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Ontogenetic changes in body size are weakly associated with basal metabolic rate in a maternity colony of Myotis velifer

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Abstract

Basal metabolic rate (*BMR*) is a fundamental physiological trait that shapes ecological and evolutionary processes, yet its intraspecific variation across ontogeny remains poorly understood. Here, we examined variation in *BMR* across developmental stages in a maternity colony of *Myotis velifer*. Using open-flow respirometry, we quantified metabolic rate in pups, juveniles, and reproductive and non-reproductive adults. To characterize developmental changes in body size, we evaluated the relationship between body mass (M_b) and forearm length across ontogenetic stages. We also tested the relationships among M_b, *BMR*, and ontogenetic stage. Body mass scaled positively with forearm length, although the strength of this relationship differed markedly among age classes, indicating ontogenetic shifts in growth dynamics. Basal metabolic rate also scaled positively with M_b, with an estimated exponent (0.62) broadly consistent with previously reported interspecific values for bats (~ 0.74–0.77). However, M_b explained only a small proportion of the variation in *BMR* (~ 7%), and we found no significant effects of sex, age class, or reproductive condition on metabolic rate. These results indicate that substantial individual-level heterogeneity in *BMR* persists despite pronounced ontogenetic differences in body size relationships. Our findings suggest that metabolic variation within maternity colonies is only weakly structured by M_b and developmental stage, highlighting the importance of additional intrinsic physiological and ecological factors shaping energy expenditure within populations.

Introduction

Energy acquisition and allocation strongly influence the ecology, behavior, and life-history strategies of endotherms because metabolic demands constrain thermoregulation, locomotion, growth, and reproduction (Mcnab 1979; Cruz-Neto and Bozinovic 2004). Consequently, understanding how endotherms acquire and allocate energy is fundamental for explaining variation in distribution, activity patterns, reproductive investment, and other ecological traits (van der Meer 2006). Basal metabolic rate (*BMR*) represents the minimum maintenance energy expenditure of an endotherm measured under standardized resting, postabsorptive, and thermoneutral conditions (McNab 1997; Frappell and Butler 2004; Genoud et al. 2018). Because of this standardized framework, *BMR* provides a useful metric for comparing energy expenditure among individuals (Nespolo and Franco 2007), populations (Wikelski et al. 2003; Broggi et al. 2007; Tieleman et al. 2009), and species (McLean and Speakman 2000; White and Kearney 2013; Genoud et al. 2018; Medina-Bello and Ayala-Berdon 2025).

In mammals, *BMR* generally scales positively with body mass (M_b), although reported scaling exponents vary among taxa and analytical approaches (e.g., McNab 2008; Packard and Birchard 2008; Sieg et al. 2009; White and Seymour 2005; White et al. 2007, among others). Variation in this relationship reflects differences in body shape and surface-area-volume ratios that influence heat exchange (Porter and Kearney 2009), as well as variation in the internal organization of metabolically active tissues and transport systems (Brown et al. 2004). In addition to M_b, *BMR* is influenced by climatic conditions, roost

characteristics, resource availability, reproductive state, organ size, life-history traits, and phylogenetic history (Cruz-Neto and Jones 2005).

Despite the extensive literature on allometric scaling of *BMR* in adult mammals —both within and across species (e.g., Lovegrove 2000; Symonds and Elgar 2002; White and Seymour 2003, 2004, 2005; McNab 2008; Sieg et al. 2009; Capellini et al. 2010; Clarke et al. 2010; Hudson et al. 2013)— much less attention has been given to understanding how this relationship changes during ontogeny (but see Hull 1973; Kooijman 2010.). Ontogeny is characterized by rapid and often disproportionate changes in morphology and physiology, including incomplete thermoregulatory capacity in early life, steep shifts in mass-specific metabolic rate, and differential growth of metabolically active organs(Hoying and Kunz 1998) These developmental transitions are expected to influence metabolic scaling relationships. Moreover, because growth, reproductive condition, and energetic state can vary substantially among individuals within maternity colonies, ontogenetic scaling relationships may also exhibit considerable individual-level variation. Nevertheless, empirical evidence on ontogenetic variation in *BMR* remains scarce in mammals. During development, changes in M_b may reflect both structural growth and variation in energetic reserves, whereas skeletal dimensions such as forearm length more directly represent somatic development in bats (Kunz 1973). Examining the relationship between M_b and forearm length across ontogeny may therefore help distinguish developmental changes in structural size from variation associated with energetic condition. Because M_b may reflect structural growth during early development but energetic condition in adults, ontogenetic changes may alter the relationship between body size and metabolic rate within populations.

