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Research Article

Effects of Surface Roughness on the Locomotion of a Long-Tailed Lizard, *Colobodactylus taunayi* Amaral, 1933 (Gymnophthalmidae: Heterodactylini)

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We analyzed the locomotor behavior of a long-tailed, forest floor, and leaf litter lizard, *Colobodactylus taunayi*, a species that retains the generalized Gymnophthalmidae *Bauplan* whilst presenting the discrete toe reduction associated with the *Bachia*-like pattern of limb reduction. We videotaped individuals moving on four substrates with increasing degrees of roughness: plastic, wooden board, glued sand, and glued gravel. Significantly higher speeds occurred on the last two substrates. As with most other limbed animals, increased speed was significantly correlated with simultaneous increases in both stride length and stride frequency. Independently of the kind of substrate, *C. taunayi* used rather slow lateral sequence walking trots. In contrast to other ectothermic tetrapods, and especially other Gymnophthalmidae, this species lacked perceptible lateral flexion of either the trunk or the tail to effectuate these slow gaits.

1. Introduction

The family Gymnophthalmidae comprises around 230 species of new world lizards [1], occurring from Central America to most of South America [2–4]. Over the last decade, several gymnophthalmid taxa have been described on the basis of comprehensive phylogenetic approaches and/or detailed studies of alpha taxonomy [5–10], suggesting that the real diversity of the family must be underestimated by the present data.

Gymnophthalmids show considerable variation regarding morphofunctional patterns as a consequence of adaptations to diverse habitats. Despite some highly specialized forms with remarkable body elongation and limb reduction (*Calyptommatus* spp., *Notobachia ablephara*, *Scriptosaura catimbau*, and also species of *Bachia*), a general gymnophthalmid *Bauplan* would characterize them as small-sized lizards (<6 cm snout-vent length), with a thin and elongated body, short limbs (loss of fingers and toes is rather frequent), and a well-developed tail [3, 4]. This body plan plays an important role for locomotion among Gymnophthalmini *sensu* Pellegrino and coauthors [11–16] and among Heterodactylini [16].

Body proportions, such as leg or tail length, and the ability to produce large undulations of the trunk control locomotor skills in terrestrial lizards. Stride length (the amplitude of limb movement) and stride frequency (the rhythm of limb movement), both components of speed (speed = stride frequency × stride length), are directly related to the body geometry and to the amplitude of body curvature (increasing the girdle inclination to gain forward displacement for the limb) [17]. The intensity of body undulation may provide an additional contribution to stride length, where the increased body length results from an increase in the number of presacral or tail vertebrae. Limb frequency is related to the motor control [18] characterizing each species and is based on the time taken by both phases of the limb cycle: stance and swing duration.

According to this *Bauplan*, which is representative of a specific morphofunctional status, modulation of both frequency and amplitude of movement adjust locomotion to the environmental mosaic. However, the mean adopted by the animal to cope with environmental constraints also includes the grip of the limbs (substrate roughness enhancing the exchange of forces during the stance phase) and the selection of an appropriate gait so as to reach a kinematic performance that minimizes energy expenditure [19, 20]. As first noted in lizards by Sukhanov [21], locomotion differs according to the nature of the substratum in which movement occurs. The gait can be characterized by different time lags between successive footfalls of the four limbs and by the relative proportion of stance and swing periods in the limb cycle.

Colobodactylus has been scarcely explored regarding locomotion patterns found in other Gymnophthalmidae. Its external shape reveals an elongated body with a strikingly long tail and toe reduction. The only two species, *C. taunayi* and *C. dalcyanus*, are restricted to the Brazilian Atlantic Rain Forest [22]. Pellegrino and coauthors [11] and Rodrigues and coauthors [23] placed *Colobodactylus* among the Heterodactylini, as a sister-group of *Heterodactylus,* and also related to *Acratosaura*, *Alexandresaurus*, *Colobosaura, Iphisa,* and *Stenolepis*. According to these authors, the Heterodactylini and Gymnophthalmini comprise the subfamily Gymnophthalmidae. *Colobodactylus taunayi*, the species studied here, is distributed along Southeastern Brazil, occurring on the Atlantic Plateau, in the lowlands at sea level and on local islands [22, 24, 25]. It is clearly associated with leaf litter on the floor of forest areas, and such an environment indicates a heterogeneous substrate in terms of roughness, which probably influences lizard performance.

This study addresses the following questions. (i) Does surface roughness affect the kinematic variables of *C. taunayi* locomotion, especially those linked to speed modulation? (ii) Are these effects similar to other Gymnophthalmidae [12–16] under the same experimental conditions?

2. Material and Methods

2.1. Animals Studied. Individuals of *Colobodactylus taunayi* (Figure 1(a)) were collected in three localities in São Paulo State, Brazil (Miguel T. Rodrigues, Proc. Ibama 02001 006003/2002-12: 046/2006-cgfau/lic and M. Dixo, Proc. Ibama 02010.002890/05-13: 0177/05-RAN). Variation in morphological parameters among them ($n = 4$) was small (mean ± standard deviation; range in parenthesis): weight = 2.3 ± 0.72 g (1.5–3.3), snout-vent length (SVL) = 4.8 ± 0.50 cm (4.2–5.3), and tail length = 12.1 ± 1.7 cm (10.9–14.6). The four specimens were kept at the Instituto de Biociências, Universidade de São Paulo, in individual terraria reproducing their natural conditions in tropical forest litter rich in moss and dry leaves (see [26]), at an average temperature of 25°C, and fed on nymphs of captive cockroaches (*Nauphoeta cinerea*).

2.2. Body Proportions and Number of Presacral Vertebrae. The body form of *C. taunayi* (Figure 1(a)) is markedly dorsoventrally flattened and notably laterally keeled, mainly at tail level. The tail length in this species is remarkable, representing between 2.1 and 2.8 times the snout-vent length (SVL). These data were compared with the body proportions of lizards from other gymnophthalmids [11, 23] collected from literature [27–35] or by direct measurement of specimens used in previous studies [12, 14–16]. In all cases, we selected the highest values for the tail length provided by authors. The number of presacral vertebrae (PSV) of *C. taunayi* was counted directly in cleared and stained specimens; for the other species data were taken from literature [23, 33, 35, 36].

2.3. Experimental Protocol. For imaging, animals could move freely inside a 0.6 × 0.4 m opaque plastic box that allowed the introduction of different kinds of 0.3 × 0.4 m horizontal supports within the field of a camera. To mitigate stress, the lizards returned to the terraria between filming sequences. Specimens were videotaped under natural light at 60 frames$*$s^{-1}, with a camera (Panasonic PV-DV910) on a tripod set perpendicularly to the 0.3 × 0.4 m filming field. A 0.01 m scale was a reference for calculation of still enlargements.

As previously used for the study of other gymnophthalmid lizards [12–15] and caecilians [37], specimens inside the box were able to freely pass over one of four different substrates: polyethylene plastic (PLAS), wooden-board (WOOD), glued sand (SAND), and glued gravel (GRAV) (Figure 1(b)). Average roughness (RA) was estimated for five different samples (5.0 mm^2) from each substrate type. For PLAS and WOOD, RA was measured with a profillometer (Kosaka Subcorder 1700 α). For SAND and GRAV, RA was estimated from direct measurement of grains under an optical microscope. So, the four substrates can be rated in an increasing RA spectrum: PLAS = 3.0, WOOD = 9.8, SAND = 546.0, and GRAV = 1560.0. Trials indicate that the animals were unable to move on perspex (RA = 0.2). This slippery substrate (methyl methacrylate) probably represents the limit for motion in such extremely unnatural conditions.

2.4. Data Acquisition. Film sequences showing several cycles of limb and spine motions on each substrate were initially analyzed frame-by-frame using an image processing software selector (SigmaScan, Jandel). Data for graphical analysis were stored directly as computer spread sheets. On frame intervals of 1/60 s, the touchdown of each limb was detected from dorsal view by two simultaneous criteria: start of hand (or foot) immobility and start of body motion. We only selected sequences in a straight-line motion for displacement, discarding those showing sharp change of direction.

(a) (b)

Figure 1: (a) *Colobodactylus taunayi* on litter; (b) experimental substrates with a gradient of increasing roughness average (RA): 1, plastic (RA = 3); 2, wooden board (RA = 9.765); 3, glued sand (RA = 546), and 4, glued gravel (RA = 1560).

Within the continuous phase of a sequence, we retained 18 cycles for each individual, yielding 72 data points for each of the four substrates, a total of 288 cycles for all individuals on all substrates. Since there are elements for two different diagonal pairs, only kinematic variables of the ipsi-lateral limb cycles (right, fore, and hindlimbs) were used.

