repeated in successive trials. The manoeuvrability performance of the bats tested during the different trials can therefore be compared to a situation in the wild where the bats are flying in an unknown, cluttered habitat. When a bat completed a flight through the obstacle course (including the first flight without obstacles), it was prevented from flying back and was rewarded with 3 - 5 mealworms. Each individual completed 5 - 8 trials consecutively, with a short break of usually 5 - 10 min between each flight and was tested in this way once or twice per night. The trials were repeated once in the case of technical problems, e.g., if the

bat was disturbed by the observer shortly before flying through the course, or if the bat showed certain behaviours (starting from the wall less than 1 m from the obstacle course, touching the wall, crawling or landing without touching an obstacle while flying through the course). The obstacles were flexible and yielded slightly when touched by a bat. Collisions with the obstacles produced no apparent signs of injury, though the bats were checked regularly. Each trial was monitored directly by the observer using a headlamp with a red light, and the trials were recorded for further analysis using four infrared-sensitive cameras (WAT-902H2 Ultimate, Watec, Tsuruoka, Japan) and Digi Protect (Abus, Affing, Germany) surveillance software. Infrared light was provided through a stroboscope (875 nm wavelength, flash rate 50 Hz, i.e., one flash per video half-frame, custom made, University of Tuebingen).

We assumed that the bats would attempt to avoid touching the obstacles and eventually make an unintended landing on the ground. Under natural circumstances, even slight contact with vegetation might be risky because some branches have spines or thorns that could lead to wing injuries (Davis 1968). Likewise, unnecessary and uncontrolled landings could increase the risk of injuries and predation (Lima and O'Keefe 2013). Therefore, using the video recordings for every trial, we counted each time when one of the obstacles was touched and each unintended landing (landing on the ground after touching one or more obstacles) within or shortly behind the obstacle course.

Differences in manoeuvrability between the species

We employed generalised linear mixed effects models (GLMMs) in R (Bates et al. 2013; RcoreTeam 2013) using the glmer function to check for differences in manoeuvrability between the species. We first tested the differences between species, based on their performance in obstacle avoidance, by comparing the total number of touched obstacles and the number of unintended landings on the ground in a basic GLMM. The basic GLMM included the function of spacing between the obstacles and species identity modelled with a Poisson error distribution, accounting for individual differences and pseudo-replication by using individual identity as a random factor. Furthermore, we tested whether repeated measures for a given spacing had any effect.

Incorporating morphometric variables into the basic GLMM

We examined the assumed species differences more closely for the purpose of determining which morphometric variables best explain the observed species-specific differences. Therefore, the morphological measures and ratios (Table 2 and 3) obtained for the 14 individuals tested in the obstacle course were added to the same basic GLMM, except that we did not include the species identity in this case. Each time, only one variable was added to the basic model (20 variables = 20 models). All of the measured and calculated morphological variables were included in the modelling process. None of the correlating variables was removed because thefact that two variables are correlated does not guarantee that they both have the same functional importance for the tested manoeuvrability performance. For the added morphometric variables in the differing models, the *p*-values were corrected for multiple testing with a Bonferroni correction factor. The morphological variables and their *p*-values were directly compared and discussed regarding their influence, or lack of thereof, in relation to the manoeuvrability performance.

Forward selection modelling procedure with morphological variables

Subsequently, we tested whether there were minimum adequate models consisting of several important morphological variables that best explained the differences in the manoeuvrability of the tested bats as a function of morphological differences. To obtain the best minimum adequate models, we used the forward selection procedure based on a minimising Bayesian information criterion (BIC). In the first step, we compared the BIC values of the 20 models (each included one morphological variable) with each other and searched for the models with the lowest BIC values. We tested these BIC models further by adding one of the 19 other variables each time. Whenever one of the new models showed a BIC value that was at least two units lower

compared with the simpler model, it was considered to be a better model. The modelling process was continued by adding further variables until no better models could be found (Table S 2[3] and S 3[3])

Comparison of individuals with injured wings

During the bat capture events, two individuals with old wing membrane injuries were captured. Because the two bats (one female *M. myotis* and one male *M. blythii*) belonged to our target species and there have been only a few studies on naturally occurring injured bats, we decided to obtain wing pictures for these bats and to test their manoeuvrability performance under the same conditions applied to the other individuals in our obstacle course. We compared the obstacle avoidance behaviour of the injured individuals with the performance of the unharmed conspecifics. Because of the small sample size, we did not carry out statistical testing.

RESULTS

Morphology

Eight of the twelve length and area measurements for the body and wings of the bats and the body mass were significantly greater in the *M. myotis* individuals compared with *M. blythii* (Table 1 and 2). The tail length (Kruskal-Wallis test, χ^2 (Chi-Square) = 6.49, df = 1, p = 0.141), tail membrane area (Kruskal-Wallis test, χ^2 = 0.032, df = 1, p = 1.0), body area (Kruskal-Wallis test, χ^2 = 4.24, df= 1, p = 0.515) and handwing length (Kruskal-Wallis test, χ^2 = 8.02, df = 1, p = 0.060) did not differ significantly between the two species (Table 2). In the case of handwing length, the difference between the two species tended toward significance, with lower values being found for *M. blythii,* which is consistent with the other length and area measurements. Regarding the body area, most *M. myotis* individuals (N = 12) exhibited higher values than *M. blythii* (N = 9), but the results were not significant (Table 2). The 95 % confidence interval of the tail length of *M. myotis* ranged from 5.1 to 5.4 cm (median: 5.2) and that of *M. blythii* from 5.2 to 5.8 cm (median: 5.6). Thus, the tail lengths strongly overlapped, but the median length was greater for the generally smaller species, *M. blythii*. A similar result was found for the tail membrane area (Table 2).

Among the size-independent ratios and indices, we found no significant differences regarding the aspect ratio, relative wing loading or tip area ratio (Table 1 and 3). However, the tip length ratio (Kruskal-Wallis test, χ^2 = 12.73, df = 1, p = 0.003) and the wingtip shape index (Kruskal-Wallis test, χ^2 = 7.29, df = 1, p = 0.049) were significantly different.

Because we found no significant differences for tail length and tail membrane area, and none of the size-independent ratios or indices that we calculated were explicitly related to the tail, we decided to define two new ratios: the tail-to-body length ratio and the tail-to-wing area ratio. The tail-to-body length ratio (TBl) is the ratio of the length of the tail (Lt) to the length of the body (Lbl); $TBl = Lt / Lbl$), and the tail-to-wing area ratio (TSs) is the ratio of the area of the tail membrane (St) to the wing area, but without the tail area ($TSs = St / (2 Shw + 2 Saw + Sb)$. Accordingly, a higher value for the tail-to-body length or tail-to-wing area ratio indicates a longer tail or larger tail area in relation to the body or wing. We found a significantly higher tail-to-body length ratio for *M. blythii* than for *M. myotis* (Kruskal-Wallis test, χ^2 = 20.67, df = 1, p < 0.001). For the tail-to-wing area ratio, we did not find a significant difference (Kruskal-Wallis test, χ^2 = 4.39, df = 1, p = 0.253).

The cluster dendrogram (Fig. 3) presented four clusters, each of which exhibited highly correlated variables. In the case of clusters 6 and 9, the length or area measurements were one of the main elements of the corresponding and highly correlated ratio (tail-to-body length ratio or tail-to-wing area ratio). In cluster 13, both relative variables included the wing area within their formula.

Cluster 14 consisted of the variable weight and all of the length and area measurements, except for the tail length

and tail area. Within cluster 14, a clear separation between the morphometric measurements for the same wing, body or tail region was observable in some cases (e.g., body area and body length or body width). Cluster 14 included all of the length and area measurements that were significantly different between *M. myotis* and *M. blythii*, with the exception of the handwing length and body area, (Table 2). The measurements of cluster 14 all showed greater values for *M. myotis*, and they therefore represent the overall size differences of the two species most clearly.

Manoeuvrability

All seven *M. myotis* and *M. blythii* successfully completed 26 valid trials on average (max. 27 trials, min. 22 trials). We recorded 181 valid trials for *M. myotis* and 182 for *M. blythii* in total. The narrowest obstacle spacing that a *M. blythii* individual was able to negotiate without touching any obstacle was 29 cm (average min. negotiated spacing: 43.1 cm, $N = 7$) (Video S 1[4]). For *M. myotis*, the narrowest spacing that could be negotiated without any touches or unintended landings was 38 cm (average min. negotiated spacing: 44.7 cm, $N = 6$). One *M. myotis* did not manage to fly through the course without any touches, even at the broadest spacing of 52 cm.

Differences in manoeuvrability between the species

The narrower the selected spacing, the greater the difference in the performance of the two species (Fig. 4). Therefore, we included the spacing as a variable in all of our GLMMs. Significantly lower numbers of unintended landings (effect between obstacle spacing and unintended landings, parameter estimate (Est.) $\pm$ standard error (SE) = -0.08 $\pm$ 0.00, z = -10.19, p < 0.001; effect between species and unintended landings Est. $\pm$ SE = -0.87 $\pm$ 0.27, z = -3.19, p = 0.001) and obstacle touches (spacing Est. $\pm$ SE = -0.05 $\pm$ 0·00, z = -13.40, p < 0.001; species Est. $\pm$ SE = -0.17 $\pm$ 0.08, z = -2.21, p = 0.027) were recorded for *M. blythii* compared with *M. myotis*. We found no effect regarding repeated measures for a given spacing, either for the obstacle touches (Est. $\pm$ SE = -0.04 $\pm$ 0.04, z = 0.96, p = 0.340) or for the unintended landings (Est. $\pm$ SE = 0.02 $\pm$ 0.07, z = 0.23, p = 0.816).