Bats represent a particularly relevant group in which to explore this question. With approximately 1,511 species described worldwide (Simmons and Cirranello 2026), Chiroptera is one of the most diverse mammalian orders. Many species form large maternity colonies in which individuals experience rapid postnatal growth, major thermoregulatory transitions, and high energetic demands associated with lactation, weaning, and the acquisition of powered flight. These developmental transitions occur over relatively short periods and provide an excellent framework for examining metabolic scaling under natural conditions. Interspecific analyses indicate that *BMR* in bats scales with $M_b^{0.75–0.77}$ (Speakman and Thomas 2003; Ayala-Berdon et al. 2025), yet no study has quantified how metabolic rate varies with M_b during ontogeny within a natural bat population.

To address this gap, we measured *BMR* in individuals from a maternity colony of *Myotis velifer* inhabiting the “Agua Fría” cave in the Sierra de Huautla Biosphere Reserve (SHBR), Central Mexico. This species forms large, thermally buffered maternity aggregations and exhibits a well-defined developmental sequence during the reproductive season, ranging from newborn pups to fully volant juveniles and adults. This system provides an ideal opportunity to examine ontogenetic metabolic scaling within a natural population. Given the positive interspecific relationship between *BMR* and M_b reported across Chiroptera, and the marked physiological transitions that occur during development, we hypothesized

that: (1) *BMR* would scale positively with M_b within the colony, and (2) sex, age, and reproductive condition would contribute to variation in metabolic rate among individuals.

Materials and methods

Study Site

Bats were captured in the Quilamula region of the Sierra de Huautla Biosphere Reserve, Morelos, Mexico (N 18º32´32.7" W 98º59´56.9") (Fig. 1). The region is characterized by warm to semi-warm subhumid climate and tropical dry forest vegetation (Beltrán-Rodríguez et al. 2014; Cruz-Aguilar et al. 2018). The "Agua Fría" cave hosts seasonal colonies of insectivorous bats, including *Mormoops megalophylla*, *Ptenorotus parnelli*, and *Myotis velifer*. *Myotis velifer* typically occupies the cave from late May to October-November, during which females give birth and rear their young. Cave temperatures range from 22° to 35° C, with relative humidity between 70 % and 90% (Ávila-TorresAgatón 2008; Estrada 2019).

Bat captures and handling

Sampling was conducted monthly from June to October 2024 and from May to June 2025, corresponding to the maternity period of *M. velifer* (Ávila-TorresAgaton 2008; Estrada 2019). Sampling from July to October 2025 was not possible due to heavy rains that limited access to the study site. Each sampling session lasted three consecutive days. Bats were captured either inside the cave using a sweep net or at the cave entrance using a 3 x 3 m mist net, depending on cave accessibility and flooding conditions. To minimize disturbance, time spent inside the cave was restricted to less than 5 min per sampling event. Ambient temperature (T_a, ºC) and relative humidity (RH, %) were recorded once inside the cave using a thermohygrometer (FLUKE 971®). Captured bats were placed individually in cloth bags and transported to our on-site holding facility where environmental conditions approximated those inside the cave. Age class was determined based on the degree of epiphyseal ossification of the metacarpals. Individuals were classified as pups (pre-weaning individuals carried by their mothers), juveniles (visible metacarpal gaps), or adults (completely epiphyseal closure). Forearm length (± 0.1 mm) was measured using digital calipers, and body mass (M_b, ± 0.2 g) was measured using a digital scale (Ohaus, Newark, NJ, USA). Reproductive condition was assessed by visual inspection of testes position in males and nipple condition or pregnancy in females.