The following variables were recorded for each stride cycle: ASP = absolute speed observed (measured in $m{*}s^{-1}$), ASL = absolute stride length or the horizontal distance traveled (in m), SFR = stride frequency or the inverse of the period (s^{-1}), STA = stance duration or the duration of foot contact with the substrate during the stride cycle (s), SWI = swing duration or the duration of absence of substrate contact by the foot (s), SDU = stride duration or the period of a stride cycle (s), and DUT = duty factor or the stance duration as a fraction of the stride cycle. To adjust individual size differences, SVL was used to calculate relative measurements, despite Gatesy and Biewener's [38] preference for the use of hip height in this correction. This provides two new variables: RSP = relative speed or the ratio of absolute speed to SVL (in $\text{SVL}{*}s^{-1}$) and RSL = relative stride length or the ratio of absolute stride length to SVL (in SVL units). These relative values allow direct comparisons with other published works.

All movements recorded for the lizards were "voluntary" and correspond to spontaneous locomotion adopted without any artificial stimulus such as treadmills. Note that, in uniform movement, we expected ASP = ASL∗SFR and, consequently, RSP = RSL∗SFR. So, stride length and stride frequency are direct determinants of speed. Also note that SDU = STA + SWI and DUT = STA/SDU, indicating that stance and swing duration are causal components of duty factor.

2.5. Statistical Analyses. Data from all substrates were pooled so as to gauge the performance across a wide range of roughness such as are likely to be encountered by these leaf litter dwelling lizards. Analyses of contrast in locomotor performance on different substrates focused on the kinematic variables with nonparametric Friedman and *a posteriori* Wilcoxon tests (both pairing by individuals) to examine all six pairwise combinations of the four substrates. A Bonferroni correction was used to maintain the experiment wise α-level at 0.05. Both contrast tests were applied with 100,000 randomizations of the data, minimizing intra individual dependence.

Previous findings [14, 15] have indicated that locomotion performance should respond to a roughness gradient across substrates. Substrate roughness varied by four orders of magnitude, justifying the use of their log transformed values. Moreover, log transforming the nine kinematic variables reduced departures from normality. A straight forward expectation was that the log means of such variables would be linearly related to log roughness. We tested whether the response of kinematic variables fitted this model by (i) examining the coefficient of determination of such relationship and (ii) examining the residuals for each substrate in these linear regressions. The experimental design leads to data dependence due to several measurements with the same individuals, resulting in variance underestimation, which may inflate the value of test statistics in comparisons [39]. However, contrasts among substrates are reliable because such effects would be the same in each of them, as the same individuals were the source of data.

The causal relationship between relative speed, relative stride length, and stride frequency in uniform movement (RSP = RSL∗SFR) could be explained by the additive model $\log \text{RSP} = \log a + b_1 * \log \text{RSL} + b_2 * \log \text{SFR} + e$; where $\log a$, b_1, and b_2 are parameters of a multiple linear regression (MLR), and e is the random error. The expected values for a perfect fit ($r^2 = 1$) are $a = b_1 = b_2 = 1$ and $e = 0$. Any significant discrepancy corresponds to nonlinearities in the relationship among the model's variables, that is, an accelerating movement. It should be noted that RSL and SFR are not fully independent variables, as any given value of speed may be attained by several combinations of stride frequency and stride length, and they could even be inversely related. But multicollinearity does not affect the MLR analysis, except for rendering large standard errors for coefficients [40]. Comparison of regression coefficients for the MLR model between pairs of substrates were made by *t* tests (with a Bonferroni correction for multiple contrasts).

Modulation of speed was studied within stride cycles by direct examination of the relationship between stride length and stride frequency. *Z*-transformation of both RSL and SFR was employed so as to render the modulation of each variable with respect to the other interpretable in the same units (standard deviations (SD)).

For the two substrates SAND and GRAV, maximum average values for RSP, RSL, and SFR obtained for *C. taunayi* were compared with those obtained for other gymnophthalmid species, namely, *Vanzosaura rubricauda*, *Procellosaurinus tetradactylus* (see [15]), *Colobosaura modesta,* and *Micrablepharus maximiliani* (see [14]).

3. Results

3.1. The Bauplan of C. taunayi within the Gymnophthalmidae. Body proportions (SVL and tail length) and PSV of some Gymnophthalmidae species show some notable differences. The tail of the Gymnophthalmidae is long in four-footed forms with more than 1.5 times SVL, although species with short tails also occur in the four tribes. The longest tails are found in the Cercosaurini; the Heterodactylini also possesses a slightly longer tail than the great majority of the Gymnophthalmini (Figure 2). In general, in the limbless taxa, long-tail (*Bachia* spp.) or short-tail (*Calyptommatus* spp.) designs are not related to PSV. Overall, tail length generally is in accordance with the limb reduction process that occurs in the Gymnophthalmidae; that is, a more pronounced reduction of the hindlimbs is associated with the long-tail design, and a more pronounced reduction of the fore limbs is associated with the short-tail design. In the Cercosaurini, most species of the genus *Bachia* show a more pronounced reduction of the hindlimbs than of the fore limbs, and the genera *Heterodactylus*, *Colobosaura, Colobodactylus* (Heterodactylini), and *Anotosaura* (Ecpleopini) have been referred to as examples of this *Bachia*-like hindlimb reduction, whereas the Gymnophthalmini *Calyptommatus* spp. shows an inverse process of limb reduction, the fore limbs being absent and possessing vestigial hindlimbs. *Nothobachia* and, to a lesser degree, *Psilophthalmus* (Gymnophthalmini) are also examples of this *Calyptommatus*-like process of limb reduction [11, 28]. This pattern was indicated [36] for *Calyptommatus* in the phylogenetic analysis of the Gymnophthalmidae.

3.2. General Patterns in C. taunayi Locomotion. Individuals of *C. taunayi* placed on the four substrates used gaits between walk and trot, which corresponded to moderately slow speeds as defined by Hildebrand [41]. The walking trot is characterized by a lateral sequence, which is typical of Squamata-quadruped locomotion. The kind of limb coordination does not change and is independent of the substrate used. During displacement under experimental conditions at ground level, whatever the gait adopted there was no lateral bending of the vertebral axis, especially in the tail, which remains stretched throughout the limb movement sequence. Large undulation only appeared at higher speeds. The comparison of progression on four substrates showed (i) a greater rigidity of the body on all substrates at low speed; (ii) a greater flexibility of the trunk and the root of the tail (through large undulations) at higher speeds (>5 SVL$*$s^{-1}) on the substrates having the highest roughness, SAND, and GRAV; (iii) such undulations were rarely seen on smoother substrates, PLAS, and WOOD.

3.3. Contrasts among Substrates. Considering all substrates together, ASP had a minimum of 0.048 m$*$s^{-1} on WOOD and a maximum of 0.578 m$*$s^{-1} on SAND (Table 1). In terms of RSP, minimum and maximum were, respectively, 1.0 SVL$*$s^{-1} on PLAS and 12.6 SVL$*$s^{-1} on SAND. RSP significantly differed among substrates (Friedman $\chi^2_3 = 95.3$; $P < 0.001$), and in *a posteriori* tests, all pairs of substrates significantly differed, except SAND and GRAV.

ASL pooled for all substrates had a minimum of 0.0116 m on WOOD and a maximum of 0.0617 m on GRAV (Table 1). RSL varied between 0.34 SVL on GRAV and 1.26 SVL on SAND (Table 1). The contrast of RSL among substrates was significant (Friedman $\chi^2_3 = 49.1$; $P < 0.001$), and pairwise comparisons resulted in PLAS differing from all, with no significant differences among the other substrates.

SDU on all substrates pooled for all had a minimum of 0.083 s on SAND and a maximum of 0.443 s on PLAS (Table 1). Accordingly, SFR varied across substrates from 2.26 s^{-1} on PLAS to 12.00 s^{-1} on SAND (Table 1). A well-established principle for limbed vertebrate locomotion is that when animals move at a given constant speed, the values of stride frequency are similar at fore and hindlimbs. Both SDU and SFR differed among substrates (resp., Friedman: $\chi^2_3 = 80.1$, $P < 0.001$ and $\chi^2_3 = 86.7$, $P < 0.001$). Pairwise comparisons between substrates for both variables were broadly in agreement: no difference was found between PLAS and WOOD, but all other pairs of substrates showed significant contrasts.

Both STA and SWI were monotonically and positively correlated with SDU (resp., $r_s = 0.875$ and $r_s = 0.652$; $n = 288$ and $P < 0.001$ for both), when all substrates are considered together. Thus, longer stride durations were due to increases in both stance and swing duration. SDU was nonlinearly related to STA (log-transformed variables: $b = 0.727$; $r^2 = 0.795$) and to SWI (log-transformed variables: $b = 0.513$; $r^2 = 0.426$). As the slopes of the above relationships indicate, as the lizards moved more slowly they increased the time the foot was off the ground at a slower rate than the rate of increase for the time the foot was on the ground. Both STA and SWI significantly differed among substrates (resp., Friedman: $\chi^2_3 = 73.0$ and $\chi^2_3 = 23.9$; $P < 0.001$ for both, Table 1). Pairwise comparisons between substrates showed that there were no significant differences in STA between either PLAS and WOOD or SAND and GRAV, but all other contrasts were significant. Only PLAS × WOOD and WOOD × GRAV showed significant difference in SWI.