Incorporating morphometric variables into the basic GLMM

When we tested all of the obtained morphological variables to determine their influence on the number of unintended landings each time in the same basic model, only two morphological variables exhibited significant corrected *p*-values: the tail-to-body length ratio, with a corrected *p*-value of p <0.001, and body length, with p = 0.013 (Table 4). The model with the second lowest BIC included only the tail length and showed a lower BIC value compared with the model including body length, but in this case, the *p*-value for the tail length alone was not significant. The variable body length showed the only significant corrected *p*-value related to the overall size differences between the two tested species, although it was found to be correlated with other overall size-related variables, such as body width, wing span and wing area (cluster 14, Fig. 3).

For the response variable touches, none of the models exhibited significant variables (Table S 3).

Forward selection modelling procedure with morphological variables

The forward selection procedure resulted in three models (with the lowest BIC values) that best accounted for the number of unintended landings (Table 5 and S 2). In addition to the spacing between obstacles and the random variable individuals, the models included the following variables: tail-to-body length ratio, body length, tail length, tip area ratio, relative wing loading and aspect ratio (Table 4). When the variables included in the three best models were compared with the cluster dendrogram, we did not find any highly correlated variables within each of the models. Only the second and third best models differed in presenting highly correlated variables relative to wing loading and the aspect ratio. The best model included only one additional variable, the tail-to-body length ratio. All variables exhibited significant *p*-values ranging from 0.005 to < 0.001 (Table 5).

For the response variable touches, there was no best model with significant variables (Table S 3).

Comparison of individuals with injured wings

The injuries of both injured individuals were clearly visible (Fig. 5). The injured *M. myotis* individual showed a longer wing span, of 43.7 cm, compared with the othertested *M. myotis* individuals, with intact wing membranes. However, the weight of the injured *M. myotis* on the first night after capture was 25.0 g, which was slightly lower than the weights of most of the unharmed *M. myotis* (Table 2). All of the wing measurements for the left side of the injured *M. myotis* exhibited lower values compared with the right side. In the case of the armwing area, nearly 40 % of the area was missing on the left side compared with the right wing (Table S 2).

The wing span of the injured *M. blythii* was 37.2 cm, slightly lower than in most of the other tested individuals from the same species. The injured *M. blythii* was also lighter, showing a body weight of 20.0 g, compared with all of the unharmed tested *M. blythii* (Table 2). Due to holes in the wing membrane of the injured *M. blythii*, 7.6 % of its left and 1.4 % of its right handwing area was missing (Fig. 5, table S 4[5]). In both injured individuals, the aspect ratio (*M. myotis*: 8.38 and *M. blythii*: 7.32) and the relative wing loading (*M. myotis*: 36.80 N/m² and *M. blythii*: 38.21 N/m²) were greater than in the individuals with intact wing membranes.

Both injured bats were successfully tested in the obstacle course. The injured *M. myotis* completed 23 valid trials (see for example video S 1), and the narrowest spacing that it could negotiate without touching any obstacle was 48 cm. The injured *M. blythii* completed 27 trials, and the narrowest spacing that it could negotiate without touching any obstacle was 31 cm.

DISCUSSION

Morphology

Thedifferences observed between the two sibling species for most of the wing and body measurements (smaller values for *M. blythii* compared with *M. myotis*) were consistent with our assumption that the overall difference in size is the main factor that accounts for their differing manoeuvrability. However, not all of the morphometric measurements were significantly smaller for *M. blythii*. In these cases, the species showed deviation from simple overall size differences due to differences in shape (Table 1). We found significant differences in wing shape with regard to the tip length ratio and, more importantly, in the wingtip shape index, independent of size. The wingtip shape index was lower for *M. blythii* compared with *M. myotis*. A lower wingtip shape index indicates a more pointed wingtip and is known to enhance roll agility, which can increase manoeuvrability (Norberg and Rayner 1987). The more pointed wing tips of *M. blythii* would therefore be favourable for performing quick movements around bushes and other vegetation. Conversely, the more rounded wingtip of *M. myotis* can be an advantage when hovering (Norberg and Rayner 1987), for example, when flying over the ground searching for prey (Russo et al. 2007, Dietz et al. 2009).

Unfortunately, there is no available index to test for differences in tail-tip shape, such as those observed for the wing. The longer tail of *M. blythii* relative to its size and the not significantly different tail-to-wing area ratio might indicate a more pointed tail compared with that recorded for *M. myotis*. Another possible explanation could be that the tail area measurements were not sufficiently accurate to reveal significant differences between the tail area ratios. While obtaining the wing pictures, we had difficulty in fully extending the tail membrane. We therefore suppose that, at least in some cases, the tail membrane area was underestimated. The longer tail of *M. blythii* and the possibly larger tail membrane in relation to its size might represent adaptations to its hunting strategy. In contrast to *M. myotis*, *M. blythii* appears to be better adapted to catching prey from vegetation such as grass stalks during flight (Arlettaz 1996, 1999; Rainho et al. 2010), in which case a larger tail membrane could be advantageous. A longer tail and a larger tail membrane are thought to increase manoeuvrability and

agility and can improve the likelihood of capturing insects at slower flight speeds (Norberg 1994; Dudley 2002; Gardiner et al. 2011*a*; Gardiner et al. 2011*b*; Adams et al. 2012).

Body area measurements showed no significant differences between the studied species, whereas the body length and body width were clearly significantly different. Overall, the body shape of *M. blythii* was more compact (body width was not reduced as much in a caudal direction) than that of *M. myotis,* as can be seen, for example, in the direct comparison of the body shapes of the two injured bats (Fig. 5).

The differing shapes of the wingtip, body and especially the tail of *M. myotis* and *M. blythii* might be a consequence of character displacement (a process caused by competitive interactions among organisms that leads to divergent trait evolution) (Pfennig and Pfennig 2010). Further measurements conducted in individuals from the two species from allopatric populations might help in validating this assumption.

Manoeuvrability

Differences in manoeuvrability between species

The obstacle course experiment confirmed our hypothesis that *M. blythii* demonstrates greater manoeuvrability compared with its sister species *M. myotis.* The species differences were more significant for unintended landings than for touching the obstacles, but both results were well in line with each other. The weaker significance observed for the touches might have occurred because touching an obstacle is less harmful (and happens in nature as well), while landing on the ground can be dangerous and is energetically much more demanding (Davis 1968; Voigt and Lewanzik 2012; Lima and O'Keefe 2013). Another possible explanation is that due to their different foraging behaviours, *M. myotis* lands on the ground more often than *M. blythii.* However, in this case, we would have expected to record many more invalid trials among the *M. myotis* individuals, including landing in front of the obstacles without obstacle touches or crawling through the course. Instead, we were only obliged to exclude a few trials, by one individual of *M. myotis* (2 trials) and two individuals of *M. blythii* (a total of 5 trials) due to repeated crawling or landing on purpose (without any touches). Furthermore, it is important to mention that we did not record how forcefully the bats touched the obstacles. A light touch with the wing tip was counted in the same way as a strong touch with the inner wing area (armwing area) or even with the body. Strong touches could change the flight path more dramatically than a light touch. In most cases of unintended landings, one or several strong obstacle touches occurred just beforehand and forced the bat to land on the ground. Therefore, we consider the results obtained for unintended landings to be more powerful proof of manoeuvrability than the results for touches.

Incorporating morphometric variables into the basic GLMM

Of the two variables included in the models showing significant corrected *p*-values, body length seemed to play a major role because it was included in the tail-to-body length ratio measurement as well. At first glimpse, it might appear that the tail length only reached significance because it was related to the body length. On the other hand, one should take into account the fact that body length is well in line with the species-specific overall size differences, whereas this is not the case for tail length. Therefore, in the model, tail length must be considered in relation to overall size to show a significant difference in performance. We could still have obtained a significant *p*-value for the relative tail length if we had generated the ratio with a different variable representing overall size differences, such as wing span or forearm length. However, the obtained results also showed that the morphometric variables that contribute to overall size differences (cluster 14, Fig. 3) do not have the same importance for the manoeuvrability performance with regard to unintended landings. Contrary to our assumption, no significant *p*-value was found for the wing span. This result confirms findings reported by Gardiner et al. (2011*a*). We therefore concluded that in our experiments, wing span did not significantly affect the differences in the manoeuvrability performance of *M. myotis* and *M. blythii.*

Forward selection modelling procedure with morphological variables

The most important morphometric variables affecting unintended landings were body length, tail length and especially the newly defined tail-to-body length ratio (best model), which proved to be a highly significant morphological ratio differentiating the two species. Body length was the only variable that belonged to cluster 14 in our hierarchical clustering dendrogram describing the overall size differences between the two tested species. Interestingly, body length, tail length and the tail-to-body length ratio refer to the sagittal plane of the bat, and not, as initially assumed for the wing span, to the transverse plane. Differences in the sagittal plane might have a greater influence because they are closer to the centre of mass (Iriarte-Diaz and Swartz 2008). We therefore concluded that the closer the impact was to the centre of mass of an obstacle, the higher the risk of an unintended landing. Furthermore, if we assume that the body length can only be slightly adjusted during flight, in contrast to the position of the wing, we suggest that during tight, quick turns close to obstacles, a greater body length would be unfavourable due to causing a reduced yaw ability and therefore a higher risk of obstacle touches or unintended landings on the ground (Swartz et al. 2012). Additionally, the longer tail of *M. blythii* appears to enhance the speed of body rotation and, thus, increases torsional agility, thus resulting in a lower risk of obstacle touches or unintended landings on the ground (Dudley 2002).

