

Body size and wing shape as predictors of the initial flight acceleration in bats of the Brazilian Atlantic Forest

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Abstract. Bat body size and some aspects of the wing shape are considered efficient indicators of bat flight performance. Here, we evaluated how body size and wing shape can be predictors of initial flight acceleration (0–10 meters) in 15 bat species (3 families) occurring in the Atlantic Forest. Two body size variables (wingspan and body mass) and three wing shape variables (relative wing loading, aspect ratio and wing tip index) were taken from 74 individuals. We carried out flight experiments with another 59 individuals, to evaluate the Initial Flight Acceleration (IFA). We used generalized linear models (GLM) to evaluate which variables were the best predictors of initial flight acceleration. Furthermore, we tested the phylogenetic signal for initial flight acceleration, and the hypothesis of phylogenetic autocorrelation for this behavior was discarded ($p > 0.05$). Our results show that larger species with narrow wings need to develop greatest initial accelerations to take off flight. We suggest a morphological restriction on flight, since most bat species analyzed have low values in both variables and those that have high values are only in one of these variables.

Keywords. Aspect ratio; Chiroptera; Flight performance; Wing morphology.

INTRODUCTION

The evolution of flight was an important evolutionary novelty, being one of the factors responsible for the evolutionary radiations of insects, pterosaurs, birds and bats (Kunz & Pierson, 1994; Fenton & Simmons, 2014). The great diversity of bats species is also expressed in the great diversity of eating habits, including insectivorous, piscivorous, carnivorous, frugivorous, nectarivorous and hematophagous species (Fenton & Simmons, 2014; Sadier *et al.*, 2021). The diversity of eating habits implies different ways of foraging and habitat use, which can be determined by body size and wing shape of each bat species (Norberg & Rayner, 1987; Norberg, 1998; Marinello & Bernard, 2014; Marciente *et al.*, 2015). Information or inferences about habitat use by bats can be important to understand how different species coexist in the same location, being a way to assess spatial niche

overlaps between species (Marinello & Bernard, 2014). However, as most bats have nocturnal and crepuscular habits, direct and systematic observation of their flying activities can be difficult. Thus, traditionally, morphological/morphometric studies have been used to predict or create hypothesis about the use of space or even flight performance in bats (Bininda-Emonds & Russell, 1994; Norberg & Rayner, 1987; Norberg, 1998). These studies usually analyze the morphology/morphometry of bats and theoretically analyze their relationships with use of space or flight performance, and only a few studies empirically tested the relationship between bat morphology and flight performance (*e.g.*, Hopkins *et al.*, 2003; Akins *et al.*, 2007; Hixon *et al.*, 2012; Marciente *et al.*, 2015).

Bat flight performance can be assessed by skills such as acceleration, braking, speed, agility, and maneuverability (Norberg & Rayner, 1987). The first three metrics are simpler to understand

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and measure, but the last two are more complex phenomena. Agility could be defined as the speed that an animal can change the direction of its flight, while maneuverability would be the smallest radius in a turn that the animal can make, without losing speed (Norberg, 1998). A common way of evaluating flight performance in bats is the speed and/or acceleration test, where bats fly a known distance and the time taken to travel that distance is measured (*e.g.*, Kennedy & Best, 1972; Hopkins *et al.*, 2003; Akins *et al.*, 2007; Hixon *et al.*, 2012).

Among the several complex movements involved in flight, takeoff can be considered quite costly from an energetic point of view, and thus can be subject to great selective pressure for wings with different shapes associated with different types of flight (Dawkins, 2021). Indeed, understanding the relationships between the form and function of organisms had been an important goal of natural history and biology since the beginnings of evolutionary thought (Mayr, 1982). More recently, this type of study has gained more modern approaches from a technological, analytical, and scientific perspective (Swartz *et al.*, 2003; Marinello & Bernard, 2014). The take-off flight, more specifically the initial acceleration of the flight, is a behavior that can be measured and, therefore, can be analyzed regarding its relationships with evolutionary, functional and morphological aspects, bringing to light which factors explain the variation in the behavior of the flight, as well helping to understand the spatial niche of bats.

The aim of this study was to test whether the initial acceleration of flight can be predicted by morphological aspects (such as body size and wing shape) and by the aspects of their evolutionary history (phylogenetic distances) in 15 bat species occurring in the Brazilian Atlantic Forest.