DUT significantly differed among substrates (Friedman $\chi^2_3 = 24.7$; $P < 0.001$). DUT on PLAS differed from all other substrates, which did not differ among themselves (Table 1). Interestingly, DUT had the smallest coefficient of variation of all variables studied ($\text{CV} = 5.5\%$), indicating

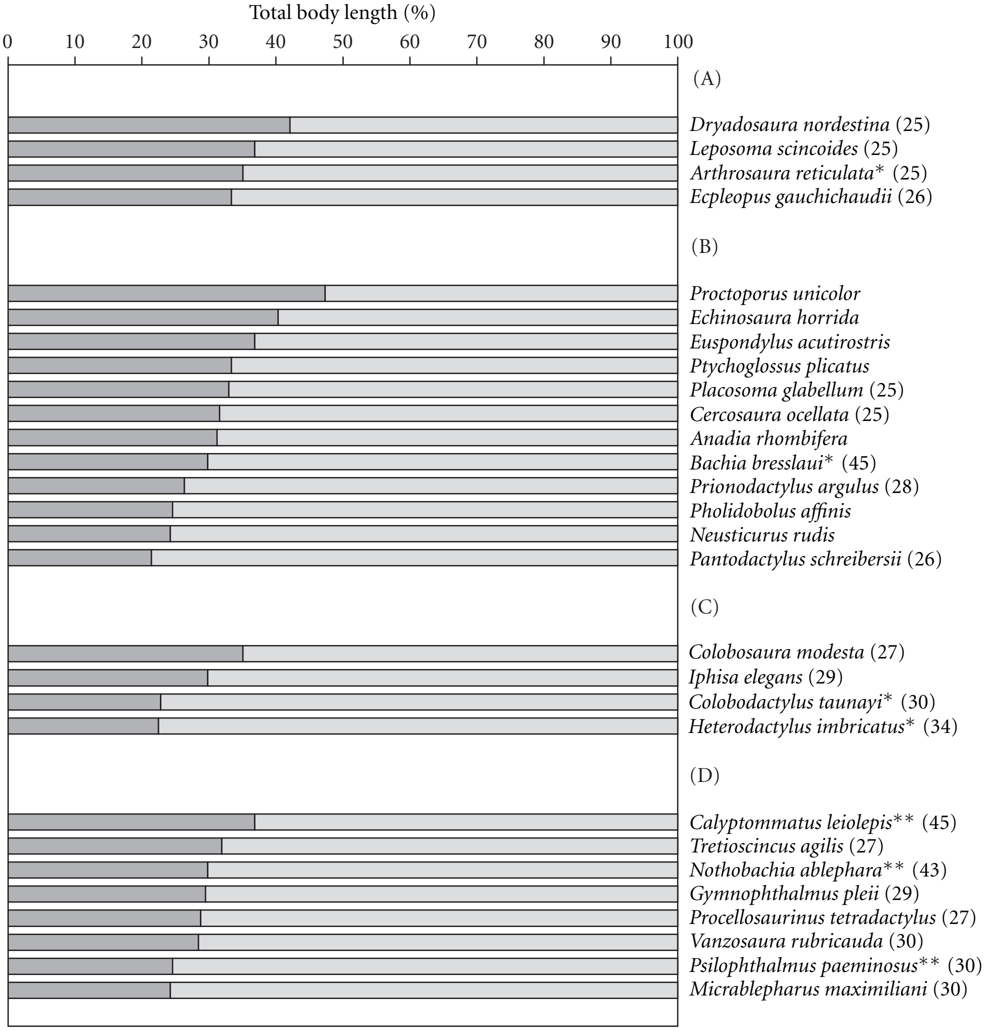

Figure 2: Body proportions of representatives from four Gymnophthalmidae tribes (*sensu* Pellegrino and coauthors [11]). Snout-vent length (dark grey) and tail length (light gray) are shown as relative measures of total body length. When available, the number of presacral vertebrae is shown in parenthesis. (a) Ecpleopini; (b) Cercosaurini; (c) Heterodactylini; (d) Gymnophthalmini. ∗*Bachia*-like limb reduction. ∗∗*Calyptommatus*-like limb reduction.

that, at the voluntary speeds chosen by the lizards, DUT was maintained within a restricted range. Despite the autocorrelation involved, as in the calculation of DUT the denominator is SDU, it is of interest to note that there was a positive, rather than negative, correlation between them ($r_s = 0.132$; $P = 0.025$; $n = 288$); note, however, that as lizards moved slower, DUT tended to increase slightly, but the explained variance is only 1.7%.

In the contrast to the raw variables (Table 1) for PLAS and WOOD, there were differences in SDU components, namely, SWI and DUT, but these were not sufficient to cause a difference between the substrates in either SDU or in SFR. Note that the difference in DUT occurred despite the absence of differences in either STA or SDU. The difference in RSL alone was sufficient to cause a difference in RSP between PLAS and WOOD. The pattern of similarities and differences was the same for the contrasts PLAS × SAND and PLAS × GRAV. The difference found in STA was sufficient to cause a difference in both SDU and SFR and in DUT, between the two pairs of substrates. In addition, there was a difference in ASL and in RSL between these pairs of substrates. Altogether, these differences caused differences in both ASP and in RSP in the two pairs of substrates.

Both WOOD × SAND and WOOD × GRAV formed contrasting pairs for which the pattern of similarities (and dissimilarities) was exactly the same. Both SDU components, namely, STA and SWI, were different between substrates in each case. These differences were responsible for the differences detected in both SDU and SFR and were sufficient to cause a significant difference in RSP. Note, however, that there was also a difference in ASP and in ASL in both contrasts between pairs of substrates. The contrast SAND × GRAV resulted in the lowest number of differences between substrates: only SDU and SWI diverged. The latter differences were insufficient to cause a difference in SFR. Moreover, as there was no difference in RSL, no difference

Table 1: Kinematic variables recorded for *Colobodactylus taunayi* on different substrates. Mean ± SD, range in parenthesis, and $n = 72$ for each cell. Relative measures result from raw values divided by individual snout-vent length (SVL). Friedman tests indicated significant differences ($P < 0.001$) among substrates for all variables. After Bonferroni correction, significant Wilcoxon pairwise contrasts among substrates for each variable were shown as different letters (a, b, and c).

Variable	Substrate				
	PLAS	WOOD	SAND	GRAV	Total
ASP	12.5 ± 5.10^{a} (5.1–29.3)	13.0 ± 4.11^{a} (4.8–23.3)	19.2 ± 10.77^{b} (6.6–57.8)	18.0 ± 8.27^{b} (5.9–40.0)	15.7 ± 8.06 (4.8–57.8)
ASL	2.96 ± 0.816^{a} (1.81–4.89)	3.09 ± 0.914^{a} (1.16–5.44)	3.60 ± 0.951^{b} (2.20–5.78)	3.39 ± 1.064^{b} (1.78–6.17)	3.26 ± 0.969 (1.16–6.17)
RSP	2.7 ± 1.15^{a} (1.0–6.4)	2.9 ± 0.92^{b} (1.2–4.6)	4.0 ± 2.31^{c} (1.4–12.6)	3.8 ± 1.76^{c} (1.1–7.8)	3.3 ± 1.72 (1.0–12.6)
RSL	0.63 ± 0.193^{a} (0.37–1.06)	0.70 ± 0.144^{b} (0.41–1.07)	0.75 ± 0.207^{b} (0.43–1.26)	0.71 ± 0.209^{b} (0.34–1.21)	0.70 ± 0.195 (0.34–1.26)
SFR	4.16 ± 0.830^{a} (2.26–6.00)	3.95 ± 0.852^{a} (2.5–6.00)	5.03 ± 1.712^{b} (2.73–12.00)	5.20 ± 1.401^{b} (2.86–8.57)	4.58 ± 1.361 (2.26–12.00)
STA	0.172 ± 0.0409^{a} (0.113–0.283)	0.170 ± 0.0502^{a} (0.083–0.287)	0.134 ± 0.0463^{b} (0.033–0.283)	0.132 ± 0.0433^{b} (0.067–0.250)	0.152 ± 0.0489 (0.033–0.287)
SWI	0.079 ± 0.0265^{a} (0.050–0.160)	0.093 ± 0.0244^{b} (0.050–0.133)	0.085 ± 0.0367^{a} (0.033–0.217)	0.074 ± 0.0258^{a} (0.033–0.150)	0.083 ± 0.0295 (0.033–0.217)
SDU	0.251 ± 0.0578^{a} (0.167–0.443)	0.263 ± 0.0558^{a} (0.167–0.400)	0.219 ± 0.0647^{b} (0.083–0.367)	0.206 ± 0.0555^{c} (0.117–0.350)	0.235 ± 0.0627 (0.083–0.443)
DUT	0.688 ± 0.0650^{a} (0.500–0.813)	0.640 ± 0.0910^{b} (0.385–0.851)	0.614 ± 0.1070^{b} (0.333–0.850)	0.636 ± 0.0912^{b} (0.462–0.857)	0.644 ± 0.0934 (0.333–0.857)

