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RESEARCH ARTICLE

The Impact of Substrate Properties on the Kinematics of Locomotion in a Limb-Reduced Skink, *Ablepharus kitaibelii* (Squamata: Scincidae)

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ABSTRACT

The environment through which animals move is rarely homogenous and requires animals to change their kinematics. Especially for small animals, even seemingly minor variations in substrate characteristics may have strong impacts on their locomotor speed and kinematics. In most quadrupedal animals, obstacles are avoided by adapting the movements of the limbs and body, allowing animals to effectively negotiate a diversity of terrains. However, how limb-reduced animals change their kinematics in function of variation in locomotor substrates remains poorly known. Here we study the limb-reduced skink *Ablepharus kitaibelii* moving on two different substrates (sand and bitumen) across a range of speeds. Our results show an effect of speed as well as significant differences between substrates in most spatio-temporal gait parameters studied. Moreover, speed modulation differed between the two substrates, suggesting that the kinematic and motor control strategies used by this species are substrate-dependent. Axial movements were strong determinants of overall locomotor speed in *A. kitaibelii,* suggesting that in limb-reduced species, the axial system drives variation in locomotor speed. Our data provide a baseline for future studies on other limb-reduced and non-limb-reduced species.

1 | Introduction

Locomotion is a critical component of an animal's biology. Not only is locomotion essential in the context of feeding or foraging (Montuelle et al. 2009, 2012) and predator escape (Husak 2006; Fu et al. 2019), it is also an important trait linked to territory defense (Husak et al. 2006) and dispersal (Cote et al. 2022). As such, selection on locomotor performance is strong and has most likely driven the exceptional variation observed in the limbs of tetrapods (Rothier et al. 2022, 2023, 2024). However, locomotion is highly dependent on the environment in which an animal lives (Renous et al. 2010). Consequently, the physical attributes of the (micro)habitat in which an animal lives can exert strong selection pressures on locomotor performance and the underlying morphology of an animal (Losos and Sinervo 1989; Lowie et al. 2019). A classic example is the convergent evolution of *Anolis* ecomorphs across the Greater Antilles where species living in similar microhabitats have converged on similar limb and body proportions due to selection on locomotor capacity in these different microhabitats (Losos 1990, 2009; Losos et al. 1998).

For many animals, the type of substrate upon which they move is critically important and impacts the kinematics and

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Summary

- We study the limb-reduced skink *Ablepharus kitaibelii* moving on two different substrates (fine sand and bitumen) across a range of speeds.
- The speed modulation differed between the two substrates, suggesting that the kinematic and motor control strategies used by this species are substrate-dependent.
- Despite its strongly reduced limbs and small size, *A. kitaibelii* is a species that can move relatively fast. In all cases, limbs were used, but when moving very slowly this species can use only its forelimbs.
- Axial movements were strong determinants of overall locomotor speed in *A. kitaibelii*, suggesting that in limb-reduced species, the axial system drives variation in locomotor speed.
- Our results confirm experimentally that limb-reduced lizards like the Snake-eyed Skink have a flexible locomotor repertoire and adapt to different soils and terrains by modulating both limb and body kinematics. Further studies are clearly needed to test the generality of the observed patterns.

performance of locomotion (Vanhooydonck et al. 2005, 2015; Höfling et al. 2012; Tulli et al. 2012; Sathe and Husak 2018; Morinaga and Bergmann 2020; Bergmann et al. 2020; Chong et al. 2022). As locomotion is dependent on forces exchanged between the animal and the substrate, differences in the substrate that impact the efficiency of force transmission will impact locomotor performance (Clifton et al. 2023). Interestingly, many lizards have reduced limbs which can be expected to impact the interactions between the animal and the substrate upon which it moves (Gasc 1984; Gans 1986; Gasc and Gans 1990; Vanhooydonck et al. 2011; Morinaga and Bergmann 2020; Chong et al. 2022). Limb reduction is extremely common in lizards and is typically associated with the evolution of a snake-like body shape (Greer 1991; Camaiti et al. 2021). The genomic basis of limb loss shows few shared elements in different taxa (Roscito et al. 2022), and similarly, the anatomical stages of limb reduction vary across clades (Camaiti et al. 2021; Smith-Paredes et al. 2021; Olson and Bergmann 2025). Limb-reduction poses specific problems when negotiating different substrates, as friction between the body and the substrate is likely greater in these species, and consequently, axial movements can be expected to contribute to a greater degree to locomotion depending on the type of substrate.