MATERIAL AND METHODS

Data collection

The field data were collected between 2012 and 2016 throughout some projects developed in five localities from the southern Atlantic Forest: (1) Parque Natural Municipal das Araucárias, municipality of Guarapuava, State of Paraná (25°21'16"S; 51°28'58"W); (2) Parque Municipal São Francisco da Esperança, municipality of Guarapuava, State of Paraná (25°3'48"S; 51°17'51"W); (3) Jardim Botânico Faxinal do Céu, municipality of Pinhão, State of Paraná (25°54'28"S; 51°35'50"W); (4) Sítio Alento da Terra, municipality of Florianópolis, State of Santa Catarina (27°31'01"S; 48°28'00"W) e Parque Nacional Aparados da Serra, municipality of Praia Grande, State of Santa Catarina (29°11'13"S; 50°04'05"W). The captures were made under licenses (SISBIO 34 884 and 44 193) and the flight experiments were authorized by the Ethics Committee on the Use of Animals at Universidade Estadual do Centro-Oeste (Unicentro).

The bats were captured with mist nets, placed in cloth bags and taken to the field base for screening. The

standard screening of captured animals consisted of species identification, determination of age (young or adult), sexing, determination of reproductive status for adult females (pregnant, lactating, post-lactating or inactive), measuring of the forearm length (mm) and the body mass (g). Species identification was made using identification keys available in the literature (Barquez *et al.*, 1999; Gardner, 2008; Díaz *et al.*, 2016). The nomenclature and taxonomic ordering followed the latest review of bats in Brazil (Garbino *et al.*, 2024). The age of the captured individuals was determined based on characteristics of animal's coat and from the ossification of the epiphyses of the phalanges of the fingers (according to Trajano, 1984). The reproductive status of adult females was determined through abdominal palpation and breast examination (according to Trajano, 1984). The length of the forearm was measured with the aid of a Mitutoyo® analog caliper to the nearest 0.05 mm. The body mass was measured using a Pesola® dynamometer marked every 0.5 g.

Individuals could have three destinations after the standard screening: (1) Those individuals classified as young or adult females with reproductive status as pregnant or lactating were ringed with numbered metal omega rings and released at the capture site. (2) The first captured adult individuals of each species (except for pregnant or lactating females) from each location were collected as vouchers (Miranda & Zago, 2015; Miranda *et al.*, 2019) and the collection numbers of these individuals are found in the scientific research data repository Dataverse, in Scielo, under <https://doi.org/10.48331/scielodata.UQC78>. After euthanasia, these collected specimens were used in morphometric analysis (see below). Finally, (3) the other adult individuals captured of each species were used in the Initial Flight Acceleration experiment (see below). After this experiment, these animals were marked with the same rings described above and released at the capture site.

Morphometric data

The individuals used in the morphometric analysis came from the first four locations mentioned above. In the analyses, two size variables were used: body mass (MASS) and Wingspan (WS) and three variables referring to the shape of bat wings: Aspect Ratio (AR), Relative Wing Loading (RWL) and Tip Shape Index (TSI) (according to Norberg, 1998 and adapted by Norberg *et al.*, 2000). The body mass was taken from living individuals inside cloth bags; then, the empty bag was weighed, and its weight was subtracted from the initial measurement to obtain the weight of the bat alone. The WS was taken in centimeters as the greatest distance between the wing tips, when extended. AR was calculated as $AR = WS^2/S$, where S is the wing area (m^2). The wing area was estimated by summing the areas of the two wings, the uropatagium, and the animal's belly from a photograph, as proposed by Norberg (1998) and Norberg *et al.* (2000). The RWL was calculated as $RWL = (Weight/S)/Weight^{0.33}$, where Weight is equal to the body mass (in grams) multiplied

by the gravity acceleration (9.81 m/s^2) and S is the wing area. The TSI was calculated as $TSI = TS/(TI-T_s)$, where TS is the ratio between the area of the handwing and the armwing and TI is the ratio between the length of the handwing and the armwing.

