6

https://doi.org/10.1038/s44182-024-00011-2

Coordinating limbs and spine: (Pareto-) optimal locomotion in theory, in vivo, and in robots

Check for updates

Robert Rockenfeller^{1,2,3} , Robert L. Cieri⁴, Johanna T. Schultz², Robin Maag^{2,5} & Christofer J. Clemente²

Among vertebrates, patterns of movement vary considerably, from the lateral spine-based movements of fish and salamanders to the predominantly limb-based movements of mammals. Yet, we know little about why these changes may have occurred in the course of evolution. Lizards form an interesting intermediate group where locomotion appears to be driven by both motion of their limbs and lateral spinal undulation. To understand the evolution and relative advantages of limb versus spine locomotion, we developed an empirically informed mathematical model as well as a robotic model and compared in silico predictions to in-vivo data from running and climbing lizards. Our mathematical model showed that, if limbs were allowed to grow to long lengths, movements of the spine did not enable longer strides, since spinal movements reduced the achievable range of motion of the limbs before collision. Yet, in-vivo data show lateral spine movement is widespread among a diverse group of lizards moving on level ground or climbing up and down surfaces. Our climbing robotic model was able to explain this disparity, showing that increased movement of the spine was energetically favourable, being associated with a reduced cost of transport. Our robot model also revealed that stability, as another performance criterion, decreased with increased spine and limb range of motion detailing the trade-off between speed and stability. Overall, our robotic model found a Pareto-optimal set of strides – when considering speed, efficiency, and stability – requiring both spine and limb movement, which closely agreed with movement patterns among lizards. Thus we demonstrate how robotic models, in combination with theoretical considerations, can reveal fundamental insights into the evolution of movement strategies among a broad range of taxa.

The greatest advantage legged robots provide over standard wheeled robots is improved mobility over irregular terrain¹. This is particularly important on steep or vertical inclines that wheeled robots are unable to access^{2,3}. Several climbing legged robotic designs have been developed (see Supplementary S1, Table A1 or [ref. 4, Fig. 3 and Table 1]) but these designs are generally less efficient than wheeled robots, particularly on flat surfaces². Yet actuation of the limbs need not be the only mechanism of propelling a legged robot, with several studies incorporating movement in the spine^{5–8}. While both mechanisms are viable ways of achieving forward movement, we lack a cogent theoretical framework for assessing the relative use of limb vs spine actuation and their interdependency with body geometry. Understanding and optimising the performance and efficiency of legged strides could thus yield important advances in the field of legged robotic locomotion.

As a source of bioinspiration, there is considerable variation among extant vertebrates in the coordination of limb and spinal motion and the relative contribution of each movement to locomotion. Many fish propel themselves using predominately spine-based lateral undulation⁹. Among extant terrestrial mammals¹⁰ and especially birds¹¹ locomotion is dominated by limb movements, although both lateral and dorsal-ventral spinal movements contribute to locomotion. Extant sprawling squamates, such as lizards, appear as an intermediate group, locomoting using a highly variable combination of retained lateral spinal undulation and protraction and retraction of the limbs^{12–15}. Despite this known variation in locomotor pattern, there is little information on the relevant advantages or disadvantages of relying more on limb vs spine movement to locomotion, and although there appears to be a macroevolutionary trend towards limb based

¹Mathematical Institute, University of Koblenz, Koblenz, Germany. ²School of Science, Technology and Engineering, University of the Sunshine Coast, Sunshine Coast, QLD, Australia. ³School of Biomedical Sciences, University of Queensland, Brisbane, QLD, Australia. ⁴Department of Zoology, University of British Columbia, Vancouver, BC, Canada. ⁵Department of Biomimetics, City University of Applied Sciences, Bremen, Germany. ^{Columbia}

locomotion^{10,16}, limbless body forms have evolved independently at least 25 times among squamates^{17,18}.

Many reasons for the retention of LSU in lizards have been suggested, mainly relating to enabling increased speed^{19,20}. This increase in speed has often been attributed to an increase in stride length associated with lateral bending¹⁴, see also, e.g., refs. 7,21–23, and [ref. 24, Fig. 1]. Intuitively, this belief can be based on the observed gain in reach of the feet²⁵. Alternatively, a geometric-mechanics explanation^{6,26} suggests that the coordination of leg and spine motion phases during gait has substantial impact on stride length. This becomes particularly important as LSU was found to transition from a standing to a travelling wave in some squamates at higher speed^{13,14}.