In some limb-reduced lizards, locomotion may not involve the use of the limbs at all. For example, the sandfish *Scincus scincus* (Linnaeus, 1758) propels itself within the sand using a large amplitude traveling-wave oscillation of its body without using its limbs (Maladen et al. 2009, 2011). In contrast, fossorial skinks of the genus *Lerista* actively use their short limbs and significantly elongated bodies during terrestrial locomotion (Gans and Fusari 1994). As friction is critical for locomotion, most limb-reduced lizards still use their limbs irrespective of the degree of limb reduction. For example, elongated and limb-reduced microteiid lizards typically use their limbs during locomotion on different substrates (Höfling et al. 2012; Renous et al. 1995, 2008), yet the importance of the limbs versus the axial system in driving variation in locomotor speed on different substrates remains poorly understood.

Ablepharus kitaibelii Bibron and Bory de Saint-Vincent, 1833 is a small scincid lizard with a slender body, a long tail, and short legs, adapted to a semi-fossorial lifestyle. This species moves in leaf litter, through short grass, and sometimes on rocky terrain in nature (Fejérváry 1912; Fuhn 1970; Gruber 1981; Stojanov et al. 2011). Interestingly, Herczeg et al. (2007) suggested that *A. kitaibelii* avoids rocky areas because of its inefficient locomotion on inclined and vertical rocky surfaces. However, the species was recently observed climbing on the vertical trunk of an eucalyptus tree in north-western Peloponnese, Greece (Tzoras et al. 2025). Although little is known about the kinematics of locomotion in this species, Beshkov and Nanev (2006) stated that *A. kitaibelii* moves in a snakelike fashion without using its limbs. A similar observation was previously reported by Gruber (1981), where the author described that, because of its very short limbs, locomotion is dependent on snakelike movements of the body. Moreover, Gruber (1981) suggested that the species uses its fore limbs more than its hind limbs.

Here, we quantify the kinematics of locomotion on two substrates mimicking natural substrates: fine sand and a hard surface. We hypothesize that this species can move efficiently on different substrates by using its short limbs and elongated body. We further quantify the contribution of the axial system and limbs to variation in locomotor speed and explore the possible occurrence of body-mediated propulsion in this limb-reduced species.

2 | Material and Methods

2.1 | Material

Seven adult individuals with intact tails were captured near Bezden Village (FN75), Bulgaria (mean snout-vent length: 43.5 mm). All animals, captured for the high-speed filming, were released to their natural habitat after filming. The Snake-eyed Skink inhabits mainly thermophilic oak forests, or the ecotone between such forests and meadows, where the animal can easily hide in the soft soil or beneath the fallen leaves (Fuhn 1970; Gruber 1981; Stojanov et al. 2011). According to Fejérváry (1912), the species inhabits meadows with less humidity and composed of limestone and clay. In Greece, the species can be found on sandy and salty soils surrounded by saltpan (Ramsey and Todd 2009). Fuhn (1970) further mentions that *A. kitaibelii* was found on a sandy beach in Albania. The subspecies *A. kitaibelii fabichi* inhabits several Aegean islands, where the terrain is rocky (Štěpánek 1944). Another subspecies *A. kitaibelii fitzingeri* is associated with different substrates in Hungary, based on their rock basement and soil types—sandstone, dolomite and limestone, andesite, volcanic gabbro, basalt, and sand (Herczeg et al. 2004). Overall, this suggests that this species is capable of moving across a variety of substrates, ranging from hard-packed and rocky to sandy soils.