Metabolic rate measurements

Metabolic rate was measured using an open-flow respirometry system (FoxBox®, Sable Systems International, Las Vegas, NV, USA). Measurements were conducted in post-absorptive, euthermic individuals during their inactive circadian phase (09:00–18:00 hrs) and within the thermoneutral zone (28 ºC) following Ayala-Berdon and Medina-Bello (2023). All individuals were measured under standardized conditions typically used for estimating basal metabolic rate (*BMR*). However, because the study

included developing individuals and reproductively active adults, some measurements may slightly exceed strict basal values as classically defined for non-reproductive adults (McNab 1997; Genoud et al. 2018). Nevertheless, we retained the term *BMR* throughout the manuscript because all measurements were obtained under comparable experimental conditions, allowing consistent evaluation of metabolic variation among ontogenetic stages within the colony. Adult and juveniles were measured 2–4 hours after capture, whereas pups were measured approximately 2 hours after separation from their mothers. A shorter fasting period was used for pups to avoid compromising survival due to their limited thermoregulatory capacity (Kunz and Hood 2000; Racey and Entwistle 2000). Individuals were placed in a 410 mL metabolic chamber housed inside a temperature-controlled cabinet (PELT5®; Sable Systems International, Las Vegas, USA). The chamber contained mesh surfaces that allowed bats to cling in a natural posture and preventing flight and extensive movement. Bats were allowed to acclimate inside the chamber for 60 minutes before measurements began. Behavioral observations confirmed that individuals remained largely inactive during recordings. Chamber temperature was maintained within ± 0.5°C of the target temperature. Flow rates (FR) of dry CO_2-free air scrubbed with Drierite (calcium sulfate) and Ascarite (sodium hydroxide) passed upstream with the air pushed through the respirometer chamber at a rate of $250\ mL\ min^{-1}$. Flow rate in the 450 mL chamber gave gas equilibration of 99 % in 5 min. The FR value was set between 150 and $250\ mL\ min^{-1}$ followingMedina-Bello et al., (2023) and was measured ad regulated using of a flow meter and flow controller positioned upstream of the pump. Excurrent air was dried before entering gas analyzers, and fractional concentrations (%/100) of both oxygen (FeO_2) and CO_2 ($FeCO_2$) were recorded every second. Baseline measurements of the empty chamber were obtained for 15 min before and after each trial using identical flow rates to correct for analyzer drift. Oxygen consumption $(VO_2)\left(in\ ml\ of\ O_2 * g^{-1} * h^{-1}\right)$ was calculated following Eq. 10.6 in Lighton (2018):

$$VO_2 = \frac{FRi\left[(FiO_2 - FeO_2) - FeO_2(FeO_2 - FiCO_2)\right]}{(1 - FeO_2)}$$

Where FR_i is the flow rate (in mL min^{-1}), F_iO_2 is the fractional concentration of O_2 in the incurrent (baseline) air, F'_eO_2 is the fractional concentration of O_2 in the excurrent air, F_iCO_2 is the fractional concentration of CO_2 in the incurrent air, and F'_eCO_2 is the fractional concentration of CO_2 in the excurrent air. Basal metabolic rate was estimated using the mean of the lowest continuous 5-min interval recorded during each trial, excluding the initial acclimation period (Genoud et al. 2018); Lighton 2018).

Data analysis

All analyses were conducted in R version 4.2.3 (R Core Team 2025) using RStudio version 1.2.5042. continuous variables were $\log_e$-transformed prior to analyses to improve normality and homoscedasticity and to facilitate comparison with previous studies on metabolic scaling. Statistical significance was assessed at = 0.05.

Body mass and forearm length

We evaluated the relationship between M_b and forearm length (used as a proxy for changes in body size during growth), using a linear regression model implemented with the “lm” function in the “stats” package (R Core Team 2025). To assess whether the relationship between M_b and forearm length differed among ontogenetic stages, separated regressions were fitted for pups, juveniles, and adults. Differences in slope among age-classes were formally evaluated using an analysis of covariance (ANCOVA) including age class as a categorical factor and its interaction with M_b. Pairwise comparisons among slopes were performed by sequentially revealing the reference category of the age-class factor.

Relationship between BMR and M_b

To evaluate whether metabolic rate scaled positively with M_b within the colony, we fitted a linear model with *BMR* as the response variable and M_b as the explanatory variable. We then compared the estimated scaling exponent qualitatively with previous reported interspecific exponents for bats (0.74–0.77; Speakman and Thomas 2003; Ayala-Berdon et al. 2025).

Relationship between BMR and population phenological traits

To evaluate whether variation in *BMR* was associated with ontogenetic and reproductive characteristics beyond the effects of M_b, we fitted multiple linear regression models including age, sex, and reproductive condition as explanatory variables. Interaction terms between M_b and categorical predictors were initially included to evaluate whether metabolic scaling relationships differed among groups. Model simplification was performed by sequentially removing non-significant terms and comparing model parsimony.