Additional variables in the best models with the response variable unintended landings were located in the frontal plane. The tip area ratio was included in the best models. Interestingly, neither the tip length area nor wingtip shape index appeared in the best models, although in our morphometric measurements, we found that thesevariables were significantly different between the two species. It appears that the tip area ratio measurement is more important for manoeuvrability in this case, independent of the shape of the wing tip. The tip area ratios for *M. myotis* and *M. blythii* (0.64 and 0.63, respectively) showed an intermediate value compared with other bat species, which is considered to be conducive to good manoeuvrability (Norberg and Rayner 1987). Most of the wing mass is located in the armwing area, which is a component of the tip area ratio and plays an important role in slow flight as well as in maintaining stability during flight (Norberg and Rayner 1987). Because the armwing area is closer to the body than the handwing area, the obstacle touches within the former area were stronger in most cases and were more likely to lead to landings on the ground than obstacle touches within the handwing area region (pers. observation). The relative wing loading and aspect ratio, which were also included in the three best models, were found to be highly correlated in our dendrogram. Therefore, these two models were interchangeable. The low relative wing loading and aspect ratio observed in both of the tested species enables slow flight, which should give a bat more time to manoeuvre around obstacles without touching them, or to adjust its flight path after a touch (Norberg and Rayner 1987; Norberg 1994).

The reason that we did not obtain significant variables for the response variable touches was most likely because this response variable did not differentiate sufficiently between the two species to allow investigation of the effect of the morphological variables. It might also be that factors other than the measured morphological variables, such as differences in behavioural flexibility (Clarin et al. 2013) or the flight speed while negotiating the obstacle course, played a role. On the other hand, it could be that the tested bats took light touches on the flexible obstacles into account after recognising that they were harmless.

Comparison of individuals with injured wings

The wing injuries of both injured individuals led to reduced wing membrane areas. In the injured *M. myotis* individual, the injury was particularly severe, as a large area of the left armwing membrane was missing. During flight, the asymmetrical wing areas may have generated differing lift and thrust forces on the two wings, which would likely have made it difficult for the bat to achieve straight or manoeuvred flight (Muijres et al. 2008; Song et al. 2008; Voigt 2013). The injuries observed on the injured *M. blythii* individual were of a different kind, as less of its wing area was missing, and the injuries were spread over both handwing areas. Therefore, we would assume that achieving straight or manoeuvred flight should not have caused difficulties as

severe as those for the injured *M. myotis*.

Consistent with Voigt (2013), who also studied the manoeuvres of naturally injured bats, our injured bats exhibited a low or lower initial weight as well as higher aspectratios and relative wing loadings than most of the intact individuals of the same species. However, in our experiments, both injured bats performed well in the obstacle course, and we did not find differences in manoeuvrability compared with the tested healthy conspecifics. The injured bats successfully completed as many trials as the bats with intact wing membranes. This finding stands in contrast to the observations of Voigt (2013), who assumed that bats with wing injuries would avoid flight manoeuvres.

Conclusions

Ultimately, variations in overall size cannot account for the differences in the manoeuvrability of the two closely related species examined in this work. The morphological variables that contribute to variations in overall size were found to be of differing importance in relation to the manoeuvrability performance of the two tested species. The only variable that was related to overall size in the best models with significant variables was body length. These species show differences in several wing and body regions with respect to the overall trend in size (e.g., the smaller size of *M. blythii*), mainly regarding wingtip shape and tail length. *M. blythii* performed better in the obstacle course and is therefore considered to be more manoeuvrable. Although differences in wingtip shape exist, the most important morphological variables resulting in differing manoeuvrability in the two species were observed to be the tail-to-body length ratio and tail length, both of which are located in the sagittal plane. The tail of *M. blythii*, which is enlarged relative to its size, is therefore not only linked to its prey capture behaviour but also has an important influence on manoeuvrability. The results obtained from the two tested injured bats support the conclusion that tail morphology is more important than wing morphology in determining a bat's manoeuvrability, as the tails of these bats were undamaged. We conclude that the morphometric differences in the overall size of the two tested species, and, more importantly, in their tail dimensions, constitute their main adaptations to different foraging and feeding strategies.

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FIGURE CAPTIONS

Fig. 1. Drawing of a greater mouse-eared bat (*Myotis myotis*, Borkhausen 1797), showing all of the morphometric measurements that were taken. The lengths and areas of the wing, body and tail elements were measured from wing pictures taken from the dorsal side (A). Other measurements were conducted directly by handling the bat (B).

Fig. 2. Flight tunnel - view from above. Sketch of the experimental set up (not exactly to scale), showing the flight tunnel and the wooden plate in the middle, where the obstacles were positioned. The bats flew from the Start position, through the obstacle course, to the End, where they received a reward.

Fig. 3.Hierarchical clustering of the 20 morphometric measurements, ratios and indices. The values presented at branches are approximate unbiased *p*-values (AU, left), bootstrap probability values (BP, right) and cluster labels (bottom). Clusters showing an AU ≥ 95 are indicated by rectangles. The first left rectangle corresponds to a cluster labelled 13, with an AU = 99 and BP = 94.

Fig. 4. Performance in the obstacle course. The boxplot in 4 A shows the number of unintended landings per tested spacing and species (*Myotis myotis*, Borkhausen 1797, is indicated with light grey and *M. blythii,* Tomes 1857, with dark grey). The lower boxplot, in 4 B, shows the number of touches per tested spacing and species. The horizontal black bars are the medians; the grey boxes represent the interquartile ranges; the whiskers below and above represent the minimum and maximum values; and the circles represent outliers. The medians sometimes reach the end of the boxes because the dataset consists only of integer numbers.

Fig. 5. Wing pictures for one injured greater mouse-eared bat and one injured lesser mouse-eared bat (*Myotis myotis*, Borkhausen 1797, and *M. blythii,* Tomes 1857, respectively).

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[1] ___ Supplementary table S 1 is available in the journal website (http://cjz.nrc.ca).

[2] ___ Supplementary figure S 1 is available at the journal website(http://cjz.nrc.ca).

[3] ___ Supplementary tables S 2 and S 3 are available in the journal website (http://cjz.nrc.ca).

[4] ___ Supplementary video S 1 is available on the journal website (http://cjz.nrc.ca).

[5] ___ Supplementary table S 4 is available on the journal website (http://cjz.nrc.ca).

Schmieder et al.   Figure 1:

A. Dorsal side

handwing length (L_{hw})

armwing length (L_{aw})

hand wing area (S_{hw})

arm wing area (S_{aw})

body width (L_{bw})

body area (S_b)

tail area (S_t)

wing area (S) $= 2\ S_{hw} + 2\ S_{aw} + S_b + S_t$

B. Ventral side

wing span (L_{ws})

forearm length (L_{fa})

body length (L_{bl})

anus

tail length (L_t)
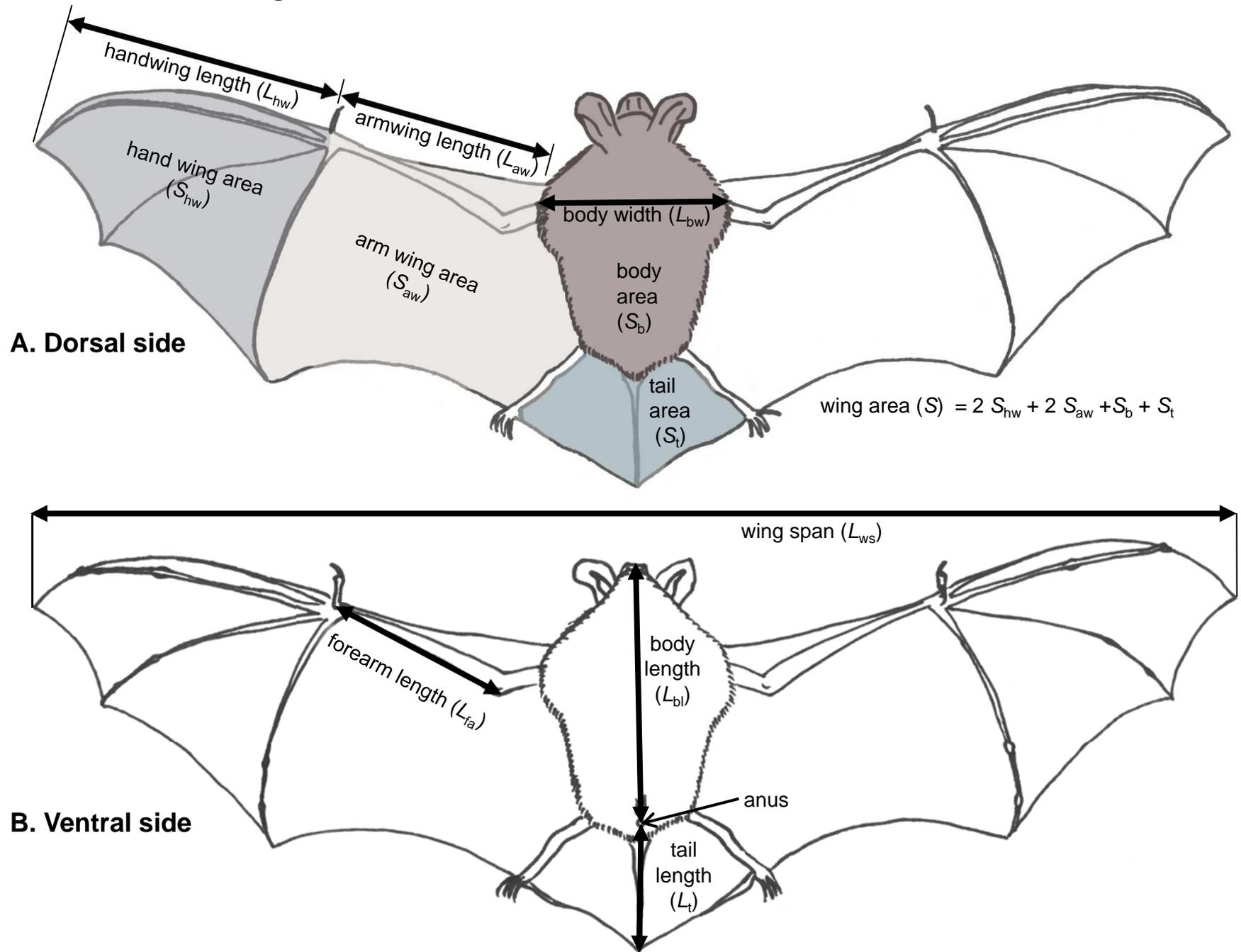
Figure 2:

Flight tunnel – view from above

infrared camera

length 8 m

4 m

1.2 m

2.8 m

Start

End

width
1.5 m

equidistant space
between obstacles,
e.g. 31 cm

perch

wooden plate,
mounted on wooden
framework

obstacles

blind,
prevented bat
to fly back

Figure 3:

Cluster dendrogram with AU/BP values (%)
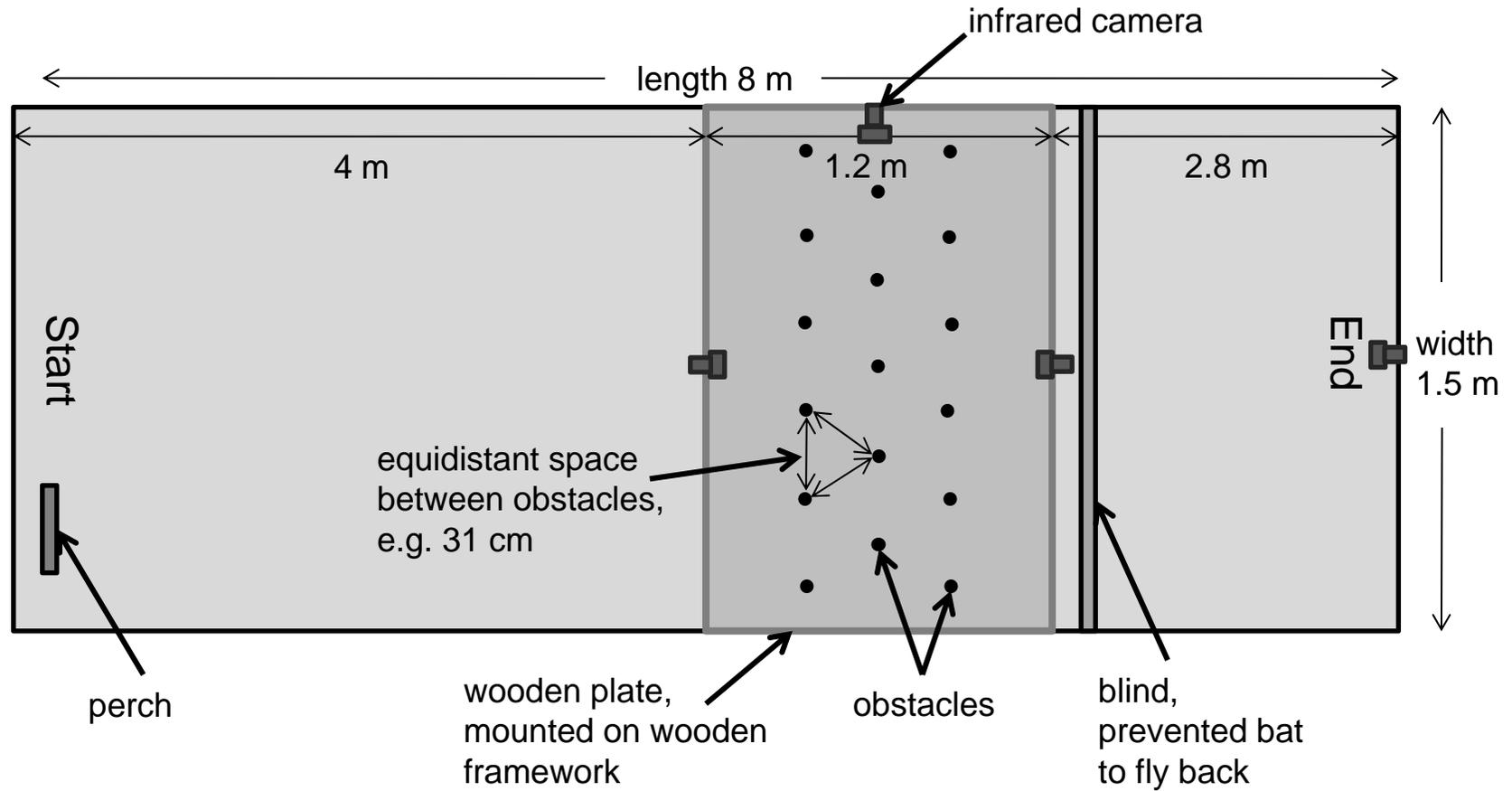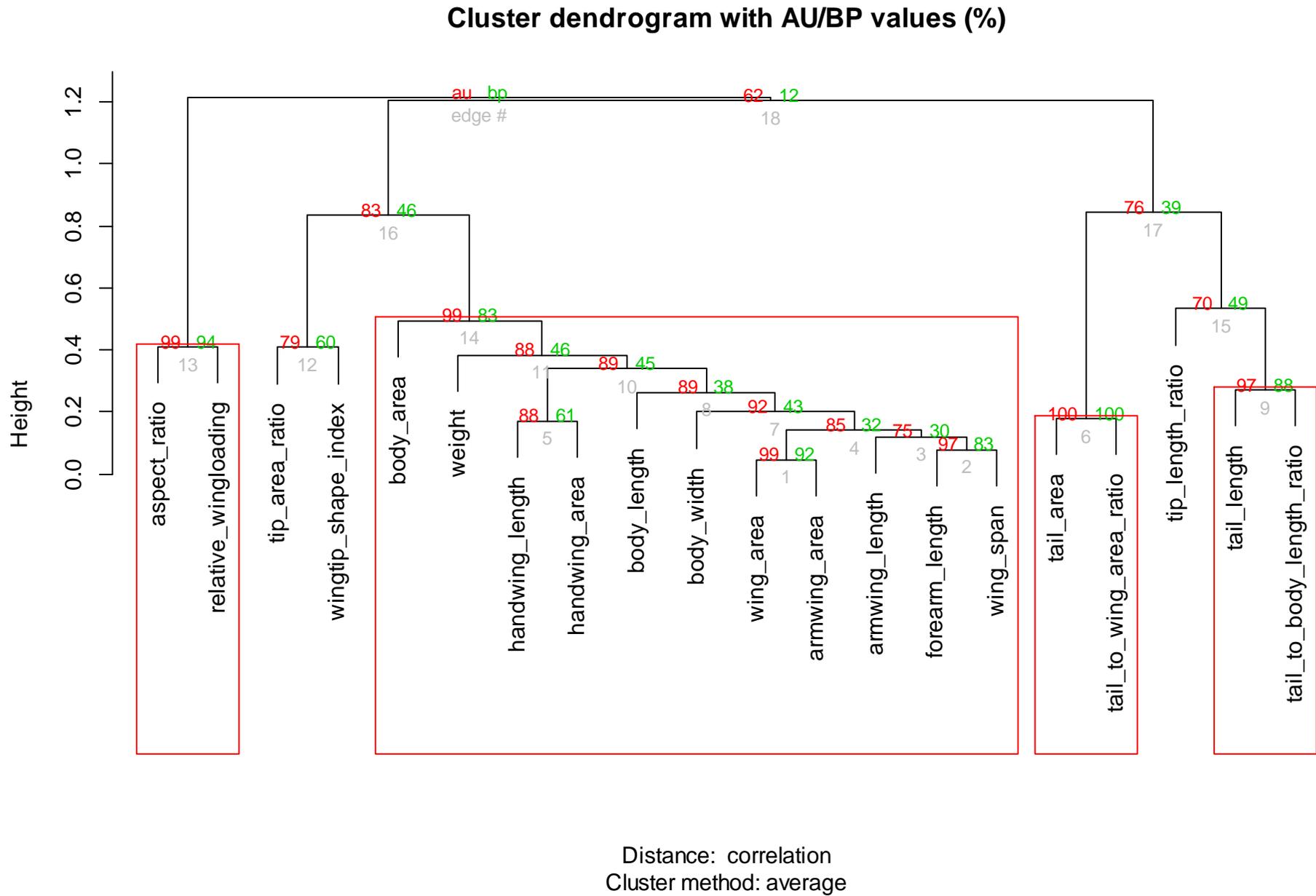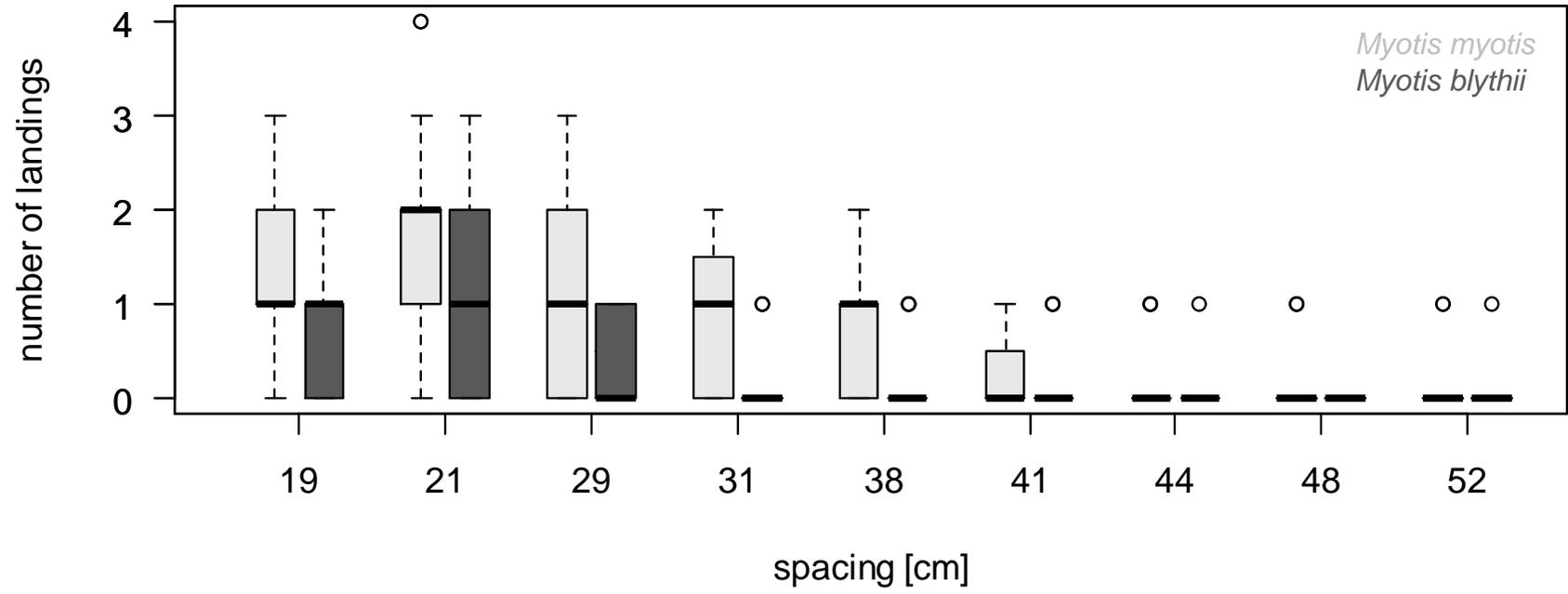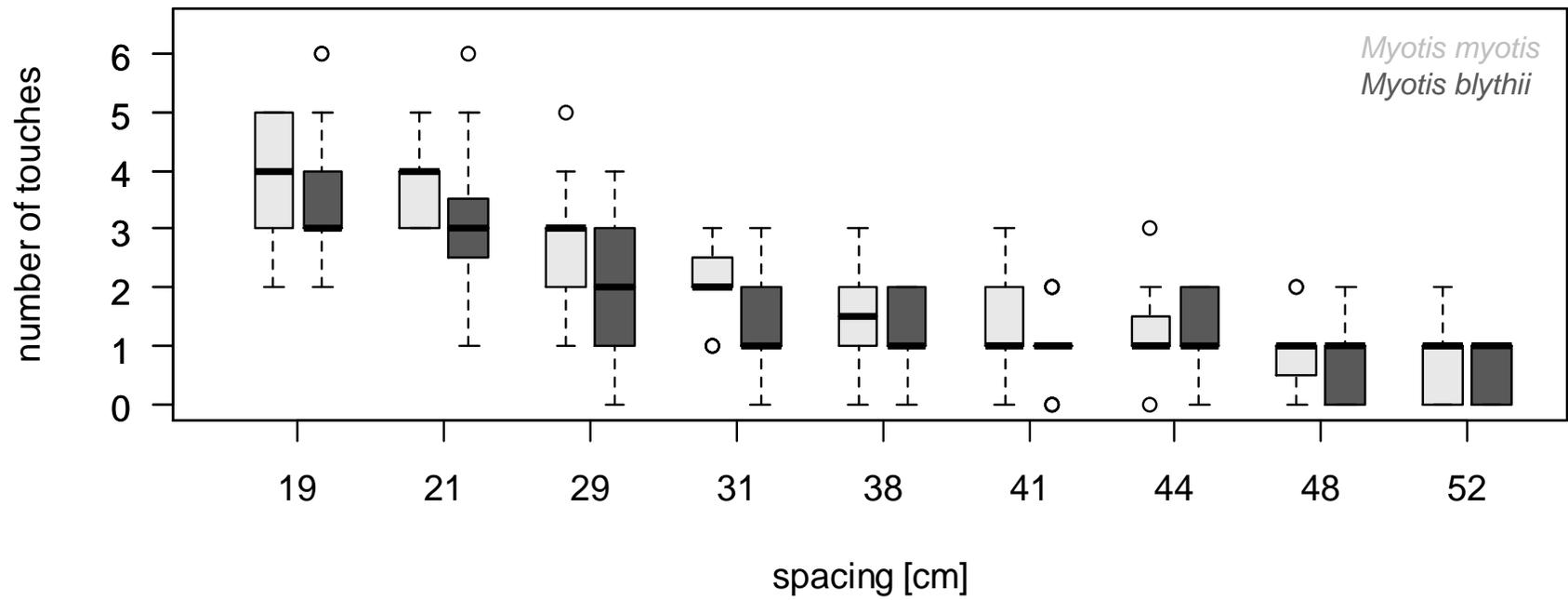
Figure 4:

Figure 5:
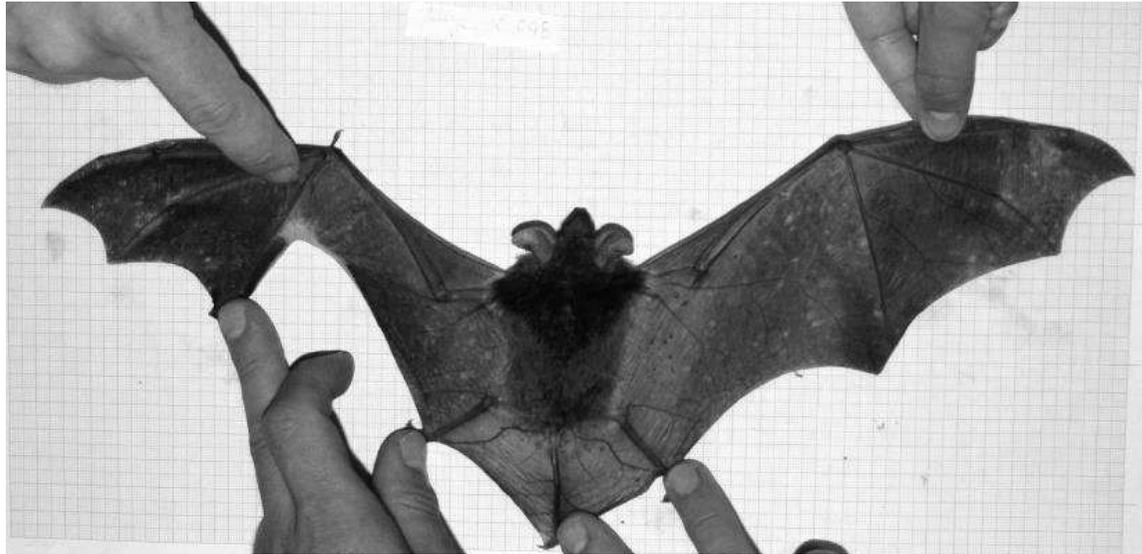
A   *Myotis myotis*

B   *Myotis blythii*
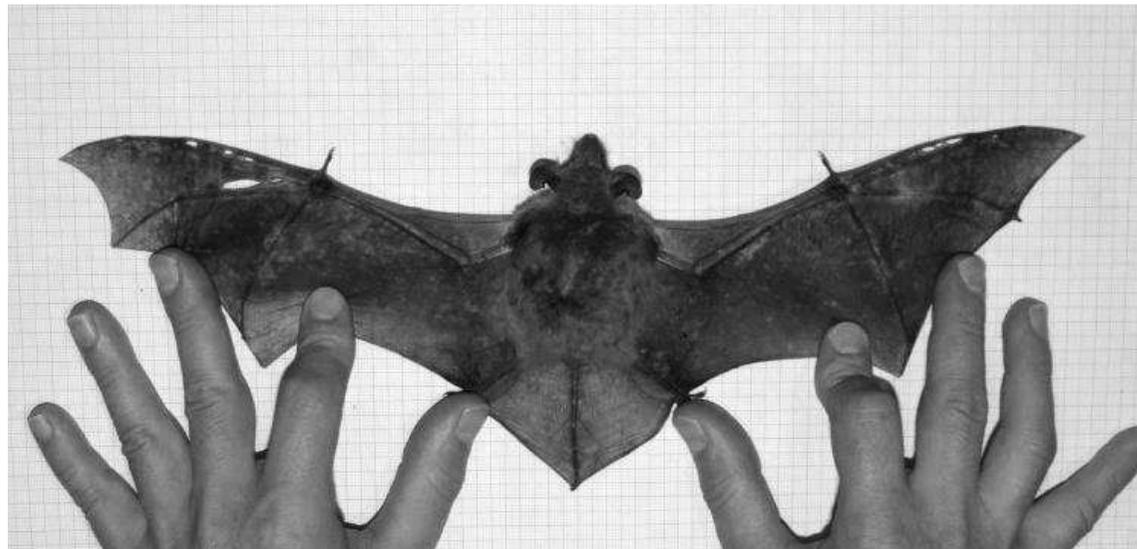
Table 1: Overview of the predictions, results and findings with regard to morphology and manoeuvrability of the greater and lesser mouse-eared bat (*Myotis myotis,* Borkhausen 1797 and *M. blythii,* Tomes 1857).