2.2 | Filming

We recorded locomotion on different substrates using a Photron FASTCAM 1024PCI high-speed camera (Photron, San Diego, USA) and control software (Photron FASTCAM Viewer, v3600_64bit). The camera was equipped with a Nikon AF D 24-85/2.8-4IF Macro objective (Nikon Corporation, Tokyo, Japan). Illumination was provided using two Dedocool lights (Dedo Weigert Film GmbH, Munich, Germany). Seventy-nine videos filmed in dorsal view were recorded. The animals were filmed on two different substrates: fine sand (7 individuals, 47 videos) and hard construction material used for waterproofing roofs, imitating a grainy rocky surface (a type of Bitumen Membrane; 6 individuals, 32 videos). To be able to film fast movements, all videos were recorded at 1000 frames per second (see Supporting Information S5: Table 1; Videos S1–S4).

2.3 | Tracking

For the tracking of the movements, each animal was painted with small white dots on the dorsal side of the body including the snout tip, a point at the level of the shoulder, a point at mid-body halfway between the pectoral and pelvic girdles, a point at the level of the pelvis, and two points on the tail—on the middle and on the tip (see Figure 1). The tracking of the movements was performed using a custom motion tracking program (designed by C. Beisser and P. Lemell, Vienna; programmed by C. Beisser, Vienna) developed in MATLAB R2015b (MathWorks, Inc., Natick, MA, USA). The software uses predictive algorithms based on a digitizing software, implemented in MATLAB (Hedrick 2008).

2.4 | Kinematic Variables

From the X- and Y-coordinates we calculated the following spatio-temporal gait characteristics: stride length (mm), stride duration (s), and stride frequency (Hz). We further calculated the wave amplitude, wave length, and frequency at the snout-tip (mm), at mid-shoulder, at mid-body, at mid-pelvis, and at mid-tail.

2.5 | Statistical Analyses

To explore how speed is modulated on the different substrates, we ran a multiple regression on the Log_{10}-transformed variables with stride length, frequency, and duration, as well as the wave amplitude, length, and frequency of the different points on the body analyzed. Next, we ran a multivariate analysis of covariance on the kinematic variables with substrate as our fixed factor and maximal velocity as our covariate to understand whether the different substrates impacted the kinematics of locomotion. Subsequently, we ran univariate ANCOVAs for each kinematic variable to test which variables differed. We incorporated individual identity as a factor in the model to account for repeated measurements for each individual.