Results

Between 2024 and 2025, we obtained metabolic data from 98 individuals (52 females and 46 males). Ten additional measurements were excluded due to anomalies consistent with recording errors. Metabolic rate was successfully measured in pups, juveniles, and adults across different reproductive conditions (**see Supplementary material**). The relative proportion of age classes varied among sampled months, with an increase in juvenile and adult males exhibiting scrotal testes toward the end of the sampling period (September and October of 2024). Metabolic measurements were obtained from individuals representing multiple ontogenetic stages, sexes and reproductive conditions.

Relationship between M_b and forearm length

We found a strong positive relationship between body mass (M_b) and forearm length across all individuals ($\beta = 0.70 \pm 0.02$, $t_{1,96} = 27.18$, $P < 0.001$). When examined by age class, the slope of the M_b-

forearm relationship was steepest in pups (β = 0.54 ± 0.05, $t_{1,17}$ = 9.39, P < 0.001), intermediate in juveniles (β = 0.46 ± 0.04, $t_{1,43}$ = 9.36, P < 0.001), and lowest in adults (β = 0.09 ± 0.05, $t_{1,32}$ = 1.60, P = 0.11) (Fig. 2), for which the relationship was not statistically significant ($t_{1,32}$ = 1.60, P = 0.11). The ANCOVA revealed a significant interaction between M_b and age class, indicating that slopes differed among groups ($F_{2,92}$ = 15.53, P < 0.001). Post hoc comparisons of slopes revealed that the allometric slope in adults was significantly lower than in pups (t_{92} = 5.57, P < 0.001) and juveniles (t_{92} = 3.91, P = 0.0005), whereas slopes did not differ significantly between pups and juveniles (t_{92} = 1.16, P = 0.48).

Relationship between BMR and M_b

The linear model revealed a significant positive relationship between basal metabolic rate (*BMR*) and M_b ($F_{1,96}$ = 7.71, P = 0.006), with an estimated slope of 0.62 ± 0.2. However, M_b explained only a small proportion of the variation in *BMR* (R^2 = 0.07), indicating substantial individual-level variability in metabolic rate (Fig. 3). Although slightly lower, the observed scaling exponent broadly overlapped the range of interspecific exponents previously reported for bats (~ 0.74–0.77).

Relationship between BMR and phenological traits

Multiple regression models including age, sex and reproductive condition, and their interactions with M_b did not reveal significant effects on *BMR* (P > 0.45 in all models). Thus, after accounting for variation associated with M_b, we found no evidence that ontogenetic stage, sex or reproductive condition explained additional variation in metabolic rate.

Discussion

In this study, we found that although pronounced ontogenetic differences in body size relationships were present, these differences were not associated with significant shifts in basal metabolic rate (*BMR*) after including M_b in the models. Nevertheless, we documented substantial intraspecific variation in *BMR* within the maternity colony of *Myotis velifer*. Despite individuals being measured under standardized conditions, metabolic rates varied considerably among individuals, suggesting that intrinsic physiological and behavioral mechanisms may contribute importantly to energy expenditure within the colony. These findings suggest that *BMR* is not a fixed trait within populations, but rather a flexible physiological parameter shaped by multiple interacting factors across development.

Ontogenetic variation in M_b*-forearm relationships*

The strong positive relationship between M_b and forearm length supports the use of forearm length as a reliable proxy for structural size in bats (Kunz 1973; Kunz and Parsons 2009; Adams and Pedersen 2013). This pattern is consistent with general mammalian growth trajectories, in which linear skeletal dimensions largely reflect somatic growth. However, energetic intake during development can influence

final forearm length, suggesting that variation in this trait may also reflect episodes of nutritional stress or differences in energy acquisition experienced in early life of bats (Davy et al. 2022).

In pups and juveniles, the relative steep slopes indicate that increases in M_b are closely associated with skeletal growth. This pattern is consistent with developmental stages characterized by rapid somatic growth and the accumulation of structural tissues (Cheng and Lee 2002; Sánchez-Garibay and Ortega 2025). The similarity in slopes between pups and juveniles suggests that this tight coupling between mass gain and skeletal growth is maintained throughout most of postnatal development. This pattern is particularly relevant in bats because newborn individuals undergo a critical developmental phase during which rapid wing growth is essential for acquiring powered flight. Achieving flight competence allows juveniles to forage independently, facilitating continuous growth and the accumulation of energy reserves necessary for survival during later energetically demanding periods such as overwintering (Wolf and Kerth 2024). In contrast, the weak and non-significant relationship observed in adults suggests a decoupling between M_b and structural size after skeletal growth is completed. In adults, variation in M_b likely reflects differences in body condition, energy reserves, and reproductive state rather than changes in skeletal dimensions. These results suggest that the biological meaning of M_b changes across ontogeny, shifting from structural growth during early development to variation in energetic condition in adults. This ontogenetic shift has important implications for interpreting scaling relationships within populations.