variable	prediction morphology	result morphology	interpretation morphology	prediction manoeuvrability	results manoeuvrability	interpretation manoeuvrability
weight	*M. myotis > M. blythii*	*M. myotis > M. blythii*	overall size difference	effect	**no effect**	
wing span	*M. myotis > M. blythii*	*M. myotis > M. blythii*	overall size difference	strong effect	**no effect**	
wing area	*M. myotis > M. blythii*	*M. myotis > M. blythii*	overall size difference	effect	**no effect**	
handwing length	*M. myotis > M. blythii*	**M. myotis = M. blythii**	handwing relatively to size longer in *M. blythii* because of differing wing tip shape	effect	**no effect**	contrary to preditcions overall size differences in these variables do not play an important role for manoeuvrability differences
handwing area	*M. myotis > M. blythii*	*M. myotis > M. blythii*	overall size difference	effect	**no effect**	
armwing length	*M. myotis > M. blythii*	*M. myotis > M. blythii*	overall size difference	effect	**no effect**	
armwing area	*M. myotis > M. blythii*	*M. myotis > M. blythii*	overall size difference	effect	**no effect**	
forearm length	*M. myotis > M. blythii*	*M. myotis > M. blythii*	overall size difference	effect	**no effect**	
tail length	*M. myotis > M. blythii*	**M. myotis = M. blythii**	tail shape differs between species	no effect	**strong effect**	longer tail increases manoeuvrability
tail membrane area	*M. myotis > M. blythii*	**M. myotis = M. blythii**	tail shape differs between species	no effect	no effect	might play a role as well, but effect was not found
body length	*M. myotis > M. blythii*	*M. myotis > M. blythii*	overall size difference	no effect	**strong effect**	important variable standing in line with overall size differences
body width	*M. myotis > M. blythii*	*M. myotis > M. blythii*	overall size difference	no effect	no effect	no importance found
body area	*M. myotis > M. blythii*	**M. myotis = M. blythii**	body of *M. blythii* more compact	no effect	no effect	no importance found
aspect ratio	*M. myotis ≥ M. blythii*	*M. myotis = M. blythii*	no difference between species	effect	effect	of general importance for manoeuvrability
rel. wing loading	*M. myotis ≥ M. blythii*	*M. myotis = M. blythii*	no difference between species	effect	effect	of general importance for manoeuvrability
tip length ratio	*M. myotis ≥ M. blythii*	**M. myotis < M. blythii**	*M. blythii* has relatively to size a longer handwing	effect	**no effect**	against our predictions does wing tip shape not play a role
tip area ratio	*M. myotis ≤ M. blythii*	*M. myotis = M. blythii*	no difference between species	effect	effect	generally important but independent from the wing shape
wingtip shape index	*M. myotis ≥ M. blythii*	*M. myotis > M. blythii*	wingtip of *M. blythii* is more pointed than wingtip of *M. myotis*	strong effect	**no effect**	against our predictions does wing tip shape not play a role
tail-to-body length ratio	*M. myotis = M. blythii*	**M. myotis < M. blythii**	tail of *M. blythii* is relatively to size longer than the tail of *M. myotis*	no effect	**strong effect**	longer tail increases manoeuvrability and in relation to overall size is most important variable for species differences
tail-to-wing area ratio	*M. myotis = M. blythii*	*M. myotis = M. blythii*	tail area might be larger, with used method tail membrane area was possibly not fully extended	no effect	no effect	might play a role as well, but effect was not found

The results column indicates found or not found significant differences between the species in regard to differences in morphology or manoeuvrability (best three models for unintended landings). In case significant differences were found for the morphology the sign < or > indicates if the values were smaller or larger for *M. myotis*. The column interpretation gives a short explanation how the results column can be interpreted for the studied species. Results that were against our predictions are shown in bold type.

Table 2: Median values of weight, length and area measurements with 95 % confidence intervals calculated with bootstrapping method in the greater and lesser mouse-eared bat (*Myotis myotis,* Borkhausen 1797 and *M. blythii,* Tomes 1857).

species	N	weight [g]	wing span, L_{ws} [cm]	wing area, S [cm²]	handwing length, L_{hw} [cm]	handwing area, S_{hw} [cm²]	armwing length, L_{aw} [cm]	armwing area, S_{aw} [cm²]	forearm length, L_{fa} [cm]	tail length, L_t [cm]	tail membrane area, S_t [cm²]	body length, L_{bl} [cm]	body width, L_{bw} [cm]	body area, S_b [cm²]
M. myotis	17	26.19 (25.9 - 27.2)	41.3 (40.9 - 42.0)	255.1 (248.3 - 262.0)	9.4 (9.1 - 9.5)	38.7 (37.9 - 40.4)	7.7 (7.4 - 7.8)	62.3 (59.1 - 64.1)	6.3 (6.2 - 6.3)	5.2 (5.1 - 5.4)	20.0 (17.6 - 20.8)	7.4 (7.2 - 7.6)	6.6 (6.48 - 6.69)	33.7 (31.9 - 36.3)
M. blythii	15	22.61 (21.8 - 23.9)	38.0 (37.5 - 38.7)	226.8 (215.4 - 233.8)	8.9 (8.6 - 9.1)	33.8 (32.1 - 35.4)	6.8 (6.6 - 7.1)	53.8 (49.7 - 55.1)	5.7 (5.6 - 5.8)	5.6 (5.2 - 5.8)	19.8 (17.4 - 22.5)	6.5 (6.3 - 6.7)	6.0 (5.6 - 6.2)	30.8 (30.4 - 32.2)
Kruskal test, df = 1	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p = 0.060$ trend	$p = 0.008$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p = 0.141$ n.s.	$p = 1.0$ n.s.	$p < 0.001$	$p < 0.001$	$p = 0.515$ n.s.

N refers to the number of individuals. The values of the two species were compared with a Kruskal-Wallis test and the resulting *p*-values were corrected for multiple comparisons with a Bonferroni correction factor. Significance is indicated by the corrected *p*-values.

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Table 3: Medians of ratios and indices with 95 % confidence intervals in the greater and lesser mouse-eared bat (*Myotis myotis,* Borkhausen 1797 and *M. blythii,* Tomes 1857).

species	N	aspect ratio	relative wing loading [N/m²]	tip length ratio	tip area ratio	wingtip shape index	tail-to-body length ratio	tail-to-wing area ratio
M. myotis	17	6.61 (6.50 - 6.86)	34.21 (32.37 - 35.30)	1.23 (1.19 - 1.25)	0.64 (0.61 - 0.66)	1.11 (1.00 - 1.15)	0.69 (0.68 - 0.74)	0.086 (0.078 - 0.090)
M. blythii	15	6.53 (86.30 - 6.68)	34.92 (33.0 - 37.35)	1.31 (1.27 - 1.34)	0.63 (0.62 - 0.66)	0.93 (0.87 - 1.03)	0.84 (0.83 - 0.89)	0.095 (0.084 - 0.109)
Kruskal test, df = 1		$p = 0.510$ n.s.	$p = 1.0$ n.s.	$p = 0.003$	$p = 1.0$ n.s.	$p = 0.049$	$p < 0.001$	$p = 0.253$ n.s.

N refers to the number of individuals. The values of the two species were compared with a Kruskal-Wallis test and the resulting *p*-values were corrected for multiple comparisons with a Bonferroni correction factor. Significance is indicated by the corrected *p*-values.

Table 4: Basic GLMM models with response variable "unintended landings" and one added morphological variable (incl. body mass) for the greater and lesser mouse-eared bat (*Myotis myotis,* Borkhausen 1797 and *M. blythii,* Tomes 1857).

	model L1	model L2	model L3	model L4	model L5	model L6	model L7	model L8	model L9	model L10+
BIC	234.9	244.4	258.4	262.7	263.6	263.6	263.7	263.9	264.3	265 - 267
Variable 2	tail-to-body length ratio	tail length	body length	forearm length	wingtip shape index	armwing length	body width	wing span	handwing length	all other morpholo-gical variables
est.	-6.71	-82.56	0.43	0.34	0.32	0.31	0.31	0.31	0.29	
SE	1.54	65.16	0.13	0.16	0.17	0.16	0.16	0.17	0.17	
z	-4.36	-1.27	3.41	2.19	1.89	1.93	1.94	1.83	1.68	
p	<0.001	1.0	0.013	0.574	1.0	1.0	1.0	1.0	1.0	1.0
		n.s.		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Variable 1 is the spacing that was always included in the models (spacing ± SE = -0.08 ±0.00, $z = -10.19$, $p < 0.001$). The p-values of the morphological variables were corrected for multiple testing with a Bonferroni correction factor.

Table 5: Forward selection results show three best models with response variable unintended landings in the greater and lesser mouse-eared bat (*Myotis myotis,* Borkhausen 1797 and *M. blythii,* Tomes 1857).

	best model 1	best model 2	best model 3
BIC	234.9	236.0	237.7
variable 2	tail-to-body length ratio	tail length	tail length
est.	-6.71	-93.4	-99.47
SE	1.54	28.03	29.71
z	-4.36	-3.33	-3.35
p	<0.001	<0.001	<0.001
variable 3		body length	body length
est.		0.69	0.51
SE		0.12	0.09
z		5.72	5.85
p		<0.001	<0.001
variable 4		tip area ratio	tip area ratio
est.		0.39	0.30
SE		0.10	0.09
z		3.81	3.30
p		<0.001	<0.001
variable 5		relative wing loading	aspect ratio
est.		0.41	0.25
SE		0.13	0.09
z		3.04	2.81
p		0.002	0.005

Variable 1 is the spacing that was always included in the models (spacing ± SE = -0.08 ±0.00, z = -10.19, p<0.001). The p-value of model 1 was corrected for multiple testing with Bonferroni correction factor.