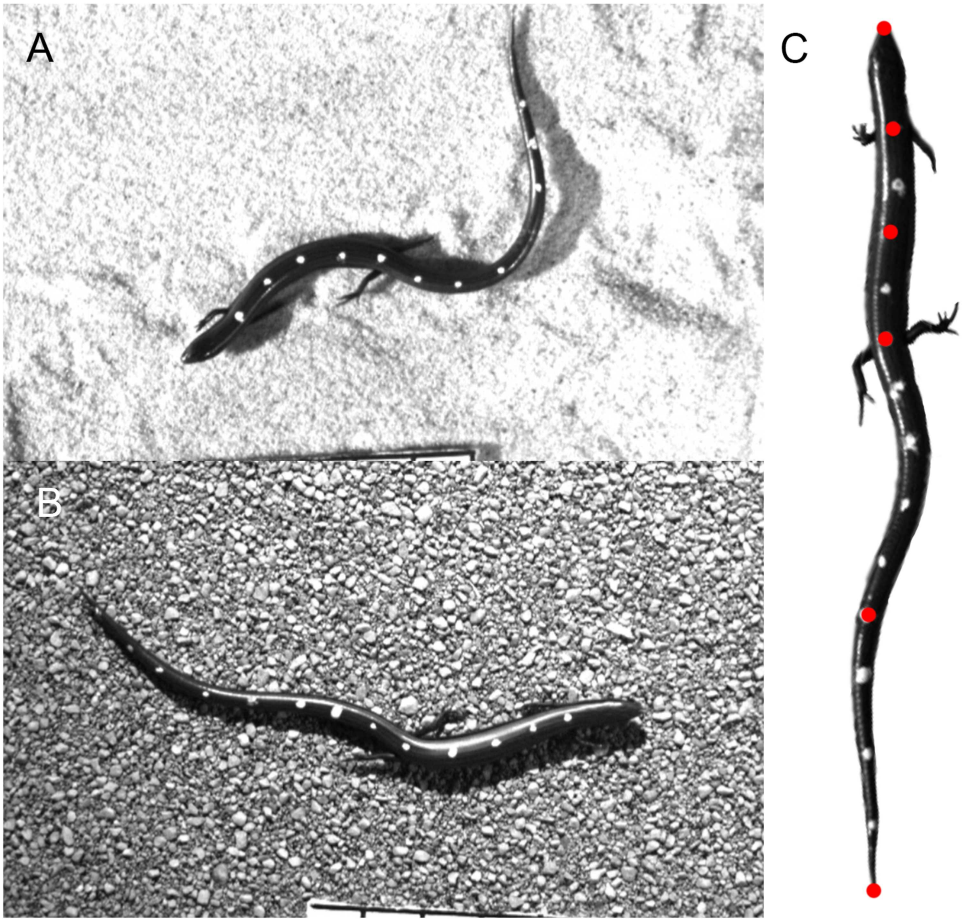

FIGURE 1 | Images extracted from a video of locomotion of adults of *A. kitaibelii* on two different substrates. (A) on fine sand; (B) on hard construction material. (C) points in red tracked for the analyses of locomotor kinematics.

3 | Results

3.1 | Speed Modulation

On fine sand a model was retained that explained 90% of the variation in velocity ($F_{4,24} = 55.92$; $p < 0.001$) with the wave amplitude at mid-tail ($\beta = 0.40$), the wave length at the shoulder ($\beta = 0.25$), the wave amplitude at the shoulder ($\beta = 0.22$), the frequency of the snout tip ($\beta = 0.69$) as predictors. On the hard substrate, the model explained 93% of the variation in peak velocity ($F_{3,18} = 69.95$; $p < 0.001$) with the wave frequency at mid-tail ($\beta = 0.74$), the wave amplitude of the snout tip ($\beta = 0.49$) positively impacting, and the wave amplitude at the shoulder ($\beta = -0.29$) negatively impacting peak velocity.

3.2 | Effect of Substrate on Locomotor Speed and Kinematics

An ANOVA detected differences in velocity for animals running on the different substrates ($F_{1,13} = 19.10$; $p = 0.009$), with animals running faster on average on hard substrates. The individual effect ($F_{6,6.3} = 2.11$; $p = 0.19$) and the interaction between

TABLE 1 | Results of the univariate ANCOVAs testing for the effect of the covariate and substrate.

	Variable	Mean square	*F*	*p*
Velocity (mms^{-1})	**Stride length (mm)**	0.054	32.083	0.000
	Stride duration (s)	0.339	50.356	0.000
	Stride frequency (Hz)	0.340	50.511	0.000
	Wave amplitude skull (mm)	0.283	8.849	0.005
	Wavelength skull (mm)	0.088	30.485	0.000
	Wave frequency skull (Hz)	0.336	49.228	0.000
	Wave amplitude shoulder (mm)	0.027	1.155	0.288
	Wavelength shoulder (mm)	0.082	37.474	0.000
	Wave frequency shoulder (Hz)	0.378	45.368	0.000
	Wave amplitude mid-body (mm)	0.133	3.310	0.076
	Wavelength mid-body (mm)	0.087	24.117	0.000
	Wave frequency mid-body (Hz)	0.320	40.290	0.000
	Wave amplitude pelvis (mm)	0.205	10.477	0.002
	Wavelength pelvis (mm)	0.062	25.005	0.000
	Wave frequency pelvis (Hz)	0.382	61.838	0.000
	Wave amplitude mid-tail (mm)	1.106	24.638	0.000
	Wavelength mid-tail (mm)	0.036	10.255	0.003
	Wave frequency mid-tail (Hz)	0.444	79.306	0.000
Substrate	**Stride length (mm)**	0.076	45.244	0.000
	Stride duration (s)	0.002	0.348	0.558
	Stride frequency (Hz)	0.002	0.355	0.554
	Wave amplitude skull (mm)	0.312	9.763	0.003
	Wavelength skull (mm)	0.037	12.779	0.001
	Wave frequency skull (Hz)	0.001	0.200	0.657
	Wave amplitude shoulder (mm)	0.021	0.909	0.345
	Wavelength shoulder (mm)	0.086	39.396	0.000
	Wave frequency shoulder (Hz)	0.012	1.435	0.237
	Wave amplitude mid-body (mm)	0.327	8.134	0.007
	Wavelength mid-body (mm)	0.093	25.836	0.000
	Wave frequency mid-body (Hz)	0.004	0.496	0.485
	Wave amplitude pelvis (mm)	0.357	18.233	0.000
	Wavelength pelvis (mm)	0.099	40.024	0.000
	Wave frequency pelvis (Hz)	0.002	0.391	0.535
	Wave amplitude mid-tail (mm)	0.498	11.098	0.002
	Wavelength mid-tail (mm)	0.155	44.621	0.000
	Wave frequency mid-tail (Hz)	0.011	2.017	0.162