Yet, increased stride length may not be the only selective force driving spine use among squamates; other explanations have also been proposed for the adaptive advantages of LSU. For example²⁷, have suggested that LSU may improve turning ability when combined with differential leg movement. Further, it was proposed that LSU may enhance stabilisation of the body by a combination of low height of the centre of mass (sprawling posture) as well as a coupling of lateral and fore-aft ground reaction forces in the feet^{28,29}. Alternatively, LSU may confer an advantage via increased energy efficiency during locomotion³⁰, as the trunk may serve as a visco-elastic system and reduce the oscillation of kinetic energy resulting from centre of mass dynamics, see ref. 22 for a detailed discussion.

The ability to determine the relative advantages for limb vs spine based locomotion is further complicated by the interaction between these traits with morphology. For example, increasing the spine range of motion (ROM) will limit the maximal size of the limbs, since above some length collisions would be predicted to occur between the fore and hind limbs along one side of the body. Similar limitations are likely to occur if the limb ROM is increased, meaning the interaction between limb ROM, spine ROM and morphology is likely complex.

Understanding the selective advantages of this variation in living systems is difficult since species generally occupy a relatively small proportion of the available performance space⁸. Species may be excluded from areas of the performance space if these areas are maladaptive, since this would quickly drive species to extinction. Alternatively, phylogenetic or structural constraints may limit the ability for the body form to occupy all areas of the performance map³¹. Thus species may not yet have evolved to any specific locomotor local maxima because multiple performance criteria may be selected for simultaneously, resulting in a trade-off between different optima, or because evolution selects for performance traits that are sufficient for survival and reproduction instead of optimal traits.

Therefore this study addressed three primary research aims with respect to the relative importance of LSU. (1) Determine the extent to which LSU—in combination with leg motion and morphology–can actually enhance (or limit) maximum stride lengths and thus speed (2) Detect any possible trade-offs or performance criteria driving different locomotion objectives (speed, efficiency, stability) when utilising LSU and (3) Define the Pareto-optima for combinations of LSU and limb ROM for multiple performance objectives, which can act as a source of inspiration for the design of legged robots.

To answer these research questions we utilise the reciprocal interplay between robotics, biology, and mathematics as illustrated in Fig. 1. First, we propose a theoretical model of two-dimensional lizard locomotion. This model can derive predictions on maximum leg lengths and thus maximum stride lengths possible and so predict a realm of (near-)optimal body plans. This mathematical model predicted a theoretical optimum not obstructed by any physical and morphological limitations.

We then validate the model in reality by introducing the robotic system SQUAMATAR (Spine-bending, QUAdrupedal, Manually Adjustable, TAiled Robot). This biologically mimicking robot was designed to posses a similar number of degrees of freedom as lizards. We use our robotic model to build a performance landscape for two other key features associated with climbing locomotion; stability and efficiency. These latter features are not easily predicted by the theoretical model and difficult to measure in vivo; the



bio-inspired robot will thus help to estimate how variations in limb ROM, spine ROM and limb length influence the performance of legged locomotion utilising LSU.

Finally, we then compare our findings to in-vivo measurements of 40+ species among running and climbing lizards to determine the extent to which different groups have optimised these traits. The interplay between theoretical model, robot, and in-vivo data provides a sound basis to understand the advantages (or disadvantages) of body plans and movement patterns for lizards and why evolution has yielded the observable morphological variety.

Results

The theoretical versus in-vivo stride lengths

We first compared theoretical predictions with in-vivo measurements to generate several important insights into stride design, depicted in Fig. 2. Model predictions were plotted as heatmaps in a spine- and leg-ROM stride space, overlain with in-vivo results of the 40+ lizards as data points, cf. Fig. D1 in Supplementary S1. We explored each component of Eqn. (2) individually, corresponding to sections "Spinal undulation: Increasing stride length per leg length", "Maximum leg length: A problem of collision", and "Maximum stride length depends solely on trunk length".

For the first component, we considered how different combinations of limb and spine ROM can optimise stride length given a fixed leg length. The first factor $(4 \cdot \sin(\frac{1}{2} \cdot (\phi_{leg} + \phi_{base}))$, red shading) represents a theoretical lizard of fixed leg length ($\ell_{leg} = 1$, i.e., TLS length), whose spine (ϕ_{base}) and legs (ϕ_{leg}) can be moved independently (Fig. 2a,d). This scenario ignores

collision between legs. For clarity, only leg ROM $40^{\circ} \le \phi_{tot} \le 140^{\circ}$ are shown, because this is the maximum range observed in vivo, and the region beyond $\phi_{base} + \phi_{leg} = 180^{\circ}$ is left blank as this combination cannot be considered biomechanically meaningful even if it is theoretically feasible. For a given leg length, increases in spine and leg ROM are shown to yield equal increases in stride length, and the maximum stride length possible is four times this leg length. *In vivo*, lizards did not occupy the whole stride space, but generally occupied the bottom right segment of the optimal plot region, suggesting that they rely more heavily on limb ROM to maximise stride length.