Figure S 1:

A. Signal without obstacle

B. Signal with echo from obstacle

125.0 kHz

93.5 kHz

62.5 kHz

31.0 kHz

0.0 kHz

10 ms
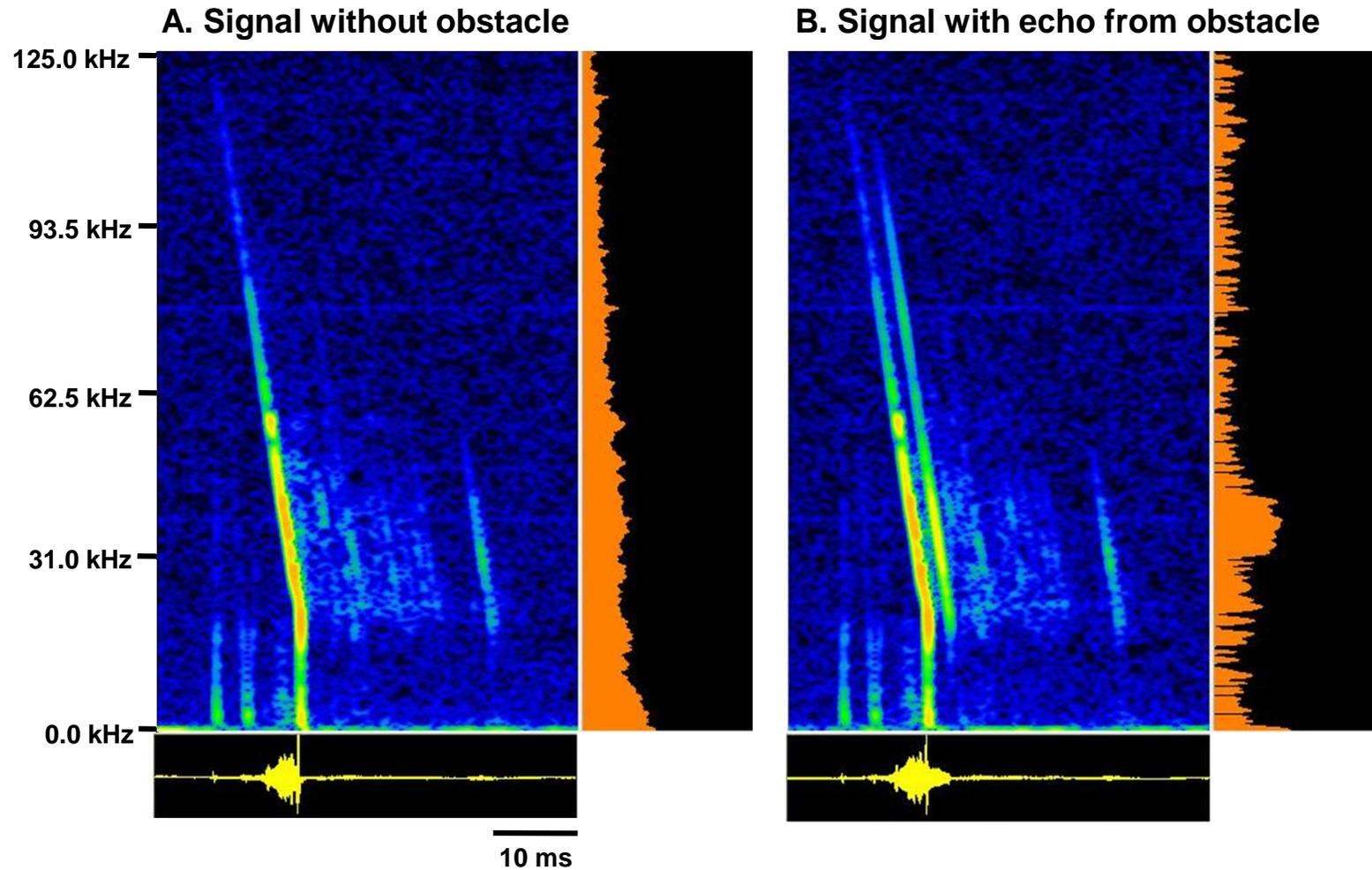
Ensonification of an obstacle. Spectrogram with time signal below and averaged power spectrum to the right shows a recording of the played back signal without obstacle (A) and with obstacle (B). In B a distinct echo from the obstacle can be seen.

Table S 1: Definitions of ratios and indices used for comparison of relative size and shape differences in the studied greater and lesser mouse-eared bats (*Myotis myotis,* Borkhausen 1797 & *M. blythii,* Tomes 1857).

name	symbol	equation	reference
Aspect ratio	AR	$AR = L_{ws}^2 / S$	Norberg 1994
Relative wing loading	RWL	$RWL = \text{weight}*g / S*\text{weight}^{1/3}$	Norberg 1994
Tip length ratio	T_l	$T_l = L_{hw} / L_{aw}$	Norberg & Rayner 1987
Tip area ratio	T_S	$T_S = S_{hw} / S_{aw}$	Norberg & Rayner 1987
Wingtip shape index	I	$I = T_S / (T_l - T_S)$	Norberg & Rayner 1987
Tail-to-body length ratio	TB_l	$TB_l = L_t / L_{bl}$	own definition
Tail-to-wing area ratio	TS_S	$TS_S = S_t / (2\,S_{hw} + 2\,S_{aw} + S_b)$	own definition

Equations for the different ratios and indices are shown with reference to the respective authors. For relative wing loading the weight was measured before the experiment started and g stands for the surface gravity (9.80665 m/s^2).

Table S 2: All models tested during forward selection process with unintended landings as response variable

BIC	# var.	model	formula	comment
261	1	L0	glmer(landings~dist+(1|ID) , data=wm, family=poisson)	basic model
235	2	L1	glmer(landings~dist+tail-to-body length ratio+(1|ID) , data=wm, family=poisson)	Best model, $p < 0.001$
244	2	L2	glmer(landings~dist+tail length+(1|ID) , data=wm, family=poisson)	$p = 1.0$
258	2	L3	glmer(landings~dist+body length+(1|ID) , data=wm, family=poisson)	$p = 0.013$
263	2	L4	glmer(landings~dist+forearm length+(1|ID) , data=wm, family=poisson)	$p = 0.574$
264	2	L5	glmer(landings~dist+wing span+(1|ID) , data=wm, family=poisson)	$p = 1.0$
264	2	L6	glmer(landings~dist+handwing length+(1|ID) , data=wm, family=poisson)	$p = 1.0$
264	2	L7	glmer(landings~dist+armwing length+(1|ID) , data=wm, family=poisson)	$p = 1.0$
264	2	L8	glmer(landings~dist+wingtip shape index+(1|ID) , data=wm, family=poisson)	$p = 1.0$
264	2	L9	glmer(landings~dist+body width+(1|ID) , data=wm, family=poisson)	$p = 1.0$
265 - 267	2	L10+	glmer(landings~dist+other variables+(1|ID) , data=wm, family=poisson)	every added variable $p = 1.0$
235	3	L29	glmer(landings~dist+tip area ratio+tail-to-body length ratio+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
239	3	L20	glmer(landings~dist+wingtip shape index+tail-to-body length ratio+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
240	3	L15	glmer(landings~dist+body length+tail length+(1|ID) , data=wm, family=poisson)	
240	3	L13	glmer(landings~dist+tail length+body length+(1|ID) , data=wm, family=poisson)	
241	3	L33	glmer(landings~dist+forearm length+tail-to-body length ratio+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
241	3	L17	glmer(landings~dist+wing span+tail-to-body length ratio+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
241	3	L23	glmer(landings~dist+handwing length+tail-to-body length ratio+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
241	3	L26	glmer(landings~dist+armwing length+tail-to-body length ratio+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
246	3	L34	glmer(landings~dist+forearm length+tail length+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
246	3	L18	glmer(landings~dist+wing span+tail length+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
246	3	L21	glmer(landings~dist+wingtip shape index+tail length+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
247	3	L30	glmer(landings~dist+tip area ratio+tail length+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
247	3	L27	glmer(landings~dist+armwing length+tail length+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
248	3	L24	glmer(landings~dist+handwing length+tail length+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
262	3	L31	glmer(landings~dist+tip area ratio+body length+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
235 - 241	3	L11+	glmer(landings~dist+tail-to-body length ratio+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
243 - 250	3	L12+	glmer(landings~dist+tail length+other variables*+(1|ID) , data=wm, family=poisson)	*except bodylength
261 - 264	3	L14+	glmer(landings~dist+body length+other variables*+(1|ID) , data=wm, family=poisson)	*except taillength
263 - 270	3	L16+	glmer(landings~dist+wing span+other variables*+(1|ID) , data=wm, family=poisson)	*except tail to body length ratio & tail length
264 - 269	3	L19+	glmer(landings~dist+wingtip shape index+other variables*+(1|ID) , data=wm, family=poisson)	*except tail to body length ratio & tail length
264 - 270	3	L22+	glmer(landings~dist+handwing length+other variables*+(1|ID) , data=wm, family=poisson)	*except tail to body length ratio & tail length
264 - 270	3	L25+	glmer(landings~dist+armwing length+other variables*+(1|ID) , data=wm, family=poisson)	*except tail to body length ratio, tail length
264 - 271	3	L28+	glmer(landings~dist+tip area ratio+other variables*+(1|ID) , data=wm, family=poisson)	*except tail to body length ratio, tail length & bodylength
264 - 269	3	L32+	glmer(landings~dist+forearm length+other variables*+(1|ID) , data=wm, family=poisson)	*except tail to body length ratio, tail length
234 - 245	4	L35+	glmer(landings~dist+tail-to-body length ratio+armwing area+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
234 - 246	4	L36+	glmer(landings~dist+tail-to-body length ratio+armwing length+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
237 - 246	4	L37+	glmer(landings~dist+tail-to-body length ratio+forearm length+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
238 - 246	4	L38+	glmer(landings~dist+tail-to-body length ratio+wing span+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
239 - 246	4	L39+	glmer(landings~dist+tail-to-body length ratio+handwing length+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
239 - 246	4	L40+	glmer(landings~dist+tail length+body length+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
240 - 246	4	L41+	glmer(landings~dist+body length+tail length+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
244 - 252	4	L42+	glmer(landings~dist+tail length+forearm length+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
245 - 254	4	L43+	glmer(landings~dist+tail length+armwing length+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
245 - 252	4	L44+	glmer(landings~dist+tail length+wing span+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
245 - 253	4	L45+	glmer(landings~dist+tail length+handwing length+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
257 - 270	4	L46+	glmer(landings~dist+body length+forearm length+other variables*+(1|ID) , data=wm, family=poisson)	*except tail length (BIC 246)
263 - 270	4	L47+	glmer(landings~dist+body length+armwing length+other variables*+(1|ID) , data=wm, family=poisson)	*except tail-to-body length ratio & tail length (BIC 245 & 245)
264 - 270	4	L48+	glmer(landings~dist+body length+wing span+other variables*+(1|ID) , data=wm, family=poisson)	*except tail-to-body length ratio & tail length (BIC 245 & 246)
266 - 270	4	L49+	glmer(landings~dist+body length+handwing length+other variables*+(1|ID) , data=wm, family=poisson)	*except tail-to-body length ratio & tail length (BIC 245 & 246)
236	5	L51	glmer(landings~dist+tail length+body length+tip area ratio+relative wingloading+(1|ID) , data=wm, family=poisson)	2nd best model
238	5	L52	glmer(landings~dist+tail length+body length+tip area ratio+aspect ratio+(1|ID) , data=wm, family=poisson)	3rd best model
238	5	L53	glmer(landings~dist+tail length+body length+tip area ratio+wing area+(1|ID) , data=wm, family=poisson)	
239 - 245	5	L50+	glmer(landings~dist+tail length+body length+tip area ratio+other variables*+(1|ID) , data=wm, family=poisson)	*except aspect ratio, wing area & relative wingloading
237 - 244	6	L54+	glmer(landings~dist+tail length+body length+tip area ratio+wing area+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
239 - 242	6	L55+	glmer(landings~dist+tail length+body length+tip area ratio+relative wingloading+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
240 - 243	6	L56+	glmer(landings~dist+tail length+body length+tip area ratio+aspect ratio+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model