Note: Bold variables indicate significant differences after sequential Bonferroni correction.

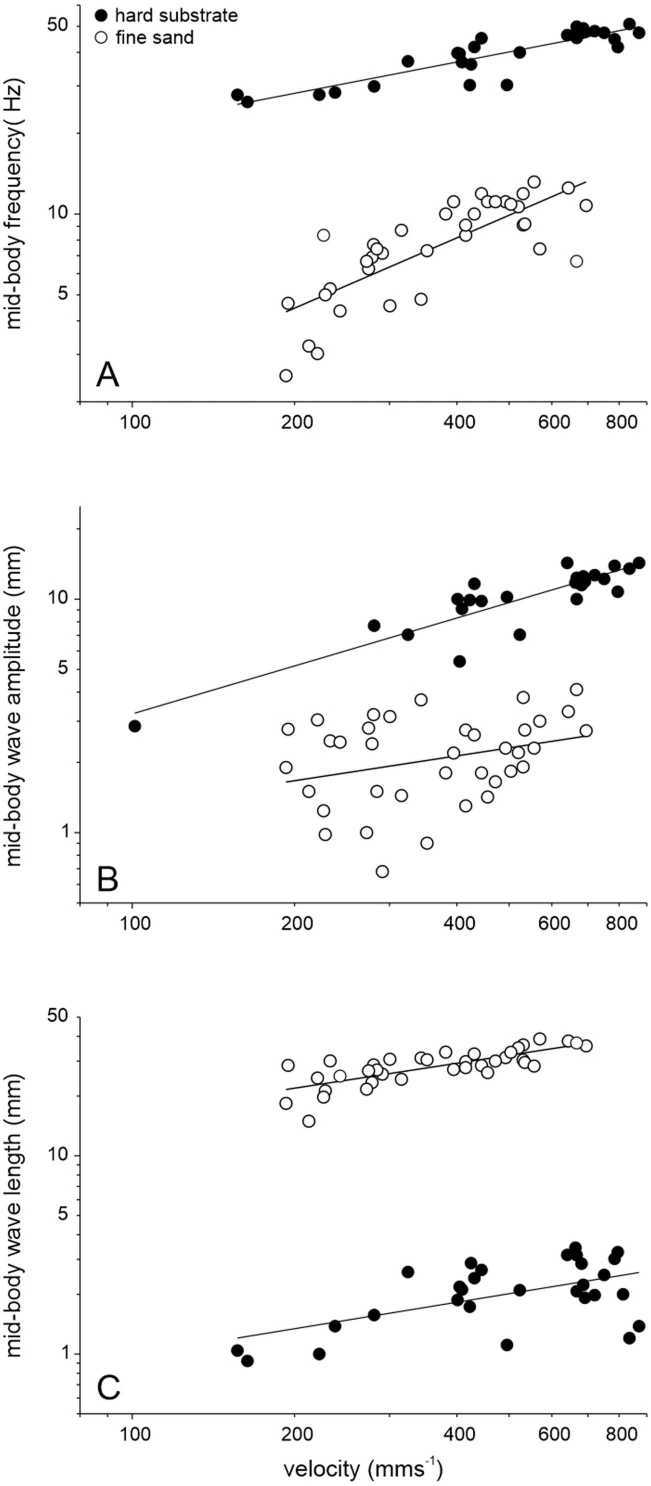

FIGURE 2 | Relationships between (A) mid-body wave frequency, (B) wave amplitude, and (C) wave length in function of peak velocity for locomotion on hard substrates and fine sand. Filled symbols represent locomotion on a hard substrate, and open symbols represent locomotion on fine sand. The contribution of axial movements clearly differs depending on the locomotor substrate.

individual and substrate ($F_{5,59} = 0.42$; $p = 0.83$) were not significant. The MANCOVA testing for differences in kinematics between substrates with velocity as a covariate detected significant differences in kinematics (substrate effect: Wilks' lambda = 0.16; $F_{18,28} = 8.47$; $p < 0.001$; velocity: Wilks' lambda = 0.09; $F_{18,28} = 15.22$; $p < 0.001$). Subsequent univariate ANOCOVAs detected significant differences in kinematics between locomotion on different substrates for most variables (Table 1; Figures 2 and 3). Moreover, velocity significantly impacted all kinematic variables except for the wave amplitude at the shoulder and at mid-body (Table 1).

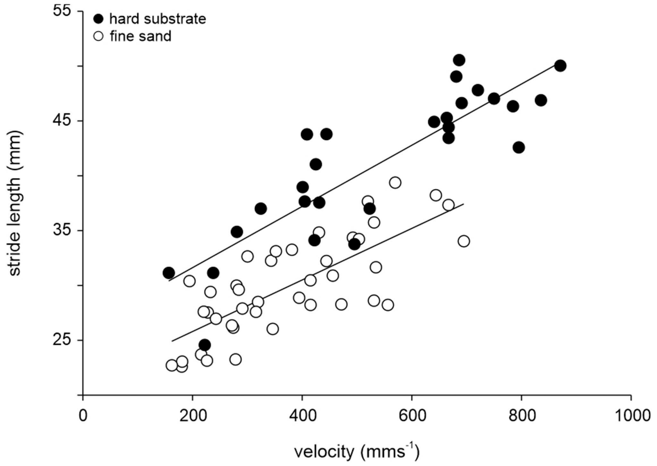

FIGURE 3 | Relationship between peak velocity and stride length. On both substrates, stride length increases with an increase in velocity but animals on hard substrates have a greater stride length for a given velocity suggesting a greater contribution of the limbs. Filled symbols represent locomotion on a hard substrate, and open symbols represent locomotion on fine sand.

4 | Discussion

