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Effects of Caudal Autotomy on the Locomotor Performance of *Micrablepharus Atticolus* (Squamata, Gymnophthalmidae)

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Abstract: Caudal autotomy is a striking adaptation used by many lizard species to evade predators. Most studies to date indicate that caudal autotomy impairs lizard locomotor performance. Surprisingly, some species bearing the longest tails show negligible impacts of caudal autotomy on sprint speed. Part of this variation has been attributed to lineage effects. For the first time, we model the effects of caudal autotomy on the locomotor performance of a gymnophthalmid lizard, *Micrablepharus atticolus*, which has a long and bright blue tail. To improve model accuracy, we incorporated the effects of several covariates. We found that body temperature, pregnancy, mass, collection site, and the length of the regenerated portion of the tail were the most important predictors of locomotor performance. However, sprint speed was unaffected by tail loss. Apparently, the long tail of *M. atticolus* is more useful when using undulation amidst the leaf litter and not when using quadrupedal locomotion on a flat surface. Our findings highlight the intricate relationships among physiological, morphological, and behavioral traits. We suggest that future studies about the impacts of caudal autotomy among long-tailed lizards should consider the role of different microhabitats/substrates on locomotor performance, using laboratory conditions that closely mimic their natural environments.

Keywords: lizard; autotomy; tail; locomotion; performance; temperature; predation

1. Introduction

Throughout evolutionary time, an “arms race” fostered varied strategies of prey capture and predator escape [1]. Autotomy—the self-amputation of a body part in response to an attack by a predator—is one of the most dramatic adaptations to avoid predation [2]. Caudal autotomy among reptiles has an ancient origin and was present in captorhinids from the Early Permian [3]. It persists to this day among squamate reptiles, in some species of snakes and most lizards, allowing them to escape while the predator is distracted by the abandoned tail part [4–7]. The detachment of the tail in most species occurs through pre-established, intravertebral fracture planes, the oldest and most common form of autotomy to date, allowing a new tail to grow supported by a calcified cartilage tube [8–11].

Despite the immediate benefit of avoiding predation, autotomy also involves energy costs that can influence survival. For instance, even when resources are limiting, tail

regeneration is a priority, probably associated with long-term survival and reproductive success [12,13]. Thus, the production of a new tail can negatively affect energy balance, immunity, growth rate, social *status*, and immediate reproductive success [2,14]. Besides, autotomy results in the temporary loss of an important mechanism to avoid predation. Therefore, autotomized individuals may alter their patterns of activity and space use, as well as foraging schedules and frequencies, to minimize exposure to predators [15,16].

In addition to affecting behavior, caudal autotomy affects the locomotor performance of some species. The tail is a counterweight, balancing the head and body during racing; therefore, its absence results in weight transfer to the forelimbs, making it challenging to move [4]. Moreover, the tail can act as an inertial damper of pelvic girdle movements, and its loss causes disordered oscillation of the hind limbs during the race [5] and reduced jump stability and performance [17]. In general, caudal autotomy leads to decreased locomotor performance [18]. However, it may not interfere [19,20] or even increase locomotor performance [21]. These opposite results may relate to interspecific differences in predation intensity throughout ontogeny, life habits, and sexual dimorphism [15]. For example, in sexually dimorphic species where males have conspicuous coloration, their locomotor performance is little affected by autotomy, as potential predators and competitors can easily see them [18,22]. Still, variation exists between and within evolutionary lineages associated with different tail shapes and functions, such as sexual displays, predator distraction, defense, balance, fat storage, stabilization, and an auxiliary organ in climbing [20,23].