Variables are ASP: absolute speed ($\times 10^{-2}$ m $*$ s^{-1}), ASL: absolute stride length ($\times 10^{-2}$ m), RSP: relative speed (SVL $*$ s^{-1}), RSL: relative stride length (SVL), SFR: stride frequency (s^{-1}), STA: stance duration (s), SWI: swing duration (s), SDU: stride duration (s), and DUT: duty factor. Substrates are PLAS: polyethylene plastic, WOOD: wooden board, SAND: glued sand, and GRAV: glued gravel.

in RSP was found. The same applies to ASP. When only the kinematic variables directly responsible for determining speed, namely, RSL and SFR were considered, an interesting pattern emerged. Thus, the only difference found between PLAS and WOOD was in RSL. The contrasts PLAS × SAND and PLAS × GRAV yielded differences in both RSL and SFR. The contrasts WOOD × SAND and WOOD × GRAV resulted in a difference only in SFR. Finally, no differences in any of the direct determinants of speed were found between SAND and GRAV.

3.4. Responses of Kinematic Variables to a Roughness Gradient. For all nine variables, the log-transformed data for all substrates together were significantly correlated with log roughness ($P < 0.001$; $n = 288$). However, the log mean of such variables was significantly correlated to log roughness only for ASP, RSP, STA, and SDU (Table 2). The small magnitude of some residuals in Table 2 indicated that kinematic variables, for certain substrates, responded accordingly to the roughness gradient, even when the linear regression as a whole was not significant. Interestingly, there was a tendency for very small residuals to occur concurrently as groups of two substrates. Thus, PLAS-WOOD formed a group for RSP and ASL, while SAND-GRAV formed another group for SFR and SDU (see Table 2). Hence, there were kinematic variables that responded closely to the gradient in roughness, whilst other variables did not, indicating overall a heterogeneity in response patterns. In addition, for certain kinematic variables two types of responses, either closely following the gradient or deviating from the gradient, could be shown to correspond to two groups of substrates.

3.5. Determination of Speed. When pooling all substrates ($n = 288$), speed increased nonlinearly with both increasing stride length and stride frequency (Figures 3(a) and 3(b)), as the relationships between (log transformed) RSP and RSL ($b = 1.446$, 95% (confidence interval) CI = 1.349–1.543) and between RSP and SFR ($b = 1.387$, CI = 1.270–1.504) resulted in slopes that differed significantly from unity. Hence, lizards increased their speed by simultaneously increased stride length and stride frequency. In addition, RSL and SFR were significantly correlated ($r = 0.465$; $P < 0.001$).

The combined action of stride length and stride frequency explained from 87.8% (WOOD) to 99.8% (GRAV) of the observed variation in speed (Table 3), thus supporting the assumption of constant speed for the empirical data on stride cycles. However, the *observed speed* (the recorded RSP values) was differed from the *theoretical speed* (product of recorded RSL and SFR values), as can be gauged by the coefficients of determination of the linear regression (r^2) between them on each substrate (PLAS = 0.972, WOOD = 0.779, SAND = 0.992, and GRAV = 0.998; all highly significant). The slopes for these relationships were as follows (b, with its confidence intervals in parenthesis): PLAS = 0.905 (0.869–0.941), WOOD = 0.908 (0.794–0.923), SAND = 1.002 (0.981–1.024), and GRAV = 1.005 (0.994–1.016), which

Table 2: Results of linear regression between the logarithm of means of nine kinematic variables and the logarithm of roughness for four substrates (codes as in Table 1). Coefficients of determination r^2 and their associated probabilities P are presented. Sample size is $n = 4$ for each linear regression. Absolute residuals of these linear regressions for each substrate are also shown, with small values (<0.01) in bold.

Variable	r^2	P	Absolute residuals			
			PLAS	WOOD	SAND	GRAV
ASP	0.926	0.0380	**0.0060**	0.0144	0.0336	0.0252
ASL	0.822	0.0930	**0.0053**	**0.0023**	0.0207	0.0177
RSP	0.936	0.0330	**0.0024**	**0.0032**	0.0295	0.0240
RSL	0.553	0.2560	0.0199	0.0209	0.0175	0.0185
SFR	0.901	0.0510	0.0194	0.0250	**0.0054**	**0.0003**
STA	0.983	0.0080	**0.0051**	**0.0080**	**0.0084**	**0.0055**
SWI	0.173	0.5840	0.0382	0.0424	0.0228	0.0269
SDU	0.904	0.0490	0.0160	0.0190	**0.0032**	**0.0063**
DUT	0.553	0.2570	0.0132	0.0142	**0.0099**	0.0109

Table 3: Results of multiple linear regression of log-transformed relative speed (RSP) versus log-transformed relative stride length (RSL) and stride frequency (SFR) for each substrate (codes as in Table 1). The coefficients of determination (r^2) were shown, as well as the intercepts (a) and the partial regression coefficients (b_1 for RSL, b_2 for SFR), with respective t tests and P values. β is standardized partial regression coefficients for each variable. Sample size for each substrate is $n = 72$. Only for WOOD the partial regression coefficients for both RSL and SFR differed significantly in pairwise comparisons among substrates.

	Substrate	PLAS	WOOD	SAND	GRAV
Fit	r^2	0.972	0.878	0.992	0.998
Intercept	a	0.018	0.378	0.001	0.001
	SE	0.044	0.047	0.017	0.008
	t	0.42	7.95	0.08	0.18
	P	0.6770	0.0005	0.9380	0.8570
RSL	b_1	0.892	1.322	1.000	1.008
	SE	0.042	0.069	0.024	0.009
	t	21.31	19.14	41.28	111.65
	P	0.0005	0.0005	0.0005	0.0005
	β_1	0.615	0.826	0.525	0.643
SFR	b_2	0.924	0.460	1.004	1.002
	SE	0.060	0.073	0.021	0.010
	t	15.39	6.33	47.65	101.04
	P	0.0005	0.0005	0.0005	0.0005
	β_2	0.444	0.273	0.606	0.581

all together indicated a slight underestimation of the actual relative speed observed. Deviation from the constant speed model indicated the occurrence of acceleration in some stride cycles.

In the MLR framework, a perfect fit of the empirical data to the constant speed model would result in partial slopes equalling unity, and this occurred on SAND and GRAV, but not on PLAS (CI $b_1 = 0.809$–0.976, $b_2 = 0.804$–1.044) and WOOD (CI $b_1 = 1.184$–1.460, $b_2 = 0.315$–0.605) (Table 3). Also, it would be expected that the intercept (log a) should be zero. A null intercept was found on all substrates, except WOOD (CI log $a = 0.283$–0.472), where the fit of empirical data to the constant speed model was the poorest (Table 3).

Increases in both stride length and stride frequency resulting in nonlinear increases in speed were corroborated by the sum of partial regression coefficients, which were greater than unity on all substrates, indicating increasing returns to scale (Table 3). It should be noted that the sum of β values (the standardized slopes, which are independent of measurement units) tended to increase according to the gradient in roughness (β values versus log roughness, $r = 0.9123$, $P = 0.045$, and $n = 4$). To evaluate the relative contribution of each independent variable in changing the dependent variable by one unit, a rough comparison of β values indicates that, on WOOD, RSL has a much higher effect on RSP than SFR (Table 3).

For individuals on all four substrates, with increasing speed, duty factor varied markedly (Figure 3(f)). This variability was highest on WOOD and PLAS, whereas on the others, it decreased at the highest speeds. However, generally, with increasing speed the animals decreased duty factor values. For example, on SAND, a DUT value of 0.86 corresponds to a relative speed of $0.017\ \text{m}*\text{s}^{-1}$, whereas that of 0.33 is for a relative speed of $0.126\ \text{m}*\text{s}^{-1}$.

The modulation of speed on each substrate was made through simultaneous increases in both stride frequency and relative stride length, as gauged by the magnitude of the coefficient of determination of the relationship between RSL and SFR (Table 4). When all substrates were pooled, SFR increased at a rate that was 0.471 SD units of the rate of increase for RSL, showing that speed modulation within the stride cycles was mainly through an increase in the latter. In each substrate, an increase in one SD unit led to increases in SFR (also in SD units) of 0.496 (PLAS), 0.216 (WOOD), 0.696 (SAND), and 0.332 (GRAV).