The locomotion of sand-swimming species often does not involve the use of the limbs, even when they are present (Maladen et al. 2009, 2011). Thus, body elongation with reduction of the limbs could be an adaptation for sand swimming and burrowing (Chong et al. 2022). Yet, most members of the family Scincidae possess elongated bodies with short limbs, irrespective of their ecology. Moreover, lizards of the genus *Lerista*, for example, actively use their very short limbs and elongated body during terrestrial locomotion (Gans and Fusari 1994). These authors explain how friction is crucial and that these animals use their limbs, irrespective of the degree of reduction. Although the species studied here, *A. kitaibelii*, is not a "typical" runner, this small species can achieve a relatively high speed (0.8–1.1 m/s) despite its reduced limbs. Locomotor velocity impacted all kinematic variables except for the wave amplitude at the shoulder and at mid-body. Thus, the front part of the body appears less modulated as animals are running faster. Interestingly, similar to other small-bodied lizards (Renous et al. 2008), the substrate affected how speed was modulated. Yet, in *A. kitaibelii* an increase in velocity is achieved by an increase in both stride length and stride frequency, different from what was observed in gymnophtalmid lizards (Renous et al. 2008). Moreover, axial movements appear to be the main determinants of variation in sprint speed in addition to stride length or frequency. Thus, in limb-reduced lizards, both limb and body movements are modulated to achieve higher locomotor speeds. The similarity in the patterns observed between two groups that have independently evolved limb reduction suggests that our results may reflect how limb-reduced lizards increase speed during locomotion. However, data on closely related non-limb-reduced species are lacking and would be critical to establish whether the patterns observed here (e.g., increased axial undulation with speed) are typical of limb-reduced species or more general features of locomotion in scincid and gymnophtalmid lizards.