Initial flight acceleration

For the Initial Flight Acceleration (IFA) experiment, 59 individuals were evaluated, representing the same 15 species analyzed for morphometrics. The IFA test consisted of measuring the time needed for the animal to travel a known distance (10 m) from rest (speed 0 m/s). Each specimen had a 10-meter-long waxed polypropylene thread ($\varnothing 0,5 \text{ mm}$; 1.83 g) attached with adhesive tape to the right foot. The other end of the thread was attached to the little finger of whoever was handling the animal (JMDM). When the animal was released, it flew and covered the initial 10 m, when began a downward tangential trajectory due to the tension of the thread. The time frame between taking off and stretching the thread (beginning of the tangential trajectory) was measured with a digital chronometer (Fig. 1). Each individual was evaluated for IFA between three and five repetitions. Only data from flights carried out on straight or approximately straight trajectories were considered for the analyses, while data from flights with tortuous trajectories were discarded. IFAs were calculated for each replicate and averaged per individual; individual means were used to calculate the species mean IFA (used in subsequent analyses). For species in which only one individual was evaluated, we used the average of the repetitions, considering that this single individual presents an IFA representative of the species.

Phylogenetic distance

To calculate the evolutionary distance between the species, we used the phylogenetic tree proposed by Shi & Raboski (2015). This phylogenetic proposal is based on a super matrix of mitochondrial and nuclear molecular data (Shi & Raboski, 2015). Of the 15 species analyzed in the present work, three species were missing in the

abovementioned phylogeny: *Neoptesicus taddeii*, *Myotis izecksohni* and *Histiotus velatus*. We included *M. izecksohni* in the phylogeny as a sister species of *Myotis nigricans*, *N. taddeii* was inserted as a polytomy with *Neoptesicus furinalis* (Díaz et al., 2016; Miranda et al., 2006; Moratelli et al., 2011), and *Histiotus velatus* was inserted as a sister group of the genus *Neoptesicus* (Yi & Latch, 2022). To obtain a phylogenetic distance matrix, this phylogeny was pruned to contain only the 15 species analyzed in this work, maintaining the original evolutionary distances. To carry out these analyses, *ape* (Paradis & Shliep, 2019) and *geiger* packages were used (Pennell et al., 2014).

Data analysis

To analyze the existence of covariation between IFA and the phylogenetic distance of the species, a phylogenetic signal test was carried out using Blomberg's "K" statistic (Blomberg et al., 2003) and the phylogenetic tree proposed by Shi & Raboski (2015). The significance test was carried out by permuting the data between the ends of the phylogeny. If $K > 1$ implies that evolutionary close species are more similar in relation to the IFA value than expected by chance (Brownian movement), resulting in a greater phylogenetic signal, while $K < 1$ implies that species resemble each other less than expected, with a lower phylogenetic signal along the tree. This test was carried out using the function "physignal" of package "phytools" (Revell & Revell, 2014) in R.

To evaluate the influence of body size (MASS and WS) and wing shape (RWL, AR, and WTI) on the Initial Flight Acceleration (IFA), we used generalized linear models (GLM) approach. As the variables (IFA, WS, MASS, RWL, AR and WTI) used are in unequal units and scales, Z standardization was used to centralizing, alignment, and sizing the variables in a more homogeneous way. To the Z-transformed data a value 10 was added to all variables, avoiding negative values, and adapting to the Gamma distribution.

A Variance Inflation Factor (VIF) analysis was performed to verify the existence of high collinearity between the predictor variables using package "fmsb" 0.7.3 (Nakazawa & Nakazawa, 2019). In this approach, variables showing VIF values above 3 were considered highly col-



Figure 1. Scheme representing the experiment to evaluate the bats' initial flight acceleration. (A) the moment that the bat took off from the researcher's hand, which is the count starting; (B) the bat's flight period and the time count; (C) the stretching of the thread, when the chronometer was stopped, ending the timekeeping.