Scaling of BMR *with* M_b

Consistent with classic metabolic theory, we found a positive association between M_b and *BMR*. However, this relationship explained only a small fraction of the total variation in metabolic rate (R^2 = 0.07), indicating that M_b alone was a weak predictor of metabolic expenditure within the colony. Although the estimated scaling exponent was broadly consistent with interspecific values previously reported for bats, the low explanatory power of the model indicates substantial residual heterogeneity among individuals. The low R^2 observed here is consistent with previous studies documenting considerable unexplained variation in the M_b–*BMR* relationship within bat species. For example,Medina-Bello and Ayala-Berdon (2025) reported substantial residual variation in adult *Eptesicus fuscus* and *Lasiurus cinereus*, which the authors associated with differences in body condition and energetic state. Additional ecological factors, such as habitat quality, resource availability, and predation risk may also contribute to metabolic heterogeneity (White and Seymour 2003). This substantial residual variation suggests that additional physiological and ecological mechanisms contribute importantly to metabolic heterogeneity within the colony.

Several mechanisms could contribute to the substantial individual-level heterogeneity in *BMR* observed in this study. First, reproductive condition may influence metabolic rate (Ricklefs and Wikelski 2002). Although measurements were conducted under standardized conditions, some individuals were reproductively active, which may elevate metabolic expenditure due to increased energetic demands and hormonal regulation. However, the effect of reproduction on *BMR* is not consistent across mammals, as

some studies report increases during pregnancy and lactation whereas others find little or no effect (Derting and Mcclure 1989; Herreid 1967). Second, variation in body condition may also contribute to residual metabolic heterogeneity. Individuals within the same colony can differ in fat reserves, muscle mass, and overall energy state due to variation in recent foraging success or individual quality (e.g., Legros et al. 2026). Such differences are expected to influence maintenance costs and consequently metabolic expenditure. Third, ontogenetic stage may further contribute to the observed dispersion in *BMR*. Pups and juveniles undergoing active growth typically exhibit elevated energetic demands associated with tissue synthesis and development (Hulbert and Else 2004; McNab 1983; Wieser 1984). Together, these mechanisms could contribute to the substantial metabolic heterogeneity observed within the colony.

Implications for metabolic scaling and ecological physiology

Our results provide novel evidence that metabolic scaling relationships can exhibit substantial heterogeneity within a single population, particularly during periods of rapid developmental change. While interspecific studies often emphasize consistent scaling exponents, our findings highlight that metabolic rate within populations is shaped by a complex interaction of developmental, physiological, and ecological processes. These findings have important implications for the interpretation of metabolic scaling. Specifically, they suggest that M_b alone may be insufficient to predict metabolic rate within populations characterized by strong ontogenetic and physiological heterogeneity, such as maternity colonies. Incorporating developmental stage, body condition, and reproductive state may therefore improve our understanding of individual variation in energy expenditure. More broadly, our study underscores the importance of considering ontogenetic processes in ecological physiology. By focusing on a natural maternity colony, we show that metabolic scaling is not static but dynamically structured across life stages. From an ecological perspective, elevated intraspecific heterogeneity in *BMR* may reflect metabolic flexibility, which could be advantageous in dynamic or unpredictable environments. Seasonal fluctuations in resource availability and environmental conditions can impose varying energetic constraints (Hooten et al. 2020), and individuals capable of adjusting their energy expenditure may be better able to cope with these changes. Thus, variability in *BMR* may represent an adaptive physiological feature rather than simple background noise (Reher et al. 2022). Our findings further suggest that scaling relationships observed across species may emerge from highly variable physiological processes operating within populations and across development.

Declarations

Competing interests

The authors declare no competing interest.