For the second component, we considered the maximum leg length possible without limb-limb collision under different combinations of limb and spine ROM (Fig. 2b). The second factor ($\ell_{leg,max}$ blue shading) concerns a theoretical lizard with given leg and spine ROM, whose maximum possible leg length has to be determined. The region beyond $\phi_{base} + \phi_{leg} = 180^{\circ}$ is again left blank, and maximum leg length is given with respect to TLS length. Here, we show that leg length is restricted relatively evenly by increases in either leg or spine ROM, and that leg length is limited to roughly 0.5 TLS length in the region of the stride space previously demonstrated to yield the greatest stride lengths (Fig. 2e).

Combining both model components by multiplication predicts the maximum possible stride length without limb collision $(2 \cdot \xi)$, green ellipse, again normalised to TLS length). Figure 2f shows that maximum stride length occurs when spine ROM is minimised. Within the range, it is also independent of leg ROM, as smaller leg ROMs are exactly compensated for by longer limbs. Regarding in-vivo spine ROM, lizards cluster between 15° and 30°, which still allow for \geq 95% of maximally achievable theoretical





ROMs and leg lengths (c) plotted vs in-vivo stride lengths for the same animals. Theoretical predictions of stride length optimising leg length and ROM are plotted as a heatmap (f) overlain with in-vivo data shown in units of TLS length. Note that Fig. 2d–f ordinates show apex angles instead of base angles, yielding a curved boundary, as derived in Supplementary S1 (Section B).

stride length. There is little observable relationship in the real lizard data between leg ROM and stride length, however, several geckos achieve high stride lengths using higher spine ROMs than predicted (Fig. 2d–f). Last, a direct comparison of theoretical predictions with in-vivo data (Fig. 2c), shows that the stride lengths of many geckos, skinks, and varanids, but less so dragons, were systematically overestimating the model predictions. Out of the 320 data points, 183 (or 57.2%) lay within the \pm 50% band around unity, indicated by dashed lines. Of the remaining points, 123 lay above and only 14 below. The centrodes of the four point clouds were located at TSL length coordinates (2.5, 3.0) (dragons), (1.8, 2.4) (geckos), (1.9, 2.5) (skinks), and (2.0, 2.9) (varanids), i.e., overestimated the model on average by 20%, 33%, 32%, and 45%, respectively.

Cluster and feature analysis

The three-dimensional mean of the measured kinematic quantities (spine ROM, leg ROM, normalised leg length) differed significantly among all species, directions, habitats, and speed by Hotelling's p, although the inter-family distinction is not as robust under Cuzick-Edwards p, particularly not for geckos and skinks (Table 1, Figs. D2-D5 in Supplementary S1). Among families, dragons use a smaller leg ROM with longer legs, geckos rely on a larger leg ROM, skinks use the largest spine ROM, while varanids locomote with a small spine ROM and shorter legs. Leg lengths and both ROMs are greater during upward climbing than in downward climbing. Compared to the climbing animals, level walking varanids have used smaller leg length but larger leg ROM. The range of motions among terrestrial lizards generally lie between arboreal (large spine ROM, large leg ROM, short legs) and semi-arboreal (small spine ROM, small leg ROM, long legs) species. Finally, faster locomotion trials were associated with increased leg ROM and decreased spine ROM compared to slower trials. A higher resolved overview of concrete kinematic values, including stride length, can be found in Fig. D6 in Supplementary S1.

Theoretical model versus level walking robot

Model predictions from Eqn. (2) were also compared with experimental data collected on the SQUAMATAR robot with three different leg length configurations (Fig. 3; short legs: 0.29 TLS; medium legs: 0.48 TLS; long legs: 0.78