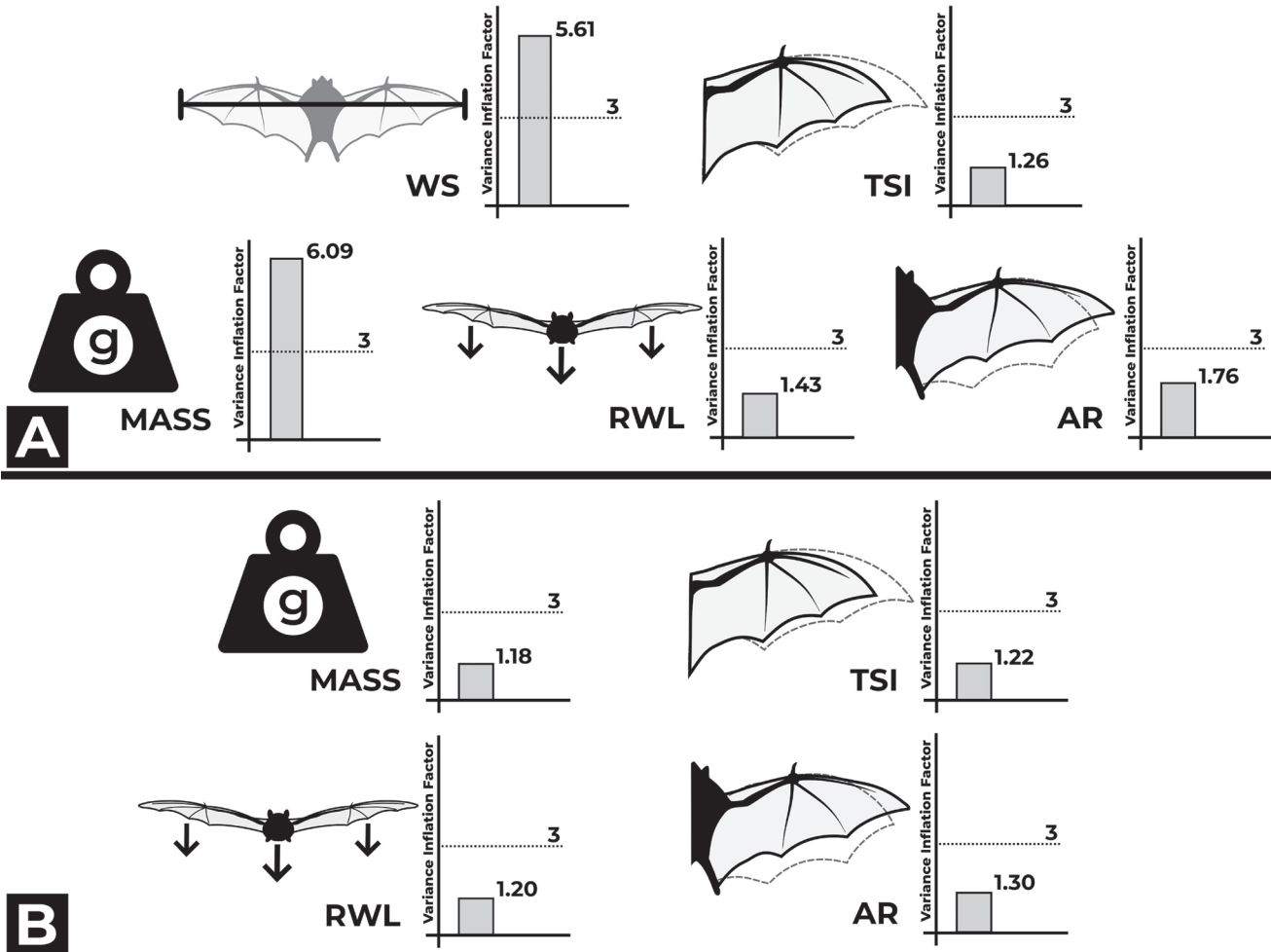


Figure 2. Variance inflation factors (VIF) for the variables predicting the initial flight acceleration. (A) Analysis of VIF with all predictor variables. (B) analysis of VIF after the WS variable was excluded from the analysis. MASS = body mass; WS = Wingspan; AR = Aspect Ratio; RWL = Relative Wing Loading and TSI = Tip Shape Index.

linear and excluded from the analysis (Fig. 2). Therefore, we decided to remove the WS Variable (keeping MASS) and a new VIF analysis was carried out resulting in all variables with low VIF values.

Thus, from four predictor variables, 16 models were constructed with all possible combinations of these variables, including a global model (with all variables) and a null model (Table 1). The best model was chosen based on the Akaike Information Criterion (AIC) and the model weight (AIC weights). In this approach, the lower the AIC value and the higher the AIC weights value, the bet-

Table 1. Generalized linear models (GLM) used to test the predictive power of the Initial Flight Acceleration (IFA) of 15 species of bats from the Brazilian Atlantic Forest. MASS = mass; AR = Aspect Ratio; RWL = Relative Wing Loading; TSI = Tip Shape Index.