3.6. Comparison with Other Gymnophthalmid Lizards. The comparison of the maximum speed achieved by *C. taunayi* with those of some other gymnophthalmids on rough substrates, as expressed by the mean of the maximum speed reached by each of the studied individuals of each species, showed that *C. taunayi* was faster than the phylogenetically

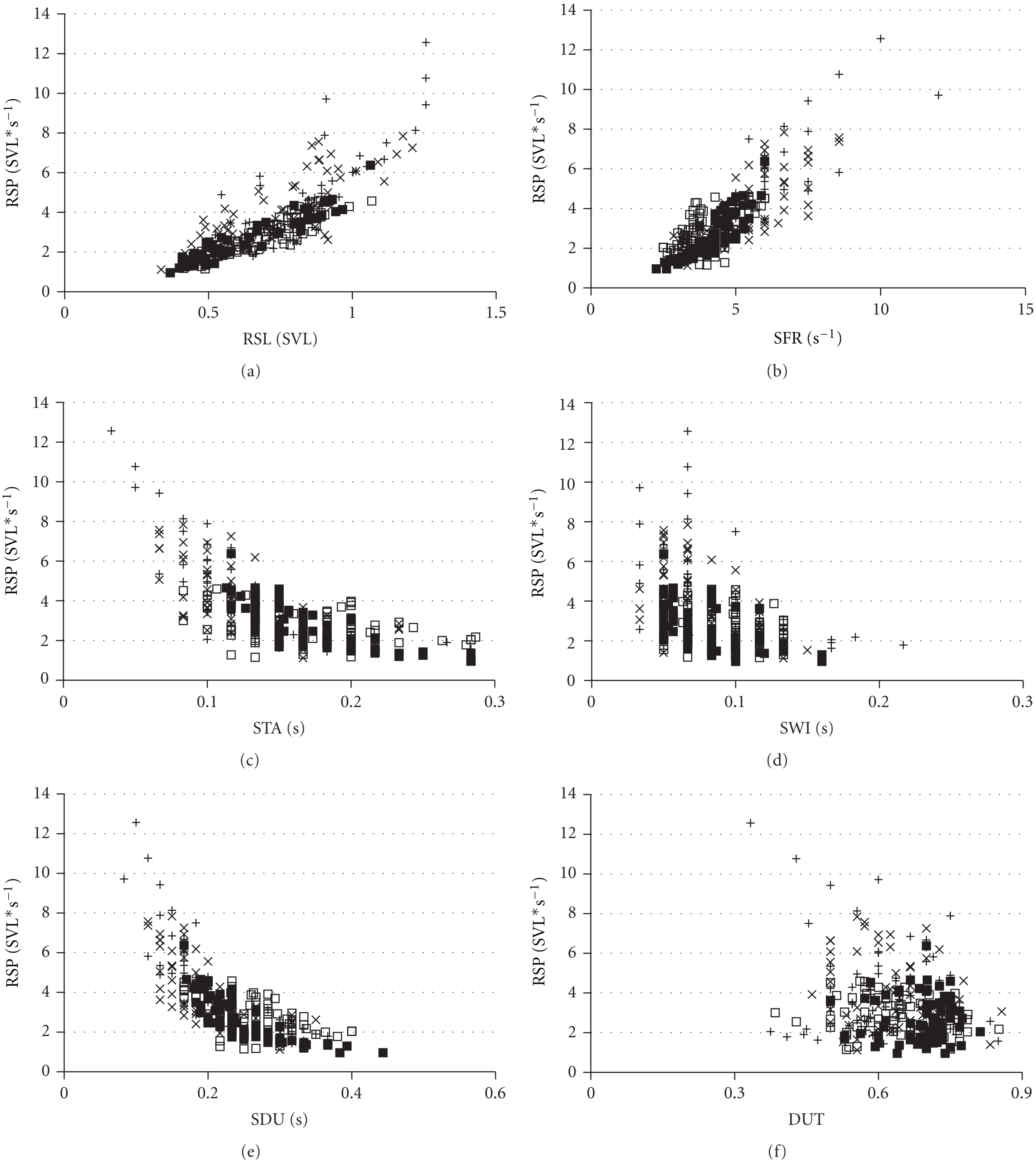

FIGURE 3: Relative speed plotted against other kinematic parameters of *C. taunayi* on four substrate types with increasing roughness level: polyethylene plastic (PLAS, black squares), wooden board (WOOD, white squares), glued sand (SAND, "+"), and glued gravel (GRAV, "×"). Relative speed (RSP) is measured in snout-vent length units per second. (a) Relative stride length (RSL, in SVL units), (b) stride frequency (SFR, in s^{-1}), (c) stance duration (STA, in s), (d) swing duration (SWI, in s), (e) stride duration (SDU, in s), and (f) duty factor (DUT). All six Spearman correlations are highly significant ($P < 0.01$).

close species *Procellosaurinus tetradactylus*, a sand specialist (Figure 4(a)). However, it was slower than more generalist species such as *Micrablepharus maximiliani* and *Vanzosaura rubricauda*, especially on sand (Figure 4(a)). The fast lizard *M. maximiliani* even has the capacity of hopping at a relative speed of 22.70 $\mathrm{SVL} * s^{-1}$, and at the initial phase of such a hop, the frequency of limb movements is always superior to 16 s^{-1}.

The mean value for the maximum stride frequency was rather low in comparison to that of most other species

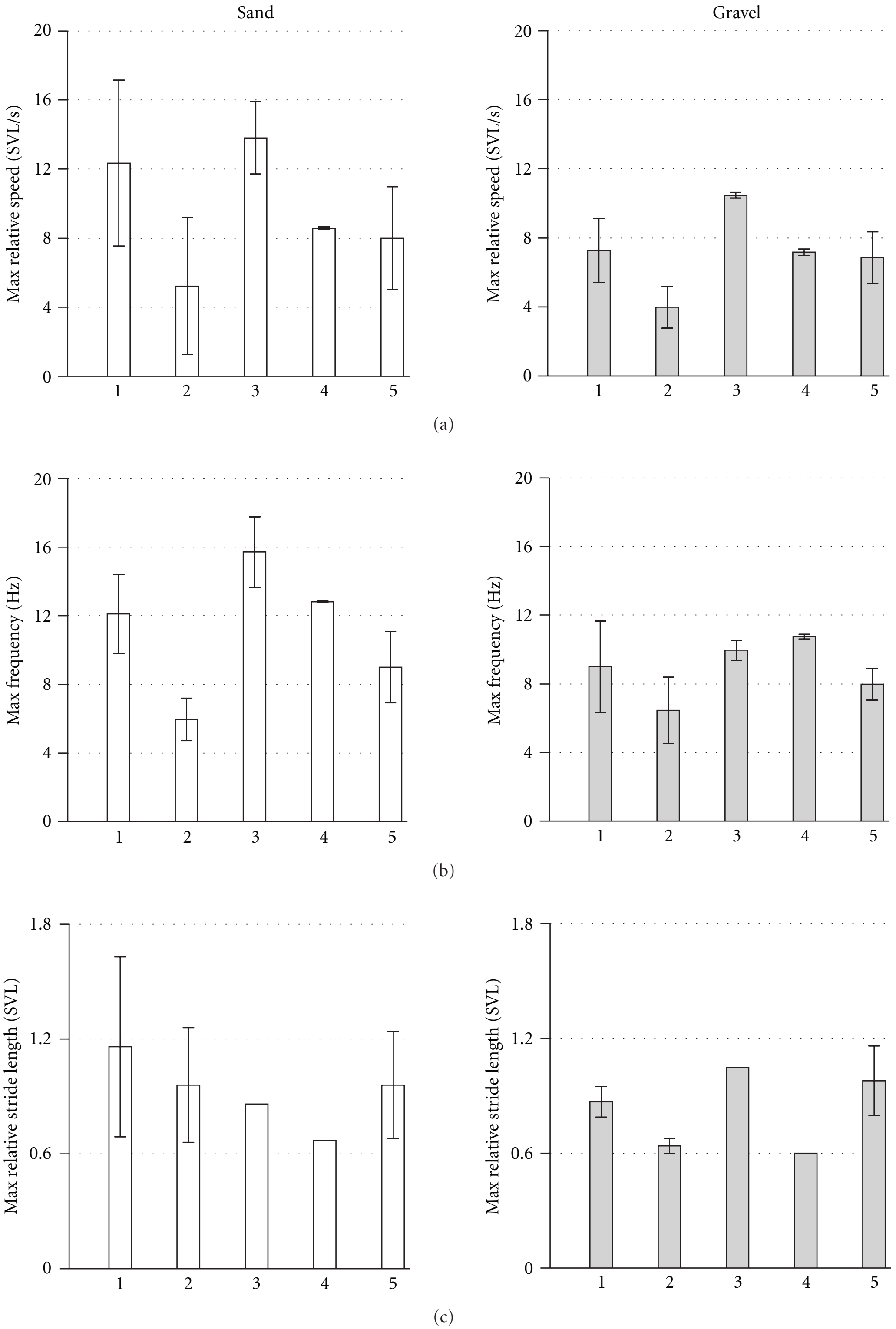

Figure 4: Comparison of the (a) maximal relative speed, (b) maximal stride frequency, and (c) maximal relative stride length of five Gymnophthalmidae species running on sand and gravel. 1 = *Vanzosaura rubricauda* ($n = 16$), 2 = *Procellosaurinus tetradactylus* ($n = 16$), 3 = *Micrablepharus maximiliani* ($n = 4$), 4 = *Colobosaura modesta* ($n = 4$), and 5 = *Colobodactylus taunayi* ($n = 16$). These are average maximal values reach by studied individuals in each species. Bars are SD. Data other than for species 5 are from Renous and coauthors [15] (1-2) and Renous and coauthors [14] (3-4).