The lizard genus *Micrablepharus* (Squamata, Gymnophthalmidae) contains two species: *M. maximiliani* (Reinhardt and Lütken, 1861), widely distributed across the South American dry diagonal, comprising the Chaco, Cerrado, and Caatinga, and *M. atticolus* Rodrigues, 1996, endemic to the Cerrado [24–27]. The two species are diurnal, semifossorial, and live among the leaf litter [28–31]. Reproductive activity peaks in the dry season, and populations undergo an almost complete annual replacement [32,33]. They share an elongate trunk and tail, short limbs, and digit reduction on the forelimbs (complete loss of digit I), whereas the hindlimbs follow the pentadactyl condition [34,35]. They exhibit intermittent quadrupedal locomotion, combining conspicuous axial traveling waves with trot-like coordination of the limbs [36–38]. The vertebral axis is the main effector of locomotion, while the limbs play an auxiliary role. On low friction substrates, the axial system of locomotion predominates, but the limbs become increasingly involved as substrate friction increases and with increasing speed [37]. *Micrablepharus atticolus* and *M. maximiliani* have a long and bright blue tail that contributes to divert attention from visually oriented predators to a non-vital part of the body at the time of an attack, which may be associated with higher rates of autotomy in more open environments [39].

Tail loss in *Micrablepharus atticolus* does not affect body condition, suggesting that the energetic costs of autotomy are low or that individuals compensate for the tail loss by increasing foraging rate [39]. Consequently, autotomy may not impair locomotor performance by reducing energy reserves [40]. However, because of the importance of the axial system during locomotion [37], tail loss may compromise sprint speed. Locomotor performance is an essential determinant of fitness, because its reduction can undermine survival, reproductive success [41,42], foraging [43,44], and social dominance [45]. Since environmental variation affects autotomy rates in *M. atticolus*, but these do not affect survival [39], studying the effect of autotomy on the locomotor performance of lizards inhabiting different environments can contribute to the understanding of possible compensatory mechanisms.

Here, we investigate the effects of caudal autotomy on the locomotor performance of *Micrablepharus atticolus* from two different environments, one in the central Cerrado and another in the Cerrado-Amazonia transition. We take into account the effects of geography, sex, body temperature, and ontogeny since (1) locomotor performance tends to be lower in females, especially during pregnancy, by the effect of the additional burden represented by the litter [46,47]; (2) there is a positive allometric relationship between body size and locomotor performance [48]; and (3) central Cerrado lizards are expected to have better locomotor performance, assuming that environmental conditions should be optimal for

performance in the core of species distributions [49]. Moreover, we investigate whether the effects of autotomy on locomotor performance are proportional to the size of the remaining or regenerated portion of the tail [50].

2. Materials and Methods

2.1. Study Sites

We collected data from lizards captured at two sites: Reserva do IBGE (15°56′06″ S, 47°52′09″ W), a protected area in Brasília, Distrito Federal, Brazil, in the central area of the Cerrado; and Parque do Bacaba (14°42′24″ S, 52°21′10″ W), Nova Xavantina, Mato Grosso, Brazil, in the Cerrado-Amazon transition. The climate in both sites is tropical with dry winter, Aw in Köppen's classification [51], with a dry season from May to September and a rainy season from October to April. In Brasília, the average annual accumulated precipitation is 1477.4 mm, and the average annual temperature is 21.0 °C; in Nova Xavantina, 1417.7 mm and 24.8 °C, respectively (<https://portal.inmet.gov.br/normais>, accessed on 30 March 2021).

2.2. Lizard Sampling

We captured lizards using arrays of pitfall traps interconnected by drift fences, as part of a long-term, mark-recapture study on their demography and community dynamics. Each array consisted of four plastic buckets of 35 L, buried to ground level and arranged in the form of a “Y”, interconnected by three 6 m long and 50 cm high galvanized steel plates that functioned as guide fences. Immediately after capture, we took the following measurements from each lizard: body mass, using a Pesola spring dynamometer (0.1 g precision); snout-vent length (SVL), total tail length, and length of the non-autotomized part of the tail—in lizards with caudal autotomy—with a metal ruler (1 mm precision); and sex, whenever possible, through palpation of the abdomen for the presence of vitellogenic follicles or eggs in pregnant females and the extrusion of the hemipenis in males. Next, we transported lizards to the lab and housed them in individual terraria, with vermiculite substrate and water *ad libitum*. Up to 24 h after capture, we carried out ecophysiology experiments (below), after which we permanently marked (by toe-clipping) and released lizards next to their exact capture sites. We captured and handled all individuals with great care to prevent any damage to the tail, such that autotomized tails resulted exclusively from natural processes. Finally, we only used adult individuals in the analyses, comprising 39 lizards from Brasília and 64 from Nova Xavantina. We considered individuals with SVL greater than 35 mm as adults [32].