For the forward selection process we added all length and area measurements (table 2) as well as all indices and ratios (table 3) and weight as explanatory variables to the basic model L0. The basic model consists of the variable space between the obstacles (dist) and the individual as a random factor (1|ID). The green colour indicates the three best models and the red colour indicates models that were excluded because their BIC value was not at least two units better than the BIC values of simpler models with one or several of the same variables. The p -values for the univariate GLMMs were adjusted for multiple testing with a Bonferroni correction factor.

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Table S 3: All models tested during forward selection process with "touches" as a response variable

BIC	# var.	model	formula	comment
183	1	T0	glmer(touches~dist+(1|ID) , data=wm, family=poisson)	basic model
176	2	T1	glmer(touches~dist+tail length+(1|ID) , data=wm, family=poisson)	p = 1.0
177	2	T2	glmer(touches~dist+tail-to-body length ratio+(1|ID) , data=wm, family=poisson)	p = 1.0
186	2	T3	glmer(touches~dist+forearm length+(1|ID) , data=wm, family=poisson)	p = 1.0
187	2	T4	glmer(touches~dist+armwing length+(1|ID) , data=wm, family=poisson)	p = 1.0
187	2	T5	glmer(touches~dist+tip length ratio+(1|ID) , data=wm, family=poisson)	p = 1.0
188	2	T6	glmer(touches~dist+wing span+(1|ID) , data=wm, family=poisson)	p = 1.0
188	2	T7	glmer(touches~dist+handwing length+(1|ID) , data=wm, family=poisson)	p = 1.0
188	2	T8	glmer(touches~dist+armwing area+(1|ID) , data=wm, family=poisson)	p = 1.0
188	2	T9	glmer(touches~dist+wingtip shape index+(1|ID) , data=wm, family=poisson)	p = 1.0
189 - 190	2	T10+	glmer(touches~dist+other variables+(1|ID) , data=wm, family=poisson)	every added variable p = 1.0
180	3	T29	glmer(touches~dist+tip length ratio+tail length+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
180	3	T14	glmer(touches~dist+forearm length+tail length+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
180	3	T32	glmer(touches~dist+wingtip shape index+tail length+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
181	3	T26	glmer(touches~dist+armwing length+tail length+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
181	3	T17	glmer(touches~dist+wing span+tail length+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
181	3	T23	glmer(touches~dist+handwing length+tail length+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
181	3	T20	glmer(touches~dist+armwing area+tail length+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
182	3	T15	glmer(touches~dist+forearm length+tail-to-body length ratio+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
183	3	T30	glmer(touches~dist+tip length ratio+tail-to-body length ratio+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
183	3	T27	glmer(touches~dist+armwing length+tail-to-body length ratio+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
183	3	T18	glmer(touches~dist+wing span+tail-to-body length ratio+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
183	3	T24	glmer(touches~dist+handwing length+tail-to-body length ratio+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
184	3	T21	glmer(touches~dist+armwing area+tail-to-body length ratio+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
184	3	T33	glmer(touches~dist+wingtip shape index+tail-to-body length ratio+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
179 - 181	3	T11+	glmer(touches~dist+tail length+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
180 - 183	3	T12+	glmer(touches~dist+tail-to-body length ratio+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
188 - 192	3	T13+	glmer(touches~dist+forearm length+other variables*+(1|ID) , data=wm, family=poisson)	*except tail-to-body length ratio & tail length
188 - 194	3	T16+	glmer(touches~dist+wing span+other variables*+(1|ID) , data=wm, family=poisson)	*except tail-to-body length ratio & tail length
188 - 194	3	T19+	glmer(touches~dist+armwing area+other variables*+(1|ID) , data=wm, family=poisson)	*except tail-to-body length ratio & tail length
189 - 195	3	T22+	glmer(touches~dist+handwing length+other variables*+(1|ID) , data=wm, family=poisson)	*except tail-to-body length ratio & tail length
187 - 194	3	T25+	glmer(touches~dist+armwing length+other variables*+(1|ID) , data=wm, family=poisson)	*except tail-to-body length ratio & tail length
189 - 194	3	T28+	glmer(touches~dist+tip length ratio+other variables*+(1|ID) , data=wm, family=poisson)	*except tail-to-body length ratio & tail length
190 - 194	3	T31+	glmer(touches~dist+wingtip shape index+other variables*+(1|ID) , data=wm, family=poisson)	*except tail-to-body length ratio & tail length
183 - 185	4	T34+	glmer(touches~dist+tail length+aspect ratio+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
183 - 186	4	T35+	glmer(touches~dist+tail length+tip length ratio+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
181 - 188	4	T36+	glmer(touches~dist+tail-to-body length ratio+forearm length+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
182 - 189	4	T37+	glmer(touches~dist+tail-to-body length ratio+tip length ratio+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
183 - 189	4	T38+	glmer(touches~dist+tail-to-body length ratio+armwing length+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model
185 - 188	4	T39+	glmer(touches~dist+tail-to-body length ratio+aspect ratio+other variables+(1|ID) , data=wm, family=poisson)	BIC not 2 units better than simpler model

For the forward selection process we added all length and area measurements (table 2) as well as all indices and ratios (table 3) and weight as explanatory variables to the basic model T0. The basic model consists of the variables space between the obstacles (dist) and the individual as random factor (1|ID). The red colour indicates models that were excluded because their BIC value was not at least two units better than the BIC values of simpler models with one or several of the same variables. The p-values for the univariate GLMMs were adjusted for multiple testing with a Bonferroni correction factor.

Table S 4: Length and wing area measurements of the injured greater and lesser mouse eared bat (*Myotis myotis,* Borkhausen 1797 & *M. blythii,* Tomes 1857).

species	N	wing span, [cm]	handwing length [cm]		armwing length [cm]		handwing area [cm²]		armwing area [cm²]		wing area [cm²]	area of holes [cm²]		aspect ratio	relative wing loading [N/m²]
			left	right	left	right	left	right	left	right		left	right		
M. myotis	1	43.7	7.1	8.0	7.6	8.4	33.9	45.6	**37.3**	61.7	227.9	-	-	8.38	36.80
M. blythii	1	37.2	8.7	8.6	6.5	6.2	**26.7**	**27.5**	43.2	43.5	189.1	2.2	0.6	7.32	38.21

The measurements are shown for the left and right wing and the bold numbers indicate membrane areas where the injuries were located.