Table 4: Results of linear regressions through the origin (zero intercept) of both Z-transformed values of stride frequency (SFR) and relative stride length (RSL). The angular coefficients (b), their respective standard errors (SE), and P values are shown with the coefficients of determination (r^2) and the Spearman correlation coefficients (r_s). Sample size is $n = 72$ for each substrate and $n = 288$ for all substrates pooled. Only WOOD × SAND ($t = 2.1$, $P < 0.05$) resulted in a significant pairwise contrast among slopes for different substrates.

Substrate	PLAS	WOOD	SAND	GRAV	All
b	0.496	0.216	0.696	0.332	0.471
SE	0.050	0.121	0.113	0.118	0.052
P	0.0005	0.0790	0.0005	0.0070	0.0005
r^2	0.586	0.043	0.347	0.100	0.222
r_s	0.747	0.289	0.564	0.329	0.457

of gymnophthalmid lizards, except for *P. tetradactylus* (Figure 4(b)). In contrast, mean value for the maximum relative stride length of *C. taunayi* was rather similar to the data obtained for the fast *M. maximiliani* on gravel and *P. tetradactylus* on sand (Figure 4(c)). Indeed, on gravel, this value was the highest for this group of lizards, underlining the importance of the stride length in the locomotion of *C. taunayi*, a species in which the SVL is rather similar to that of *V. rubricauda* and *P. tetradactylus*, and four times shorter than that of *Colobosaura modesta*, an allied heterodactylini species.

4. Discussion

4.1. Bauplan Constraints to Locomotion. *Colobodactylus taunayi* belongs to the assemblage *Colobodactylus, Heterodactylus* that differs from the remaining Heterodactylini by their more elongated body and degree of limb reduction [23], and it is included in the *Bachia*-like limb reduction group [11]. It moves in the superficial leaf litter using a lateral walking trot without the aid of body undulation. Considering that the trot is the basic form for quadrupedal fast movement in lizards [42], it is notable that *C. taunayi* is also able to adopt this gait for relatively low speeds.

In our experimental conditions, this species scarcely used body undulation, with the trunk curving little and the tail remaining rather rigid, especially at low velocities. The contribution made by girdle rotations to progress [17] was insignificant, and likewise, that of the vertebral system to four-footed movement also appeared to be largely negligible when compared with other forms [43]. Rather, the limbs became the main propellers; the stride length adopted by this heterodactylini lizard on the smoothest substrates should be attributed to the limb action rather than to any body undulation, since in straight-line displacements *C. taunayi* did not use axial undulations. This option can constitute a loss of efficiency, and the maximum extension of the limbs constitutes a limit for the stride length value (approximately 1 SVL). The great variability of the swing duration, which necessarily forms part of the stride duration and also influences the value of the duty factor, is probably due to a consequence of the propulsion that derives mainly from the limbs acting in conjunction with a relatively rigid trunk. Inversely, on the rough substrates, some mobility of the trunk evinced, as a weak undulation could amplify the stride length generated by the limbs. This longer stride length, which is a characteristic feature found in all Gymnophthalmidae studied, can effectively contribute to increase the speed.

4.2. Variation in the Components of the Stride Cycle. A number of aspects of our results may provide some insights into the locomotion process used by *C. taunayi*: (i) the highest velocities were only found when individuals moved on sand and gravel, substrates that present a marked degree of roughness in the experimental conditions, whereas lower velocities characterized the progression on smoother substrates, plastic, and wooden board; (ii) the maximum values reached by the relative stride length and the highest stride frequencies were obtained on sand and gravel; (iii) in contrast, the high speeds on sand and gravel were obtained by marked increase of the stride frequency and more moderate increase of a long stride length; (iv) in fact, this high value of the stride length on the substrates having a high degree of roughness was reached by all individuals. Facilitation provided by the axial muscular-skeletal system could explain the difference observed for the relative stride length on the rougher substrates.

There is a general biomechanical expectation that short limbs should limit stride length, and hence short-limbed lizards should have short stride lengths. Irschick and Jayne's data [44] on five lizard species showed a range from 2.32 to 4.20 BL (*mean stride lengths* by *mean total body lengths*, with BL obtained by adding average SVL to tail lengths). *Colobodactylus taunayi* had an average RSL of 0.70 SVL, ranged from 0.34 to 1.26 SVL (so, with tail excluded). The maxima relative stride lengths of *V. rubricauda* and *Procellosaurinus tetradactylus* were, respectively, 0.99 and 0.67 BL [15]. Thus, gymnophthalmids show short relative stride lengths as compared to the five species studied by Irschick and Jayne [44].

Mean stride frequency of these species [44] ranged from 11.23 to 14.50 s^{-1}; maxima were not reported. Mean stride frequency of *Hemidactylus garnotii*, which has relatively short limbs, was 13.00 s^{-1} [45]. The maximum frequency of the gymnophthalmid species *P. tetradactylus* and *V. rubricauda*, as means of the four largest frequencies attained by four individuals of each species [15], were, respectively, 8.92 and 14.41 s^{-1}. The maxima in stride frequency for one individual each of *C. modesta* and *M. maximiliani* were, respectively, 12.50 and 16.67 s^{-1}. Therefore, apparently, both short-limbed and long-limbed species can show relatively high stride frequencies. However, *Iguana iguana* has a low maximum stride frequency of 1.4 s^{-1}, *sensu* Brinkman [46], and so does *Varanus exanthematicus*, 1.8 s^{-1}, *sensu* Jayne and coauthors [47].

Alexander [48] proposed a simple rule for distinguishing gaits based on duty factor values; namely, duty factors below 50% refer to running gaits, and those above 50% refer to walking gaits. Hildebrand's classification [31] utilizes, in addition to duty factor, the relative limb phase, and an even more complex determination of gaits relies on the gait mechanics (e.g., [49]). The discussion that follows focuses exclusively on duty factor because there are more comparative data for this kinematic variable than for gait mechanics. The average duty factor for the 18 lizard species, studied by McElroy and coauthors [49], independently of gait, is 53.61% (SD = 13.05; $n = 23$). Species using walking gait mechanics 65.14% (SD = 8.82; $n = 7$) and running gait mechanics 48.56% (SD = 11.37; $n = 18$) differed statistically ($Z = 3.012$; $P = 0.003$; $n_1 = 7$; $n_2 = 18$) in the expected direction; that is, running gaits showed a lower duty factor. Indeed there was a negative correlation between absolute speed and duty factor ($r_s = -0.859$; $P = 0.0005$; $n = 22$) for these species.

Duty factor in *C. taunayi* ranged from 33.33% to 85.71% and had an average of 64.36% (SD = 0.0935; $n = 288$). Mean duty factors for the five lizard species studied by Irschick and Jayne [44] ranged from 17% to 35%, and these low means corresponded to the high mean absolute speeds of these species, as a negative correlation was also found between these variables ($r_s = -0.900$; $P = 0.037$; $n = 5$). Mean duty factor for *Hemidactylus garnotii* was 43% [45].

Thus, short-limbed lizards, such as the Gymnophthalmidae, seem to have (i) relatively short relative stride lengths, (ii) mean stride frequencies as high as those of some long-limbed lizard species, (iii) much lower average and maximum speeds than long-limbed lizards, and (iv) relatively high duty factors. However, these are only general trends, which should be subjected to a more rigorous comparative analysis due to the procedural differences in data collection by different authors.