2.3. Locomotor Performance

We recorded sprint speed on a wooden track (300 cm long × 30 cm high × 40 cm wide). We induced each lizard to run as fast as possible by manual stimulation, mimicking a predatory chase, to record the maximum speed. Due to the thermal sensitivity of sprint speed [52], we conducted runs at three different temperatures—cold (=ambient −5 °C), ambient (~20 °C), and hot (=ambient +5 °C)—in each experiment. We used gel ice packs and incandescent lamps to alter lizards' body temperature, monitored with a fast-reading cloacal thermometer (L-K Industries Miller & Weber T-6000 Cloacal 0/50 °C 0.2 precision). We conducted two trials of each lizard at each temperature, totaling six runs. We recorded runs at 420 fps with a Casio HS EX-FH25 digital camera mounted on an aluminum tripod at 1.5 m height in the center of the track. Later, we analyzed videos with Tracker 4.80 to obtain the maximum sprint speed of each lizard at each temperature.

Within at least one hour after the last run, we measured the critical thermal minimum and maximum, with a one-hour interval between them, using a fast-reading cloacal thermometer (L-K Industries Miller & Weber T-6000 Cloacal 0/50 °C 0.2 precision). We exposed lizards to the sources of heat and cold mentioned above until they lost the righting response, i.e., when they could not return to the prone position after turning in a supine position without leading the animal to death. To build performance curves (below), we

considered that sprint speed is equal to zero at the critical thermal minimum and maximum. The Animal Use Ethics Committee of the University of Brasília approved all procedures (process 33786/2016).

2.4. Statistical Analyses

To determine the effect of caudal autotomy on locomotor performance, we built generalized mixed-effects additive models—GAMMs [53] with the MGCV package [54] in the R environment [55]. We used GAMMs to generate performance curves and evaluate the influence of predictors on the shape and location of curves because they allow nonlinear responses and are flexible due to the non-parametric smoothing functions used in sections of the data [56]. In these models, we used the maximum sprint speed as the response variable; the individual as a random factor; and sex, pregnancy (gravid/non-gravid), body temperature, mass, SVL, relative tail length (total tail length/SVL), caudal autotomy (autotomized/not autotomized), relative length of the regenerated portion of the tail (length of the regenerated portion of tail/SVL), and study site (Brasília/Nova Xavantina) as fixed factors. To assess model significance, we used a likelihood-ratio test comparing its fit with that of a null model, composed only of the response variable, the intercept, and the random factor.

To evaluate predictor importance, we used a combination of model selection and averaging based on the Akaike Information Criterion adjusted for small samples (AIC_c), with the package MUMIN [57]. Model selection attempts to improve our understanding of the relationship between the response and the predictors by reducing model's complexity. However, this approach often results in biased regression parameters and too small respective standard errors in finite samples because they do not reflect the uncertainty related to the model selection process [58,59]. On the other hand, model averaging incorporates the uncertainty intrinsic to model selection by combining parameter estimates across different models [60,61]. Using this approach, we examined the complete set of possible models combining the fixed effects to obtain model-averaged standardized parameter estimates for statistical inference [62,63]. We used averages calculated across all models ("full averages"), assuming that each model includes all variables, but that in some models the corresponding coefficient (and its respective variance) is set to zero, which avoids biasing the values away from zero [64]. Moreover, we calculated the importance of each predictor as the sum of Akaike weights across all models containing that predictor.