Table 1 | Significance of stride parameter

TLS). For each leg length, model stride lengths were predicted after conversion to theoretical parameters (see Section C in Supplementary S1) and are shown as heatmaps with measured values overlain (Fig. 3a, d, g). Only the stride space that did not result in experimental collisions for each configuration is plotted, which was smaller than the theoretical range that considered the feet as points. The range of possible ROMs depended on ℓ_r (leg length): under the short leg configuration, the claws collided with the body at smaller ROM than for the medium leg length configuration, while collision between front and hind leg happened earlier in the long leg configuration. Agreement between empirically-measured and theoreticallypredicted stride lengths differed between robot leg length configurations. For short leg length, robot stride lengths were less than theoretical predictions, with the exception of very small ROM in both leg and spine. For medium and long leg lengths, the robot mostly fit within the theoretically predicted range,

large, and were less than predicted values when leg ROM was small. Robotic cost of transport during level walking (Eqn. (4)) was also calculated for each point in the stride space (Fig. 3b, e, h). For all leg lengths, moving with both small leg and spine ROM resulted in high COT. Further, the COT for travelling with shorter legs was highest while the COT for medium legs was slightly less than for long legs over the observed intervals. The absolute minimum COT for medium legs was found around a leg ROM of 60°–80° and a spinal ROM of around 20°.

but experimental stride lengths exceeded predictions when leg ROM was very

An optimal stride space, considering both stride length and COT, was determined using Pareto-optimisation (Fig. 3c, f, i), which identified the points where one of several objective functions was maximised without corresponding losses in another function. The Pareto-optimal point for stride length was always associated with higher leg ROM for a given spine ROM. While the Pareto front for short and medium legs were found in comparably small kinematic domains, for long legs the minimum COT was found for a particular spot at very low leg ROM. The Pareto front for medium legs lies at a leg ROM of 70°–90° and a spine ROM of about 25°, i.e., quite comparable to what we observed for real lizards, cf. Fig. 2. Note that this Pareto front hold for constant leg lengths (Fig. 2d) and is not to be compared to the situation of optimal leg lengths (Fig. 2f).

 fast [f]
 91
 (19.4, 101, 0.528)

 Significant differences between clusters are examined by Hotelling's *p* value for each pair of three-dimensional centres – consisting of mean spine ROM ($\hat{\phi}_{spine}$), mean leg ROM ($\hat{\phi}_{leg}$), and mean leg length ($\hat{\ell}_{leg}$) normalised to TLS length – and by Cuzick-Edwards' *p* value with respect to the *k* = 3 nearest neighbours. Values between 0.05 and 1, i.e., non-significant test statistics, are marked with 'o', values below

 0.05 with one asterisk (*), values below 0.01 with two (**), and values below 10⁻⁴ with three (***). Note that while Hotelling's tests are symmetric, Cuzick-Edwards' are not. Abbreviations (behind the groups) are given also above the *p*-matrices for a better overview.

cluster	size	$(\hat{\pmb{\phi}}_{spine}, \hat{\pmb{\phi}}_{leg}, \hat{\ell}_{leg})$	Hotelling p	Cuzick-Edwards p
family				
dragons [d]	74	(20.3, 80.2, 0.679)	$\left(\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{pmatrix} 1 & g & s & v \\ 1 & *** & *** & ** \\ *** & 1 & * & * \\ ** & o & 1 & * \\ *** & *** & * & 1 \end{pmatrix}$
geckos [g]	154	(23.6, 103, 0.576)		
skinks [s]	21	(27.6, 93.3, 0.549)		
varanids [v]	71	(19.6, 98.1, 0.469)		
direction				
up [u]	218	(24.8, 94.7, 0.621)	$ = \begin{pmatrix} u & a & 1 \\ 1 & *** & *** \\ & 1 & *** \\ & & 1 \end{pmatrix} $	$\begin{pmatrix} u & a & i \\ 1 & *** & *** \\ *** & 1 & ** \\ *** & * & 1 \end{pmatrix}$
down [d]	51	(16.4, 93.1, 0.505)		
level [l]	51	(16.6, 105, 0.442)		
habitat				
terrestrial [t]	73	(21.3, 96.2, 0.55)	$ \begin{bmatrix} t & s & a \\ 1 & *** & ** \\ 1 & *** \\ & 1 & *** \\ & & 1 \end{pmatrix} $	$ \begin{pmatrix} t & s & a \\ 1 & \ast \ast & \ast \ast \\ \ast \ast \ast & 1 & \ast \ast \ast \\ \ast \ast \ast & \ast \ast \ast & 1 \end{pmatrix} $
semi-arboreal [s]	52	(17.4, 94.7, 0.611)		
arboreal [a]	102	(25.5, 100, 0.545)		
speed				f
slow [s]	124	(22.7, 93.1, 0.574)	$\begin{pmatrix} s & m & t \\ 1 & * & *** \\ 1 & *** \\ & 1 & * \\ & & 1 \end{pmatrix}$	$ \begin{pmatrix} s & m & r \\ 1 & ** & ** \\ o & 1 & ** \\ *** & ** & 1 \end{pmatrix} $
medium [m]	105	(24, 95.8, 0.615)		
fast [f]	91	(19.4, 101, 0.528)		

robot design

long legs $\ell_r = 170 \,\mathrm{mm}$



60 80 leg ROM (deg)