Model	Predictor variables	Model	Predictor variables
1	MASS+AR+RWL+TSI	9	AR+RWL
2	MASS+AR+RWL	10	AR+TSI
3	MASS+AR+TSI	11	RWL+TSI
4	MASS+RWL+TSI	12	MASS
5	AR+RWL+TSI	13	AR
6	MASS+AR	14	RWL
7	MASS+RWL	15	TSI
8	MASS+TSI	16	Null

ter the model fits to explain the response variable (IFA). When the difference between the best model and the others (ΔAIC) is less than 2, it was considered that these models are equally predictive. This analysis was carried out using “AICcmodavg” 2.3.2 package (Mazerolle & Mazerolle, 2017) in software R 4.3.1 (R Core Team, 2023).

RESULTS

A total of 133 individuals were captured, comprising 15 species and three families. Of these, 74 were used for morphometric analyses, and 59 were used for the Initial Flight Acceleration (IFA) experiment (Table 2). The Blomberg K test to evaluate the presence of a phylogenetic signal in the IFA was not significant ($K = 0.6807$, $p > 0.05$). Therefore, it can be assumed that there is no phylogenetic signal for Initial Flight Acceleration.

The species that presented the highest average initial flight acceleration (IFA) was *Desmodus rotundus* (3.18 m/s^2), followed by *Molossus rufus* (2.6 m/s^2). The lowest IFA values were obtained by *Anoura caudifer* (0.79 m/s^2) and *Myotis izecksohni* (1.0 m/s^2). *Artibeus lituratus* presented the highest values of MASS, WS e RWL, while *Myotis izecksohni* presented the lowest values of these same variables. *Molossus rufus* had the highest AR, while

Table 2. Species obtained during the sampling in the Brazilian Atlantic Forest used for obtaining morphometric data and initial flight acceleration data; IFA = Initial Flight Acceleration; N = number of individuals measured/evaluated; R = Repetitions of the flight experiment, by species.

Taxa	IFA experiment	Morphometric data
PHYLLOSTOMIDAE		
<i>Desmodus rotundus</i> (É. Geoffroy, 1810)	N = 1; R = 5	N = 5
<i>Chrotopterus auritus</i> (Peters, 1856)	N = 4; R = 13	N = 4
<i>Anoura caudifer</i> (É. Geoffroy, 1818)	N = 1; R = 3	N = 1
<i>Carollia perspicillata</i> (Linnaeus, 1758)	N = 4; R = 12	N = 4
<i>Artibeus fimbriatus</i> Gray, 1838	N = 1; R = 5	N = 1
<i>Artibeus lituratus</i> (Olfers, 1818)	N = 5; R = 17	N = 2
<i>Pygoderma bilabiatum</i> (Wagner, 1843)	N = 1; R = 5	N = 3
<i>Sturnira lilium</i> (É. Geoffroy, 1810)	N = 31; R = 91	N = 15
MOLOSSIDAE		
<i>Molossus rufus</i> É. Geoffroy, 1805	N = 1; R = 3	N = 2
VESPERTILIONIDAE		
<i>Histiotus velatus</i> (L. Geoffroy, 1824)	N = 1; R = 4	N = 16
<i>Lasiurus blossevillii</i> (Lesson, 1826))	N = 1; R = 5	N = 2
<i>Lasiurus ega</i> (Gervais, 1856)	N = 1; R = 5	N = 1
<i>Neoptesicus furinalis</i> (d'Orbigny & Gervais, 1847)	N = 2; R = 8	N = 6
<i>Neoptesicus taddeii</i> (Miranda, Bernardi & Passos, 2006)	N = 3; R = 9	N = 4
<i>Myotis izecksohni</i> Moratelli et al., 2011	N = 2; R = 6	N = 7
TOTAL	59	74

Chrotopterus auritus, had the lowest. The highest TSI value was obtained for *Carollia perspicillata* and the lowest value was for *Lasiurus ega* (Table 3).

Model 6 presented the lowest AIC value (41.11) and the highest model weight (0.44) (Table 4). Furthermore, the Δ AIC between the best model and the second one was greater than 2, therefore, model 6, which includes body mass and aspect ratio as predictor variables, is the one that best explained the IFA variation. The coefficients of the best model were significant and positive for both MASS and AR (Table 5), with the effect of the aspect ratio on the IFA greater than the body mass effect. The graph

of AR data by MASS (Fig. 3) shows a possible size/shape restriction on flight, since there were no species with high values in both variables, which would make takeoff energetically prohibitive, and a high initial acceleration would be required.