Previous authors reported that *A. kitaibelii* folds its limbs next to the body and moves in snakelike fashion when performing fast locomotion (Gruber 1981; Beshkov and Nanev 2006). In contrast, our high-speed video recordings demonstrate that the Snake-eyed Skink effectively uses its limbs both for running on fine sand and hard substrates (see Videos S1, S2) as observed in other limb-reduced skinks (Gans and Fusari 1994). The limbs serve as anchors, allowing the animal to generate friction with the substrate and push the body forward. However, an animal released from the hand of the first author used snakelike movements without the use of the limbs (Video S3). Yet, this animal was not moving efficiently. Later, the animal used its limbs and started running. Interestingly, in one case, an animal was observed moving using only its forelimbs when moving at very slow speeds on the hard substrate (Video S4). The animal moved in a rectilinear fashion for a short period with the hind limbs folded next to the tail. A similar type of locomotion was observed in other individuals by the first author (V. Vergilov). These observations suggest that these animals may have a larger repertoire of movements that can be selected depending on the environmental constraints. As the species is observed on a variety of substrates ranging from softer soils and sand to rocky terrain, this locomotor flexibility is likely highly beneficial.

Our results show snake-eyed skinks run on average faster on hard substrates. On sand substrates, the limbs penetrate into the softer substrate, which likely causes slip and loss of propulsive force. These results mimic those for lacertid lizards (Vanhooydonck et al. 2015), where locomotion on sand resulted in generally lower sprint speeds compared to hard substrates. In contrast, Liolaemini lizards generally showed the highest speeds on sandy substrates (Tulli et al. 2012). More studies on locomotion on different substrates are needed to test the generality of these patterns. Especially, data on limb-reduced animals compared to closely related non-limb-reduced species are required to assess the role of the limbs during locomotion and the interaction thereof with substrate characteristics. Scincid and gymnophtalmid lizards appear excellent candidates for such studies and may allow a better understanding of the evolution of limb reduction in lizards and the functional consequences thereof.

5 | Conclusion

Despite its strongly reduced limbs and small size, *A. kitaibelii* is a species that can move relatively fast. In all cases, limbs were used, but when moving very slowly this species can use only its forelimbs. Our results also demonstrate that on hard surfaces, animals run generally faster. On fine sand, the velocity of *A. kitaibelii* is lower on average, likely due to the "sinking" of the limbs into the substrate. However, peak velocity was similar on both substrates, suggesting that the animals can compensate for this effect by increasing the contribution of the axial system, but likely at a high energetic cost. Our results confirm experimentally, that limb-reduced lizards like the Snake-eyed Skink have a flexible locomotor repertoire and adapt to different soils and terrains by modulating both limb and body kinematics. Further studies are clearly needed to test the generality of the observed patterns.

Author Contributions

Vladislav Vergilov: conceptualization, methodology, video recordings, analysis, writing – original draft, and writing – review and editing. **Anthony Herrel:** analysis, writing, review, and editing. **Patrick Lemell:** tracking.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.
Supporting video 1: Locomotion of an adult *A. kitaibelii* on fine sand.
Supporting video 2: Locomotion of an adult *A. kitaibelii* on hard construction material.
Supporting video 3: Snakelike movements of an adult *A. kitaibelii* with the limbs folded against the body.
Supporting video 4: Slow locomotion of an adult *A. kitaibelii*, using only its fore limbs.
Table S1: Marginal means illustrating differences in the kinematics of locomotion of *A. kitaibelii* on different substrates.