Finally, depending on the kind of substrate encountered, *C. taunayi* can use different methods to progress. On rough substrates (sand and gravel), it can adopt the general mechanism found in most lizards, that of combining the action of a horizontal undulation of axial muscular skeletal system with movement of the limbs. This mechanical association results in a long stride length which only needs a slight increase to furnish higher speeds. Conversely, on the smooth substrates (plastic and wood), *C. taunayi* can maintain its axial system rigid and only use the limbs to progress. This option, which also requires an adjustment of the stride frequency, may have an important energetic cost; it is also likely to be uncomfortable and is probably avoided in natural conditions. The adoption of this particular locomotion strategy on smooth substrates and the use of a classic lizard strategy of locomotion on sand and gravel may indicate that the species is better adapted to substrates with a high roughness coefficient. This agrees with the ecological context, since *C. taunayi* is classified as a habitat specialist living in superficial leaf litter of the Neotropical rainforests where it is semifossorial. The strategy of such ombrophilous animals, when avoiding light, is to hide under dead leaves, a dense, and heterogeneous environment composed of many rough elements. Given the well-generalized habitat in the gymnophthalmid lizards, the long-tail pattern shown by *C. taunayi* does not seem to be directly related to its habitat. However, the use of the basic locomotion of lizards only on sand and gravel and its modification (by elimination of the mechanical action of the body undulation) on smooth surfaces furnish kinematics elements that could rather characterize a litter specialist.

4.3. Responses of Kinematic Variables to a Gradient of Roughness.

Surface texture has a multidimensional nature which comprises roughness (the average distance between peaks and valleys, that is, vertical deviations of a real surface from its ideal form), waviness (the repeating irregularities with spacing greater than roughness), lay (the overall pattern created by the production process), and flaw (any unintentional surface irregularity that may be random or repeating, such as cracks and inclusions). It should thus be kept in mind that roughness can only partially describe the complexity of the surface texture of the substrates used, and lizard locomotion could conceivably respond to unmeasured aspects of the gradient.

Previous studies of other short-limbed and elongated gymnophthalmid lizard species have shown variation in locomotor performance on different substrates including perspex, plastic, cardboard, sand, and gravel [14, 15]. The substrates used in the present paper, namely, polyethylene plastic, wood, sand, and gravel formed a nonlinear gradient in roughness which encompassed four orders of magnitude (10^0–10^3). Both polyethylene plastic and wood were machine finished, the former according to industrial standards. But neither the glued sand nor the glued gravel was subjected to such processes. As roughness is only one of the components of surface texture; it is probable that the experimental substrates differed also in these additional properties, which comprised the combination of all imperfections present.

The total surface area of the sand and gravel substrates is larger than that of the other two substrates due to the higher geometrical complexity, and the probability that cracks and other discontinuities were larger in wood than in the polyethylene substrate, which has the most homogeneous surface of them all. Although such substrate differences probably surpassed the simple differences in roughness, these additional characteristics were not measured. The remarkable differences between wood and the other substrates shown for the relative contributions of both stride frequency and relative stride length were due to accelerations (positive or not) being more common on wood, and thus yielding discrepancies between the two speed estimates, that is, the independent estimate that based on the within stride cycle data.

Colobodactylus taunayi may use sandy substrates, as well as leaf litter and hence be exposed to a wide range of substrate properties. The leaf litter is a very heterogeneous substrate in terms of the surface textures and their spatial orientation, and sand presents peculiar sliding properties associated with locomotion. Given the diversity of substrates that the species is exposed to, one might expect it to be a “jack of all trades” regarding locomotor performance, rather than a specialist in one of the substrates to which it is normally exposed. The experimental gradient in roughness that would thus likely encompass the range of substrates *C. taunayi* would encounter during its ontogeny. One would expect the plantar surface of the feet and of the digits of *C. taunayi* to have suitable coefficients of friction with the type of surfaces commonly encountered by individuals, and hence it is noteworthy that *C. taunayi* is unable to progress forward on perspex, while other gymnophthalmids are able to do so [14, 15]. This locomotor limitation in *C. taunayi* indicates a lower threshold value of roughness below which propulsive friction does not occur; that is, there is a constraint in performance imposed by very low friction substrates, although, obviously, none of the cited gymnophthalmids are exposed to such low friction coefficients in their natural habitats.

When lizards are made to move on different substrates one wishes to associate variation in the substrate properties to variation in locomotor performance, ideally to identify which substrate properties induce variation in kinematic variables, and more specifically, the direction and magnitude of the variation induced. In other words, one wishes to associate substrate properties, such as roughness, with specific ways in which lizards apply forces to the substrate to generate forward thrust, and how different substrates influence the final performance, as measured by speed.

Based on our previous analyses of other gymnophthalmids [14, 15] we predicted that the locomotor performance should increase according to a gradient in friction, here roughly approximated by the gradient in roughness. Overall, these predictions have received support in the present study; namely, (i) in the MLR analysis there was a positive correlation between the sum of the partial slopes of RSL and SFR and the logarithm of roughness, thus showing that modulation of speed responded to the gradient, and the sums of slopes were greater than unity revealing increasing returns to scale according to increasing roughness; (ii) the pattern of pairwise differences between substrates for the univariate analysis of each kinematic variable expected if they responded to the rank order in roughness; (iii) some kinematic variables had log means that correlated significantly with log roughness; (iv) even when a kinematic variable did not statistically fit the model log *means* × log *roughness*, some substrates fitted the expectation well, judged by the small magnitude of their residuals in the linear fit.

However, the analyses of locomotor performance under the gradient in roughness also uncovered some important deviations: (i) some kinematic variables did not show the expected pattern of pairwise differences for the gradient, (ii) some kinematic variables simply did not show a significant correlation between log means and log roughness, and (iii) in those cases where the kinematic variable did not fit the model either all substrates significantly deviated from its expectation or at least two substrates did so. These results raise the following additional questions: why did certain kinematic variables behave according to this model whilst others did not? And why did some other variables, and for certain substrates, deviate from the model and others did not?

In order to explain the heterogeneity of responses shown by the kinematic variables and the additional heterogeneity between substrates in the response of a given kinematic variable, that is, an interaction between kinematic response and substrate, we need a model which considers the relationship between locomotor performance and roughness. Animals have biomechanical limits imposed by morphology, physiology, and biochemistry. Hence it can be expected that below a lower threshold for some substrate properties—such as roughness and friction—performance will be nil, and at an upper threshold for such substrate properties, performance will be maximized (and thus cannot increase), for instance, if adhesion is optimal. Surfaces have friction values that impose such lower and upper thresholds for locomotor performances (the lower threshold in friction for *C. taunayi* on perspex has been already mentioned). Furthermore, there will be a range of values for the substrate property in which performance is directly correlated with the substrate property values. This simple model can be slightly modified to account for differential performances of different kinematic variables in the same substrate by stating that their upper and lower thresholds do differ. In addition, the slopes of the responses of kinematic variables to the same range of variation of the substrate property may themselves be different.

When the log means of kinematic variables correlated significantly with log roughness, we take that to mean that performance was in the region of a linear response (between thresholds), and a parsimonious explanation as to why a given kinematic variable did not significantly fit the model log *means* × log *roughness* on all substrates, but only some of them would be that the performance for such a variable and for a given substrate was either below the lower or above the upper thresholds of response. In addition, one cannot rule out that deviation from such log-log model for particular kinematic variables, and for particular combinations of kinematic variables and substrates, could be due to influence of additional, nonidentified, and properties of the substrates besides roughness. Also, it should be noted that a broader range of values for relative speed, stance duration, and swing duration, as well as a narrower range of values for duty factor, were recorded only on sand and gravel. The absence of a range of values in different orders of magnitude on certain substrates—namely, plastic and wood—might have also influenced detected patterns.

4.4. Determination of Speed. The spontaneous absolute speeds recorded for *C. taunayi* ranged from 0.05 to $0.58\,\mathrm{m}{*}\mathrm{s}^{-1}$. McElroy and coauthors [49] reported the average speed for 18 lizard species. Pooling the data provided by these authors for their lizard species for both running and walking, the average speeds ranged from 0.16 to $1.84\,\mathrm{m}{*}\mathrm{s}^{-1}$. The average speed of *C. taunayi* ($0.16\,\mathrm{m}{*}\mathrm{s}^{-1}$) was the same as that of *Tracheloptychus petersi* [49]. Van Damme and coauthors [50] provided absolute speeds for 11 lizard species which ranged from 1.25 to $3.20\,\mathrm{m}{*}\mathrm{s}^{-1}$, without mentioning total body lengths (BL) of the specimens. But, as recorded by Irschick and Jayne [44], other lizards with relatively longer limbs than *C. taunayi* attained much higher average speeds, For example, *Callisaurus draconoides*: $4.00\,\mathrm{m}{*}\mathrm{s}^{-1}$, *Uma scoparia*: $3.90\,\mathrm{m}{*}\mathrm{s}^{-1}$, and *Phrynosoma platyrhinos*: $2.10\,\mathrm{m}{*}\mathrm{s}^{-1}$. Thus, as already mentioned by Renous and coauthors [15], gymnophthalmids seem to achieve low average spontaneous speeds. Note, however, that Irschick and Jayne [44] data were obtained on treadmills, whilst. McElroy and coauthors [49] allowed individuals to run on a level track, as with gymnophthalmids ([14, 15] present paper).