DISCUSSION

The differences between the sampled IFAs (between 0.79 and 3.18 m/s²) were expected, since 15 species from three different families were evaluated, comprising a variation in size (from 5 to 100 g), wing shape, feeding habits and foraging strategies. The flight performance of bats could be predicted by body size, especially regarding to the initial flight acceleration or takeoff. In fact, in larger species, there is greater energy expenditure to take flight acceleration or takeoff. This is a physical restriction on flight (from insects to planes) and larger objects need greater accelerations to takeoff (Norberg, 1998; Dawkins, 2021). Furthermore, an increase in the species aspect ratio also implies greater initial flight accelerations, that is, species with proportionally narrower wings must accelerate more during takeoff. Since the classic work by Norberg & Rayner (1987) aspect ratio has been seen as a variable that influences the flight style of bats, and in the present work this relationship was observed regarding the takeoff of these animals. In other hand, Hixon et al. (2012) pointed out that the aspect ratio did not explain the variation in acceleration in another set of species, however, probably when associated with variation in body size, the aspect ratio has the power to predict the initial flight acceleration of the species.

Some authors point out that, in addition to size, wing loading also explains acceleration and other aspects of flight performance (Kalcounis & Brigham, 1995; Hixon et al., 2012). However, wing loading (not relative wing loading, as used in this work) is a measure more associat-

Table 3. Animal size and wing shape metrics analyzed for 15 species of bats from Brazilian Atlantic Forest. AR = Aspect Ratio; IFA = Initial Flight Acceleration; MASS = Mass; TSI = Tip Shape Index; RWL = Relative Wing Loading; WS = Wingspan.

Taxa	IFA (m/s ²)	MASS (g)	WS (cm)	RWL (N/m ²)	AR	TSI
PHYLLOSTOMIDAE						
<i>Desmodus rotundus</i>	3,18 ± 0,47	39,6 ± 5,55	36,59 ± 1,19	19,43 ± 1,93	6,73 ± 0,24	3,11 ± 0,14
<i>Chrotopterus auritus</i>	1,45 ± 0,20	82,75 ± 7,41	50,17 ± 0,89	16,14 ± 0,91	5,74 ± 0,15	1,73 ± 0,11
<i>Anoura caudifer</i>	0,79 ± 0,19	11	26,67	10,38	6,85	3,18
<i>Carollia perspicillata</i>	1,06 ± 0,26	16 ± 1,63	30,58 ± 1,42	10,1 ± 1,35	6,01 ± 0,49	3,6 ± 0,67
<i>Artibeus fimbriatus</i>	2,22 ± 0,34	61	45,65	16,48	6,49	2,05
<i>Artibeus lituratus</i>	1,66 ± 0,38	84 ± 22,63	50,68 ± 1,24	20,13 ± 4,2	6,33 ± 0,09	1,11 ± 0,05
<i>Pygoderma bilabiatum</i>	1,33 ± 0,08	27,33 ± 2,3	32,2 ± 0,38	16,72 ± 1,64	6,47 ± 0,23	2,18 ± 0,44
<i>Sturnira lilium</i>	1,48 ± 0,51	21,57 ± 2,27	31,6 ± 1,44	13,69 ± 1,32	6,46 ± 0,33	2,65 ± 0,75
MOLOSSIDAE						
<i>Molossus rufus</i>	2,6 ± 0,98	17,5 ± 0,7	33,33 ± 2,12	12,64 ± 1,49	8,15 ± 0,25	1,33 ± 0,02
VESPERTILIONIDAE						
<i>Histiotus velatus</i>	1,22 ± 0,2	10,46 ± 2,35	29,06 ± 1,32	7,85 ± 1,51	6,5 ± 0,31	1,88 ± 0,47
<i>Lasiurus blossevillii</i>	1,42 ± 0,19	12,5 ± 3,53	28,02 ± 0,43	10,07 ± 2,49	6,49 ± 0,44	1,15 ± 0,04
<i>Lasiurus ega</i>	1,72 ± 0,33	15	34,38	8,86	7,12	1,07
<i>Neoptesicus furinalis</i>	1,12 ± 0,19	8,66 ± 0,87	24,45 ± 0,69	9,27 ± 0,8	6,53 ± 0,29	1,47 ± 0,27
<i>Neoptesicus taddeii</i>	1,43 ± 0,43	16,5 ± 3,51	31,66 ± 0,52	10,82 ± 1,9	6,75 ± 0,26	1,43 ± 0,1
<i>Myotis izecksohni</i>	1,0 ± 0,16	6,07 ± 1,53	23,62 ± 1,58	6,78 ± 1,01	6,44 ± 0,25	1,76 ± 0,47