3. Results

We obtained ecophysiological data from 39 lizards from Brasília and 64 lizards from Nova Xavantina (Table 1). The likelihood-ratio test indicated that our full GAMM differed significantly from a null model and adequately fitted the data ($\chi^2_{[1]} = 219.129$, $p < 0.001$, adjusted- $r^2 = 0.622$). Among the parametric terms in the model, collection site and pregnancy were significant, while among smooth terms, body temperature, body mass, and the length of the regenerated portion of the tail were significant (Table 2). Model selection and averaging indicated that body temperature, pregnancy, mass, collection site, and the length of the regenerated portion of the tail, in this order, were the most important predictors of locomotor performance in *Micrablepharus atticolus* (Table 3). The GAMM predicted maximum locomotor performance around 31 °C (Figure 1A). Gravid females had lower performance than males and non-gravid females (Figure 1B), and lizards from Nova Xavantina achieved higher performance—and at higher temperatures—than lizards from Brasília (Figure 1C). Finally, the locomotor performance increased with body mass (Figure 2A) and the relative length of the regenerated portion of the tail (Figure 2B).

Table 1. Summary statistics of ecophysiological parameters of *Micrablepharus atticolus* from Brasília and Nova Xavantina, Brazil. Values represent the mean $\pm$ one standard deviation.

Parameter	Brasília	Nova Xavantina	Total
Sample size	39	64	103
Mass (g)	1.49 $\pm$ 0.35	0.82 $\pm$ 0.19	1.06 $\pm$ 0.41
Snout-vent length (mm)	38.22 $\pm$ 3.06	34.98 $\pm$ 2.76	36.12 $\pm$ 3.26
Tail length (mm)	48.62 $\pm$ 13.74	46.37 $\pm$ 17.64	47.17 $\pm$ 16.39
Relative tail length	1.27 $\pm$ 0.34	1.32 $\pm$ 0.50	1.31 $\pm$ 0.45
Length of regenerated portion of tail (mm)	6.38 $\pm$ 10.30	9.99 $\pm$ 11.95	8.71 $\pm$ 11.51
Relative length of regenerated portion of tail	0.16 $\pm$ 0.26	0.28 $\pm$ 0.34	0.24 $\pm$ 0.32
Body temperature during runs (°C)	27.94 $\pm$ 6.72	27.53 $\pm$ 5.43	27.67 $\pm$ 5.88
Critical thermal minimum (°C)	13.90 $\pm$ 1.78	15.20 $\pm$ 3.29	14.70 $\pm$ 2.08
Critical thermal maximum (°C)	44.41 $\pm$ 1.84	40.00 $\pm$ 3.09	41.69 $\pm$ 3.43
Sprint speed (maximum)	0.07 $\pm$ 0.02	0.10 $\pm$ 0.04	0.09 $\pm$ 0.04

Table 2. Full generalized additive mixed-effects model (GAMM) relating predictors to locomotor performance (sprint speed) of the lizard *Micrablepharus atticolus*. AU: caudal autotomy (yes/no), CCR: total tail length, RCr: length of the regenerated portion of the tail, SVL: snout-vent length, NX: Nova Xavantina, edf: expected degrees-of-freedom.

Parametric Terms				
Term	Estimate	Std. Error	<i>t</i>	<i>p</i>
(Intercept)	0.0411	0.0065	6.3080	<0.0001
LocalNX	0.0220	0.0069	3.1920	0.0015
SexMale	0.0015	0.0045	0.3230	0.7467
AUYes	0.0000	0.0070	−0.0040	0.9970
Pregnancy	−0.0203	0.0068	−2.9700	0.0031
Smooth Terms				
Term	edf	Ref. df	<i>F</i>	<i>p</i>
s(Temperature)	7.976	7.976	95.569	<0.00001
s(CCR)	1.000	1.000	0.036	0.84979
s(RCr)	1.000	1.000	3.037	0.08203
s(SVL)	1.000	1.000	0.365	0.54589
s(Mass)	3.119	3.119	4.983	0.00259

Table 3. Model selection and averaging of generalized additive mixed-effects models (GAMMs) relating predictors to locomotor performance (sprint speed) of the lizard *Micrablepharus atticolus*. Models depicted are those with $\Delta AIC_c < 4$. AU: caudal autotomy (yes/no), RT: length of regenerated portion of tail, AIC_c : Akaike information criterion corrected for small samples, ΔAIC_c : difference between given and best model, $wAIC_c$: Akaike weight.