Author Contribution

Conceptualization: J.A.B.; Formal analysis: J.A.B., J.M.C.; Investigation: J.A.B., J.M.C.; Methodology: J.A.B., J.M.C., E.A.L.; Project administration: J.A.B.; Supervision: J.A.B.; Visualization: J.A.B., J.M.C.; Writing – original draft: J.A.B., J.M.C.; Writing – review & editing: J.A.B., J.M.C, E.A.L.

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Data Availability

All data associated with this study are provided as Supplementary Material

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Figures

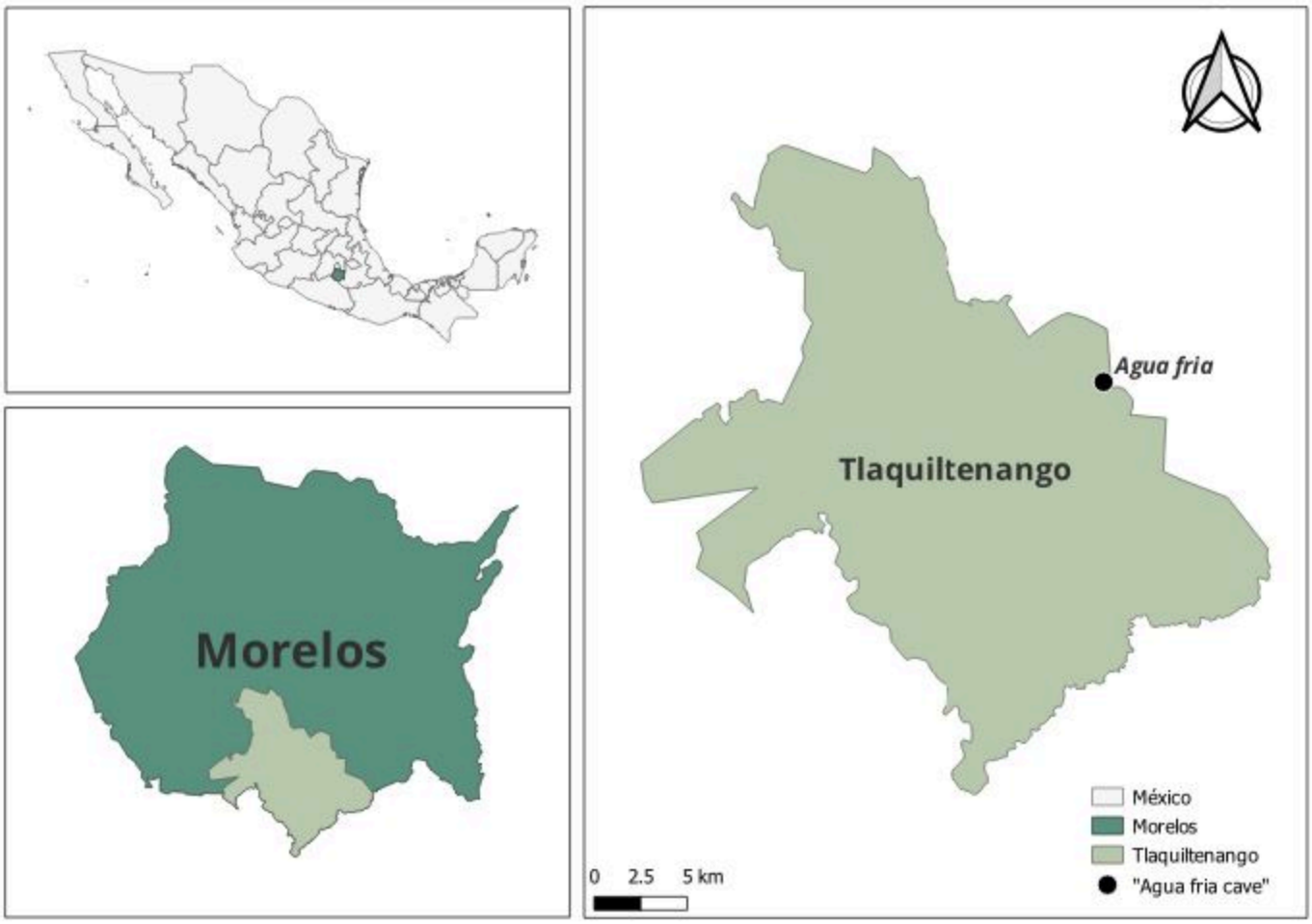


Figure 1

The map shows the location of Mexico, the state of Morelos, and the municipality of Tlaquiltenango. The black dot indicates the location of the “Agua Fría” cave. A scale bar and north arrow are included. Base map was created by using the QGIS software ver 3.42