Maximum or sprinting speeds was not measured for *C. taunayi*. The *spontaneous* maximum speed recorded was $0.58\,\mathrm{m}{*}\mathrm{s}^{-1}$. *Hemidactylus garnotii*, with a similar total body length and relatively short limbs, had maximum speed of $0.84\,\mathrm{m}{*}\mathrm{s}^{-1}$ [51]. Another gecko, *Coleonyx variegatus*, reached $5.03\,\mathrm{m}{*}\mathrm{s}^{-1}$, and a skink with short limbs, *Eumeces skiltonianus*, reached $0.75\,\mathrm{m}{*}\mathrm{s}^{-1}$[52]. The lizards studied by McElroy and coauthors [49] had maximum speeds ranging from 0.20 to $3.57\,\mathrm{m}{*}\mathrm{s}^{-1}$, but these included both walking and running mechanics. The maximum speeds for species using walking mechanics ranged from 0.20 to $1.23\,\mathrm{m}{*}\mathrm{s}^{-1}$, while those utilizing running mechanics ranged from 0.28 to $3.57\,\mathrm{m}{*}\mathrm{s}^{-1}$. Vanhooydonck and coauthors [53] reported maximum speeds for 11 lizard species that ranged from 1.09 to $3.34\,\mathrm{m}{*}\mathrm{s}^{-1}$, but without mentioning total body lengths of the specimens. Among the Gymnophthalmidae, the maximum absolute speed recorded for *Micrablepharus maximiliani* was $0.41\,\mathrm{m}{*}\mathrm{s}^{-1}$, and that for *Colobosaura modesta* was $0.50\,\mathrm{m}{*}\mathrm{s}^{-1}$ (see Renous and coauthors [14]).

Maximum relative speeds (the means of the four largest speeds of each individual studied, on all substrates) recorded for *V. rubricauda* and *P. tetradactylus* were, respectively, 9.91 and $4.37\,\mathrm{BL}{*}\mathrm{s}^{-1}$ [15], whilst for *C. taunayi* it was $8.21\,\mathrm{BL}{*}\mathrm{s}^{-1}$. Only one individual each of *M. maximiliani* and of *C. modesta* were studied by Renous and coauthors [14], and the means of the four highest speeds attained by each individual were, respectively, 4.69 and $3.49\,\mathrm{BL}{*}\mathrm{s}^{-1}$. These maxima for all gymnophthalmids are low relative speeds, even when compared to mean relative speeds (not maximum relative speeds) of other lizard species. For example, Kohlsdorf and coauthors [54] reported mean running speeds of $23.8\,\mathrm{BL}{*}\mathrm{s}^{-1}$ for *Tropidurus itambere* and $29.1\,\mathrm{BL}{*}\mathrm{s}^{-1}$ for *T. oreadicus*. Reilly and Delancey data [55] reported $9.15\,\mathrm{BL}{*}\mathrm{s}^{-1}$ for *Sceloporus clarkii*. The mean relative speeds of five lizard species running on treadmills studied by Irschick and Jayne [44] are *Callisaurus draconoides* $52.6\,\mathrm{BL}{*}\mathrm{s}^{-1}$, *Uma scoparia* $48.8\,\mathrm{BL}{*}\mathrm{s}^{-1}$, *Phrynosoma platyrhinos* $26.6\,\mathrm{BL}{*}\mathrm{s}^{-1}$, *Dipsosaurus dorsalis* $41.4\,\mathrm{BL}{*}\mathrm{s}^{-1}$, and *Cnemidophorus tigris* $36.5\,\mathrm{BL}{*}\mathrm{s}^{-1}$. Further, the sprinting speeds of some of these species are even higher; for example, *Callisaurus draconoides* may reach more than $50\,\mathrm{BL}{*}\mathrm{s}^{-1}$[44, 56]. Although, admittedly, the spontaneous speeds attained by gymnophthalmids on level substrates are not directly comparable to the speeds of lizards forced to run on treadmills or to sprinting speeds, the available data suggests that gymnophthalmids have low absolute and relative speeds, associated with the short length of their limbs.

In the constant speed model the joint effect of stride length and stride frequency is multiplicative, and both variables are correlated with each other. Hence it can be argued that simple bivariate analyses relating either RSL or SFR to RSP are not really informative regarding speed modulation because these analyses assume independent effects of each variable on speed. Modulation of speed can be made conceptually clearer by considering that any given speed can be the result of several combinations of stride length and frequency values. Thus, these combinations imply an inverse relationship between RSL and SFR, which further highlights their interdependence.

Colobodactylus taunayi individuals were allowed to choose voluntary speeds on the substrates, and thus a range of speeds was obtained, and increases in speed were attained by simultaneously increasing both stride length and stride frequency, as found in other lizard species (e.g., [15, 45, 46, 53, 57]). Thus it can be argued that speed modulation should be best viewed within the MLR framework in which (i) the joint effect of both stride length and of stride frequency can be examined concurrently, and (ii) the interdependence among these two variables is taken into account in the very structure of the MLR equation. Moreover, the possibility of rigorously examining the partial regression coefficients allows for the statistical control of the effect of either independent variable, maintaining it fixed, whilst examining the effect on speed of one unit change in the other variable. Hence we view the use of the logarithmized form of the constant speed model, that is, the fully parameterized MLR framework, as enabling a higher internal consistency in this type of kinematic analysis.

According to Vanhooydonck and coauthors [53] and McElroy and coauthors [49] short-limbed lizards would be expected to increase speed mainly by increasing stride frequency. In our study, as revealed by the MLR analysis, increases in speed—on all substrates, except wood—were attained by joint increases in both stride length and stride frequency with equal relative contributions of each. On wood, however, the increase in stride length was three times higher than the increase in stride frequency when individuals increased speed. Such asymmetrical contributions are most probably due to the two independent ways, the speeds were measured, and that, in the MLR approach, variation in speed is to be necessarily explained by the within stride cycle measurements. Thus, on wood, there probably occurred accelerations and decelerations responsible for differences between the speeds measured within and outside the stride cycle. There was thus significant heterogeneity in the way speed was modulated through variation in its direct determinators among substrates.

Nonetheless, when speed modulation was examined using only those variables measured for each stride cycle, namely, RSL and SFR, no difference in the relative modulation of stride frequency with respect to relative stride length was found among substrates, indicating a similar relative covariation of both variables in all substrates. Note, however, that the relative contributions of such variables to speed variation was such that for each SD unit in RSL, only a fractional unit in SFR occurred, showing speed modulation to be mainly through relative stride length. Furthermore, for larger values of RSL, a higher variation in SFR was found, indicating relative modulation of these two variables with respect to one another to be tighter for smaller RSL values.

5. Epilogue

Ultimately, precise knowledge of the response pattern of kinematic variables to the gradient in roughness demands more precise investigations of the biomechanics of locomotion when only a single property of the substrate varies in the gradient, thus allowing accurate and precise association of biomechanical characteristics of the locomotor system of the individuals and the specific property being examined. Nonetheless, despite the multidimensional nature of the properties of the substrates in our experimental setup, interesting intraspecific variations in locomotion performance were uncovered, including variation in speed modulation between substrates and differential responses of kinematic variables to each substrate.

A general plea for studies that examine locomotor performance in lizards varying in degree of body elongation and limb size has been made repeatedly (e.g., [58–60]). Interestingly, it has been shown that judicious use of substrate properties (e.g., roughness) allows for the experimental isolation of the use of either appendicular or axial systems of locomotion exclusively (e.g., [14], present study) in species which utilize both tetrapod and undulatory locomotion modes. In addition, given that some pairs of substrates, when compared, yielded differences in single direct determinants of speed, such as stride length on plastic-wood and stride frequency on both wood-sand and wood-gravel, and this suggests that careful choice of substrates, and of substrate properties, might allow a more precise experimental approach, focusing on single determinants of speed, and how they are associated with the degree of limb reduction. In other words, when limbs are modified, specific kinematic variables, within the hierarchical causal structure of speed determination, may be affected, and it would be instructive to know which kinematic variables are affected and the quantitative degree to which they are affected by specific morphological limb modifications (see [12]). Ideally, single substrate properties should be experimentally manipulated to elicit both qualitative and quantitative changes in kinematic variables, in a predictable manner, so as to measure how limb shortness, limb incompleteness, and limb loss quantitatively affect functional aspects of both tetrapod and undulatory locomotion.

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