Model Selection									
Model	df	logLik	AICc	ΔAICc	wAICc				
Pregnancy + Site + s(Mass) + s(RCr) + s(Temperature)	11	934.81	−1847.06	0.00	0.25				
AU + Pregnancy + Site + s(Mass) + s(RCr) + s(Temperature)	12	934.84	−1845.01	2.05	0.09				
Pregnancy + Site + s(Mass) + s(RCr) + s(Temperature)+ Sex	12	934.82	−1844.97	2.10	0.09				
Pregnancy + Site + s(Mass) + s(Temperature)	9	931.35	−1844.32	2.75	0.06				
AU + Pregnancy + Site + s(Mass) + s(Temperature)	10	932.22	−1843.96	3.10	0.05				
Pregnancy + Site + s(Mass) + s(RCr) + s(SVL) + s(Temperature)	13	934.93	−1843.07	3.99	0.03				
Model Averaging									
Importance	s(Temperature)	Pregnancy	s(Mass)	Site	s(RCr)	AU	Sex	s(CCr)	s(SVL)
Sum of model weights	1.00	0.93	0.90	0.89	0.73	0.33	0.27	0.15	0.14
Number of containing models	255	253	253	254	254	255	255	255	254

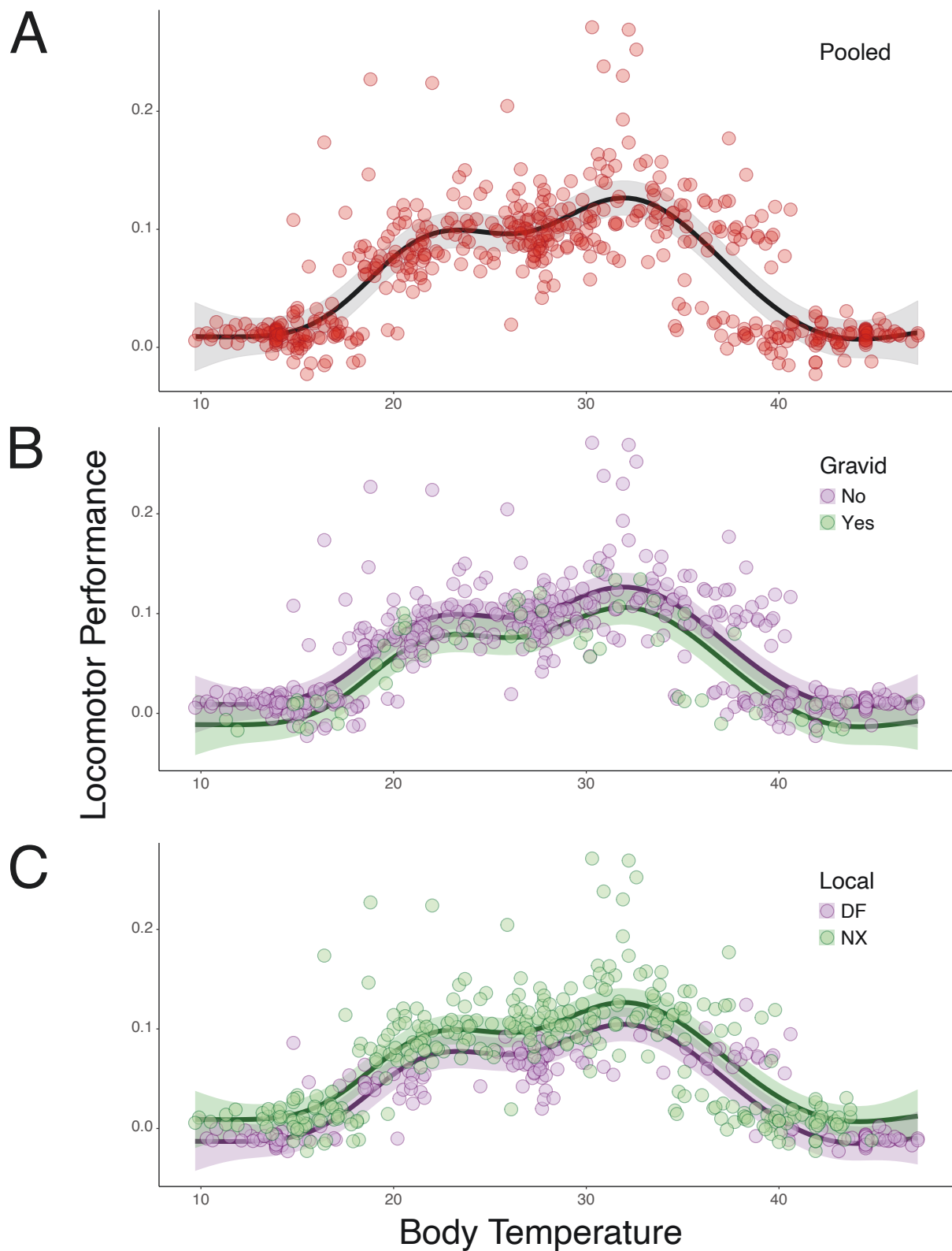


Figure 1. Locomotor performance (sprint speed) of the lizard *Micrablepharus atticolus* as a function of (A) body temperature, (B) body temperature and female reproductive condition (gravid females vs. non-gravid females and males), and (C) body temperature and geography. Points represent partial residuals of a generalized additive mixed model (GAMM), while lines and bands represent the predictions and confidence limits, respectively.