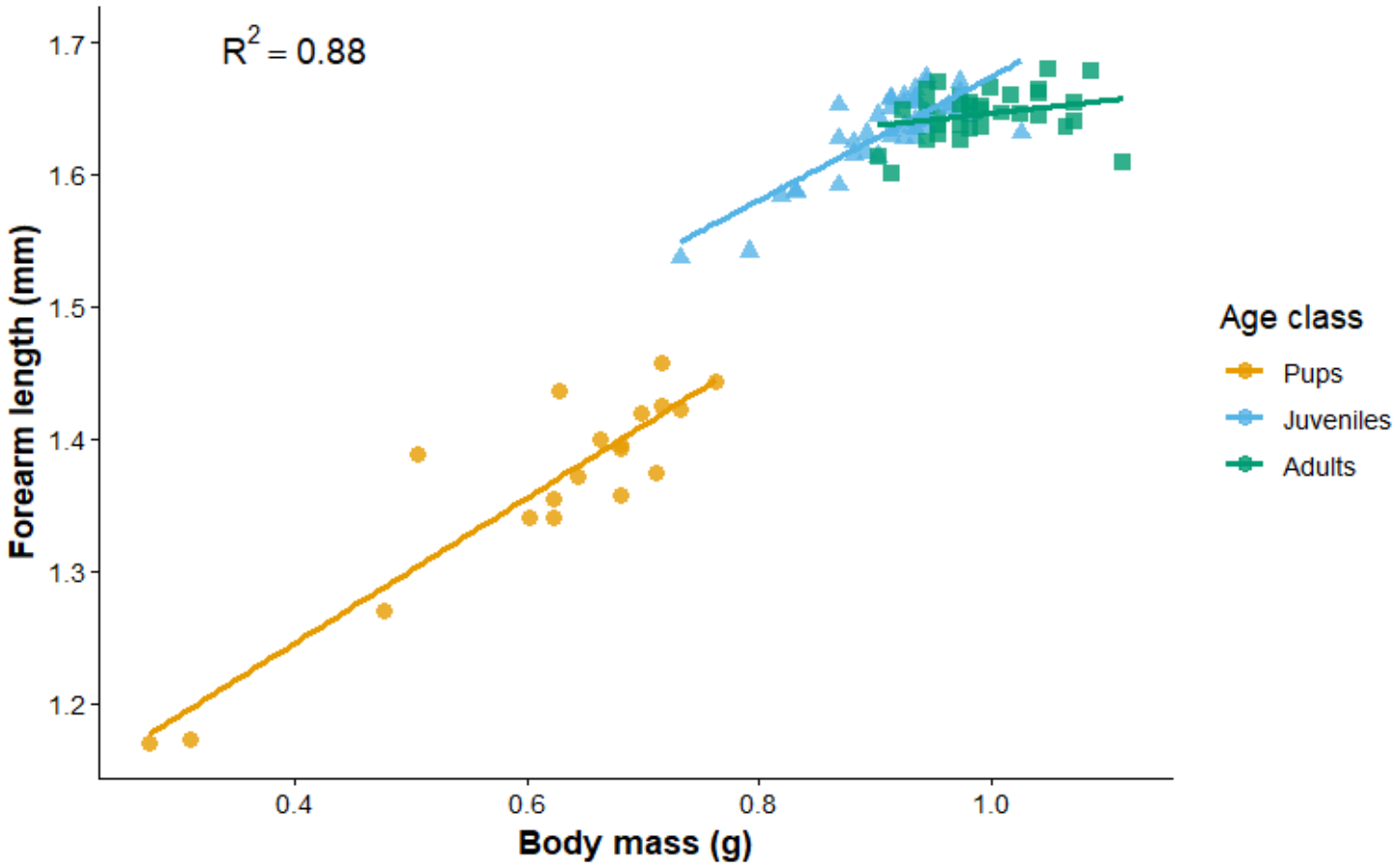


Figure 2

Log–log relationship between body mass and forearm length across ontogenetic stages in *Myotis velifer*. Points represent individuals, and colors denote age classes (pups, juveniles, adults). Lines show fitted linear models for each group. The slope of the relationship decreased with age, being highest in pups, intermediate in juveniles, and lowest in adults, suggesting ontogenetic changes in the scaling of body mass relative to forearm length.