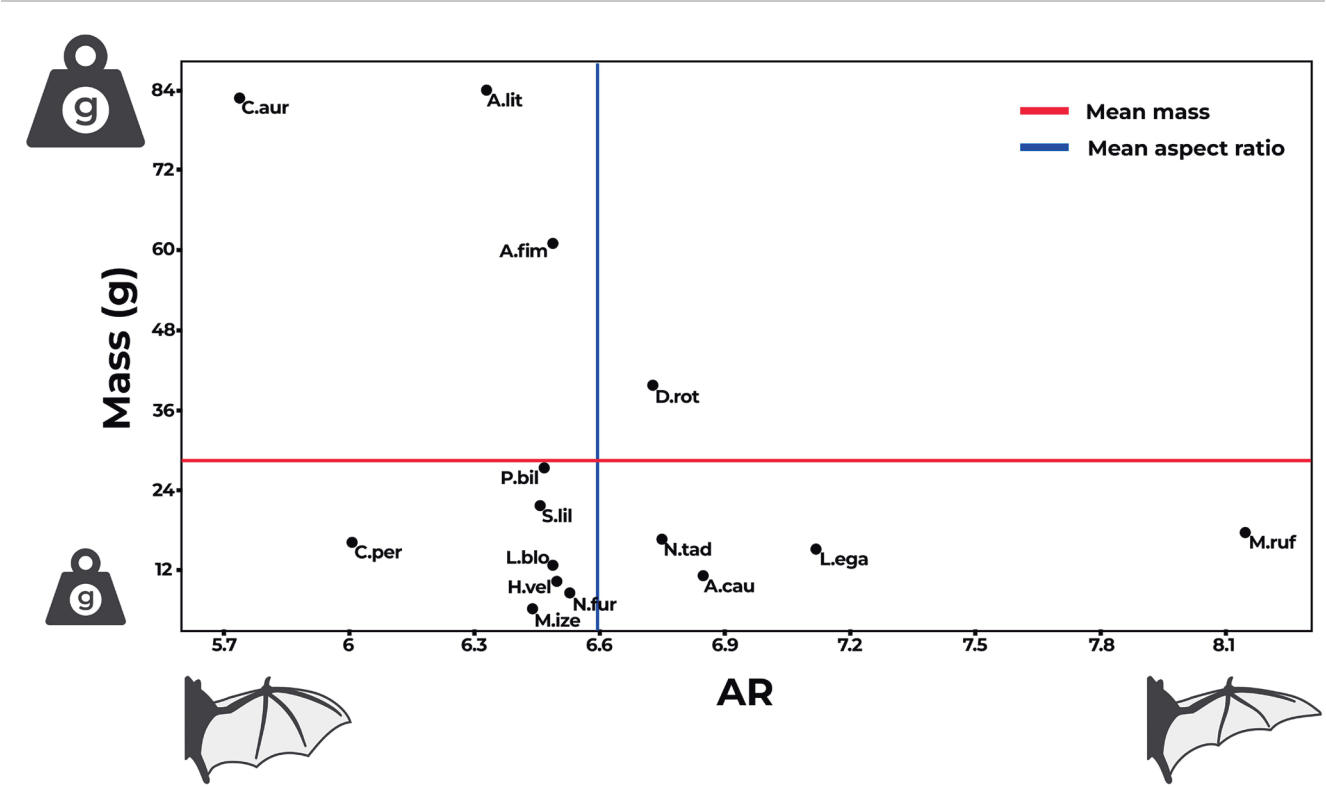


Figure 3. Biplot between the two variables (Mass and Aspect ratio) that best explained the Initial Flight Acceleration (IFA). A.cau = *Anoura caudifer*; A.fim = *Artibeus fimbriatus*; A.lit = *Artibeus lituratus*; C.aur = *Chrotopterus auritus*; C.per = *Carollia perspicillata*; D.rot = *Desmodus rotundus*; H.vel = *Histiotus velatus*; L.blo = *Lasiurus blossevillei*; Lega = *Lasiurus ega*; M.ize = *Myotis izecksohni*; M.ruf = *Molossus rufus*; N.fur = *Neopitesicus furinalis*; N.tad = *Neopitesicus taddeii*; P.bil = *Pygoderma bilabiatum*; S.lil = *Sturnira lilium*.