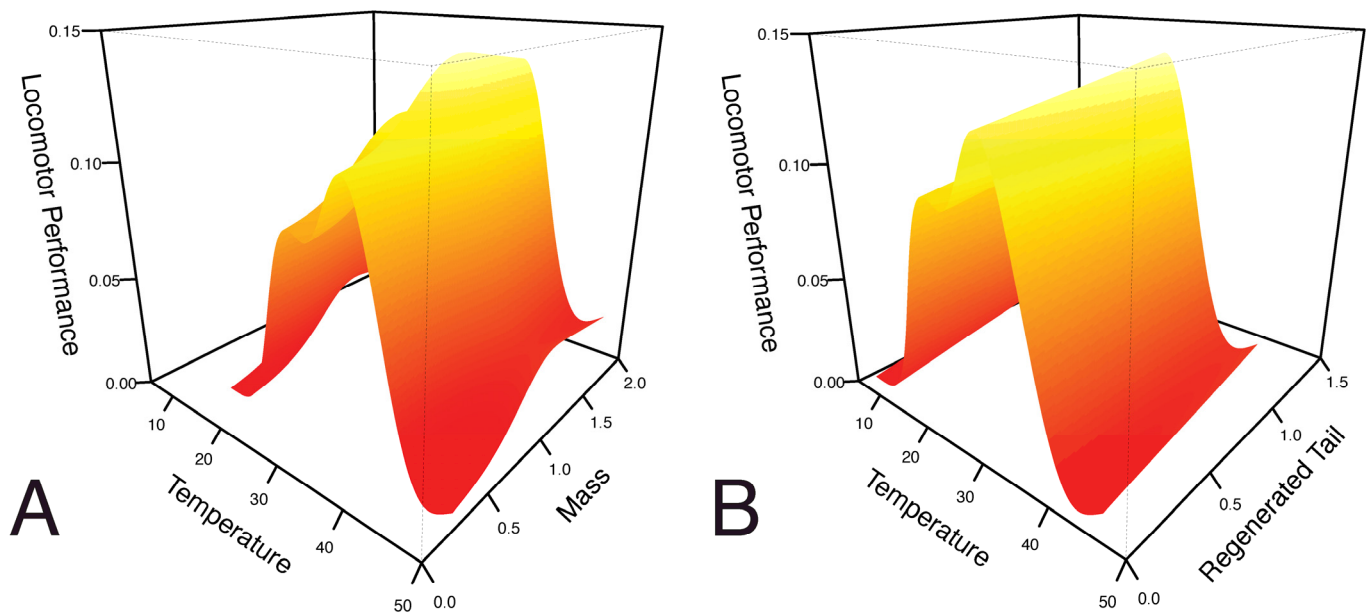


Figure 2. Locomotor performance (sprint speed) of the lizard *Micrablepharus atticolus* as a function of (A) body temperature and body mass, and (B) body temperature and length of the regenerated portion of the tail. The surface represents the predictions of a generalized additive mixed model (GAMM).

4. Discussion

We assessed the effects of caudal autotomy on the locomotor performance of *Micrablepharus atticolus*, controlling for the influence of several covariates. We found that the performance is significantly affected by body temperature, female reproductive condition, body mass, geography, and caudal autotomy. Overall, our findings highlight the complex patterns of association among physiological, morphological, and behavioral traits and that meaningful inference and prediction based on physiological performance must consider such patterns [65–68].

Body temperature was the foremost factor affecting performance. This outcome is not surprising, given that body temperature is one of the most critical ecophysiological variables affecting the performance of ectotherms [69–71]. Sprint speed peaked at ca. 31 °C, which is substantially higher than that recorded for *Capraonina itaquara* (24.51 °C) and *Colobodactylus dalcianus* (25.81 °C), two closely related gymnophthalmines from high-elevation areas in the Atlantic Forest of southeastern Brazil [72,73]. Moreover, our analyses showed that lizards from Nova Xavantina achieve higher sprint speeds at higher body temperatures than lizards from Brasília. Such differences might be related to altitudinal, latitudinal, or even lineage effects [74]. As environmental temperatures in Nova Xavantina are ca. 4 °C higher than in Brasília (and even higher than in high elevations of southeastern Brazil), our results are consistent with the notion that geographic variation of thermal sensitivity in locomotor performance is adaptive, such that organisms adjust optimal performance temperatures to prevalent field body temperatures [67]. For instance, based on the principle that biochemical and physiological systems operating at high temperatures have a high catalytic capacity, the “hotter is better” hypothesis predicts a positive relationship between maximal organismal performance and optimal temperatures [75]. This relationship holds when considering interspecific [65,76] or intraspecific comparisons [77,78].