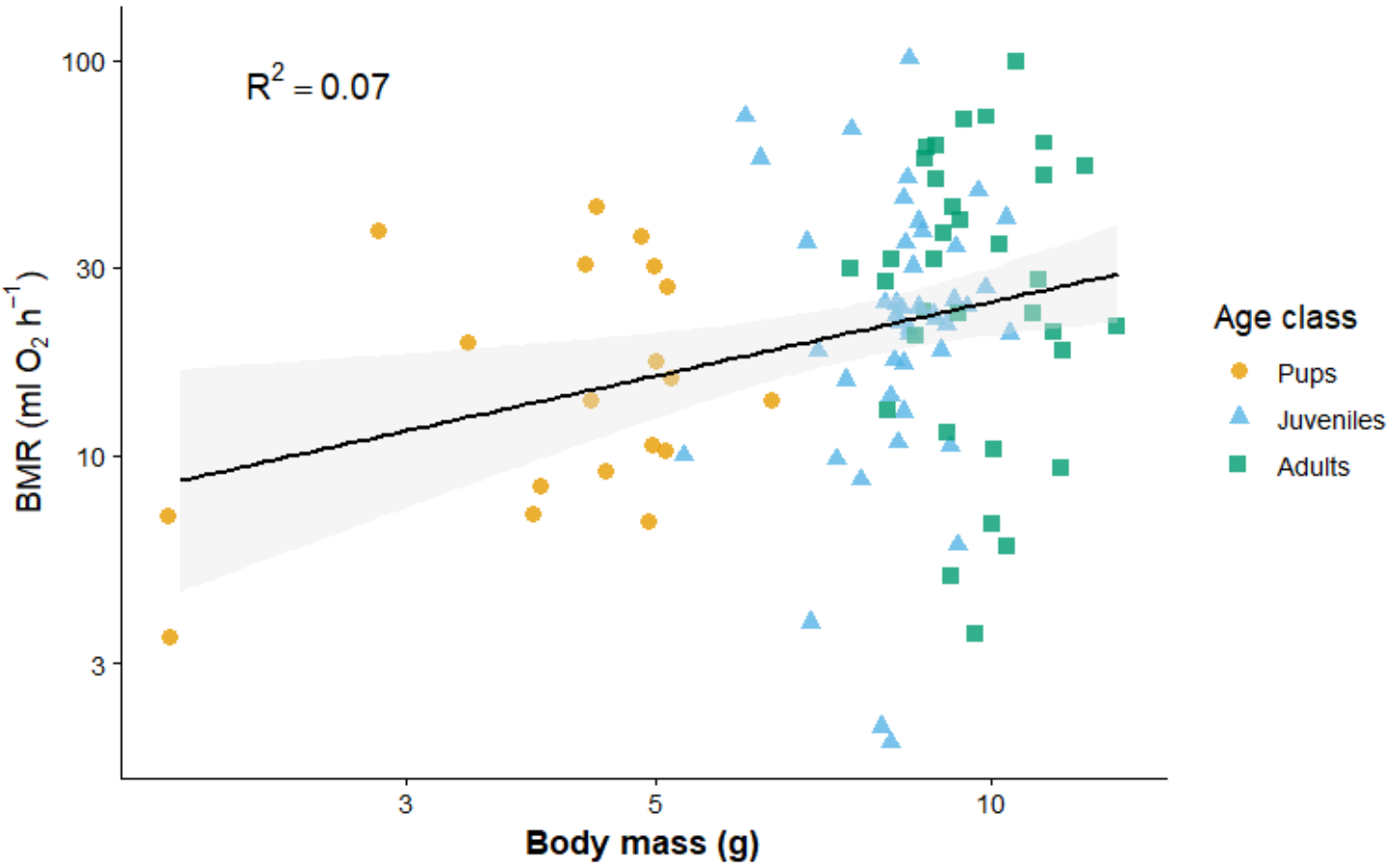


Figure 3

Relationship between body mass and basal metabolic rate (*BMR*) in a maternity colony of *Myotis velifer*. *BMR* scaled positively with body mass, although body mass explained only a small proportion of the observed variation ($R^2 = 0.07$). Points represent individual measurements across ontogenetic stages (pups, juveniles, and adults), distinguished by symbol type. The solid line represents the linear regression fitted to log-transformed data, and the shaded area indicates the 95% confidence interval.

Supplementary Files

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- SupplementaryMaterial.xlsx