ed with size than shape, *i.e.*, the relationship between bat weight and its wing surface (see discussion about these variables in Norberg *et al.*, 2000). Despite this, very high wing loading (or relative wing loading) values can probably reduce maneuverability and hindering the execution of tight turns, in addition to being able to affect flight speed of bats (Kalcounis & Brigham, 1995; Stockwell, 2001; Hixon *et al.*, 2012). However, no relationship was

Table 4. Generalized linear models (GLM) evaluated for their power to predict Initial Flight Acceleration in 15 species of bats from the Brazilian Atlantic Forest. AICc = Akaike Information Criterion. Δ AIC = Variation of AIC model; and AICWt = AIC model weights.

Model	AIC	Δ AIC	AICWt	Model	AIC	Δ AIC	AICWt
6	41.11	0.00	0.44	12	46.73	5.62	0.03
2	43.36	2.25	0.14	11	47.74	6.63	0.02
3	44.15	3.04	0.10	15	48.58	7.46	0.01
14	44.88	3.77	0.07	10	48.76	7.64	0.01
13	45.07	3.96	0.06	1	48.82	7.71	0.01
16	45.42	4.30	0.05	8	50.55	9.44	0.00
9	46.20	5.09	0.03	4	50.58	9.47	0.00
7	46.65	5.54	0.03	5	50.69	9.58	0.00

Table 5. Parameters and p-values estimated using a Generalized Linear Model explaining the variation in Initial Flight Acceleration in Brazilian bats from Atlantic Forest. MASS = Mass; AR = Aspect Ratio; SE = Standard Error.

Variable	Coefficients	SE	t-value	p
MASS	0.05865	0.02140	2.788	0.01641
AR	0.06660	0.02140	3.113	0.00898

observed between relative wing loading and the initial flight acceleration of the species analyzed here. The tip shape index was not related to the initial flight acceleration, as also found by Hixon *et al.* (2012). On the other hand, in the present work only one aspect of the flight was evaluated (initial acceleration), and it is possible that wing loading (or relative wing loading) and tip shape index are important in other aspects of the flight, such as agility and speed maneuverability, which were not analyzed here (Norberg & Rayner, 1987; Norberg, 1994).

Body size appeared to be useful when assessing spatial segregation (as in Fleming *et al.*, 1972; Miranda *et al.*, 2018), since larger bats use space differently than smaller ones (Marciente *et al.*, 2015). Although less simple to understand, the aspect ratio also plays an important role in the spatial segregation of bat communities, also implying different ways of using space, specially the using of cluttered or open spaces (Norberg, 1998).

Thus, it is understood that an increase in size and/or aspect ratio implies greater energy costs when taking off. This relationship imposes restrictions on size or aspect ratio, so that a general pattern emerges: (1) most species are small and have broad or intermediate wings, allowing for more general use of space, as seen in insectivorous bats (such *Myotis*, *Neoeptesicus*, *Histiotus* and *Lasiurus*), nectarivorous bats (such *Anoura* and *Glossophaga*) and smaller frugivores (such *Carollia*, *Sturnira* and *Pygoderma*); (2) either the species is large with proportionally wide wings (such as *Chrotopterus* or *Artibeus*) or the species has narrow wings, but cannot be large (such as *Tadarida* and *Molossus*). So, a species with

high values in both variables may present difficulties in taking off, especially from the ground, as reported for vampire bat and large molossids, which end up needing a period of free fall to be able to begin their flight (Norberg & Rayner, 1987; Schutt-Jr. & Simmons, 2006). Therefore, it can be considered that the flight experiment was efficient in evaluating the initial acceleration of flight. Takeoff is possibly one of the most critical moments in the flight of bats and a target of selection, driving their morphological evolution and diversity.

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