Whereas Brasília is at the core of *Micrablepharus atticolus*’ geographic distribution, Nova Xavantina is closer to its periphery, next to the Cerrado–Amazonia ecotone [26,79]. Therefore, we expected higher physiological performance in the core population, as predicted by the core-periphery hypothesis [49,80]. However, we found the opposite pattern, with higher performance in the more peripheral population. Several factors might account for this result. For example, despite the centrality difference between the two sites relative

to the species' range, they might have the same or even opposite patterns of environmental suitability, i.e., the geometric center of the geographic distribution may not coincide with areas of greater suitability and vice-versa [81,82]. Moreover, due to phenotypic plasticity or adaptation to local conditions, species range boundaries may not be driven by thermal performance [72,83].

Our analysis indicates no intersexual differences in sprint speed in *Micrablepharus atticolus*, most likely related to the lack of sexual size dimorphism [29]. However, we found that pregnant females have lower locomotor performance than males. This decrease likely occurs due to the additional physical load of the litter, making the body broader and heavier [84]. However, as locomotor performance increased with body mass, the lower performance in pregnant females may be related to physiological changes linked to reproduction [85], such as decreased muscle strength, reduced metabolic capacity, motivation to escape [86], and energy allocation [87]. These physiological changes ensure adequate embryonic development and remain for a while after egg-laying [85,88]. A decrease in gravid females' locomotor performance was also recorded in other lizard species [89–93]. By becoming slower, pregnant females are more susceptible to predation, and this can promote several behavioral changes during pregnancy, such as foraging near potential shelters and avoiding long races during a predatory escape.

The body mass of individuals is an essential factor in determining sprint speed [76]. We found continuously increased performance with increasing body mass, which would probably occur until the optimal mass is reached, beyond which performance decreases [94,95]. This increase in performance with body mass is typical among quadruped species [45,76,96,97]. Despite using lateral undulation when moving in the middle of the leaf litter, *Micrablepharus atticolus* can also rely on quadrupedal locomotion when on a flat substrate [36,37]. We advance that the ever-increasing locomotor performance associated with increased body mass results from the very short lifespan of *M. atticolus* [32], such that individuals never reach a critical body mass.

In most cases, the tail has an active role in improving lizard sprint speed, and caudal autotomy undermines locomotor performance [14,20]. Moreover, the greater the relative size of the intact tail, the higher the magnitude of sprint speed change following autotomy. However, we found that sprint speed was unaffected by tail loss but by the relative length of the regenerated portion of the tail, i.e., the longer the regenerated tail, the higher the sprint speed. Still, this effect was meager, unlike patterns documented elsewhere for eublepharids, lacertids, and skinks, [46,98–100]. Caudal autotomy has no impact on the locomotor performance of some lizard species [19,20]. Some researchers have argued that this reflects these species' skinny and short tails [19] or even that adverse effects of autotomy result from researchers damaging the lizards' locomotor muscles during experimental tail breakage [101]. Individuals of *Micrablepharus atticolus* have a long tail (in our samples, $\sim 1.7 \times$ SVL in individuals with intact tails), one of the longest among gymnophthalmids [102], and we used lizards with naturally broken and regenerated tails. Therefore, these explanations cannot account for the patterns we observed.

A synthesis on the effects of tail autotomy, tail size, and locomotor performance in lizards identified clear phylogenetic patterns in the data [20]. Hence, among-lineage differences in the biomechanics of locomotion and the tail function during sprinting may account for the different effects of tail loss on locomotor performance. The single previous study on the locomotion of *Micrablepharus* did not address the impact of caudal autotomy on performance [37], and to the best of our knowledge, ours is the first study on this issue within Gymnophthalmidae. This lineage comprises small, cryptic, and often fossorial or semifossorial Neotropical species, characterized by many instances of the evolution of body elongation and limb reduction [34,35,103]. Indeed, fossoriality is a critical driver of the evolution of a snake-like morphology among squamates [104,105]. Therefore, in such species, the tail may have a very context-specific role in locomotion, which may not be apparent when individuals move on a flat substrate. For instance, in *Colobodactylus taunayi*, a gymnophthalmine, the tail remains stretched during displacement on a flat

surface [102] and a similar pattern is apparent in *M. maximiliani* when moving on gravel or sand (Figures 3 and 6 in [37]). Tail loss in lizards of the genus *Takydromus*, where the tail can be three times as long as the SVL, similarly had little effect on locomotor performance [20,50,106]. These species often use a three-dimensional, cluttered environment amidst the leaf litter, much like “grass-swimmer” lizards [107,108]. We conjecture that the long tail of *M. atticolus* is more useful when using undulation amidst the leaf litter and not when using quadrupedal locomotion on a flat surface. Future studies on the impacts of caudal autotomy on long-tailed lizards should consider the role of different microhabitats/substrates on locomotor performance, using laboratory conditions that closely mimic their natural environment.

Author Contributions: N.A.S., H.M.P. and G.R.C. conceived the study, conducted the analyses, and wrote the manuscript. All authors participated in fieldwork, lab work, data collection and curation, and revised the manuscript. D.B.M., G.H.d.O.C. and G.R.C. provided planning and supervision. All authors have read and agreed to the published version of the manuscript.

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