120

0.0

35

Fig. 3 | Theoretical predictions vs performance data from SQUAMATAR for level walking. Theoretical predictions of stride lengths (heatmaps) overlain with SQUAMATAR data for stride length for short (a), medium (d), and long legs (g) vs leg and spine ROM. Differential spacing between measured data points is due to the translation of robot angles into model angles (Section B in Supplementary S1). Theoretical prediction of cost of transport overlain with SQUAMATAR data for

20

0

60 80 leg ROM (deg)

100 120

Climbing robot: Stride length and COT

Correspondence between theoretical predictions and robot empirical data were compared during climbing exclusively using the medium leg length configuration (Fig. 4) because this configuration represented the greatest variability in possible ROM, the lowest COT, and the highest agreement between theoretical prediction and in-vivo data during level walking. Robot stride length during climbing, was between 3% and 90% lower than during level walking (Fig. 4a, b). The mean decrease in stride length accounted for 36%, which is well comparable to the 33% decrease in real lizards (compare red and blue six-sided stars in the last column of Fig. D6 in Supplementary S1). COT was between 30% and 1500% (mean 100%) greater (Fig. 4c, d). Both deviations were highest for small ROMs. Stability was also found to vary with ROM during climbing in SQUAMATAR, as the success rate was always 100% for small leg and spine ROMs and decreased with increases in either ROM (Fig. 4e). Among the 100% successful trials, only the one showing maximum stride length can be considered for the Pareto front, as it dominates all other points. The resulting Pareto front (Fig. 4f), which considers stride length, COT, and success rate, lies close along the front showing 0% success rate, indicating that if successful trials were obtained, optimal kinematics were likely to be found at even larger leg or spine ROM.

Discussion

This study aimed at exploiting the interplay between a robotic model, a vast biological data base, and a theoretical-mathematical model in order to stride length for short (b), medium (e), and long legs (h) vs leg and spine ROM. COT (unit-less) as obtained from current consumption per distance travelled, Eqn. (4). SQUAMATAR's stride length versus COT for short (c), medium (f), and long legs (i), together with the Pareto front, i.e., the set of all non-dominated points, (black crosses). The two distinguished Pareto-optimal points of maximum stride length (blue square) and of minimum COT (red square) are highlighted.

40 60 80 cost of transport (

500

400 300

200 100

investigate the consequences and trade-offs of LSU regarding the running speed, efficiency, and stability of lizard locomotion. To this end, we built both mathematical and robotic models and compared these with in-vivo movement data of climbing and running lizards, cf. Fig. 1.

Mathematical optimum predicts a limb-dominated movement pattern

Our mathematical model suggested two general predictions of squamate walking locomotion. The first is that the maximum stride length is independent of the leg ROM (where limb length was maximised as to just avoid collision), but instead equals twice the trunk length at maximum bending. Thus, secondly, the fastest strategy for a theoretical lizard would be to keep a straight spine and choose a leg ROM dependent on leg length (Eqn. (2) and Fig. 2f). When measuring the movement strategy chosen for a phylogenetically diverse range of lizards, moving both up and down vertical surfaces and on level ground, we could indeed confirm this tendency (Fig. E1 in Supplementary S1), but also found some deviation from this theoretically predicted optimum. The most common strategy was to limit movement of the spine to between 10°-30°, and to allow the limb ROM to vary between 60°-130°.

A comparison with the corresponding in-vivo stride lengths (Fig. 2c) showed that model predictions tended to underestimate the observed values, particularly for geckos and varanids. Lizards were inclined to have anatomically longer limbs than predicted, or to use a greater functional leg





cost of transport ()

Fig. 4 | **Theoretical predictions vs performance data from SQUAMATAR during vertical climbing.** Heatmap of theoretical predictions of stride length given by spine and leg ROMs overlain with data recorded from the SQUAMATAR robot shown in terms of TLS length (**a**) and as a percentage deviation from level walking data (**b**). COT of SQUAMATAR, given spine and leg ROMs, shown in absolute terms (**c**) and as a percentage deviation from level walking data (**d**). Climbing success rate of SQUAMATAR is shown (**e**) at different leg and spine ROMs with points of zero

success corresponding to white panels in (a-d). Contour lines in (c) and (e) are drawn for clarity. The three-dimensional Pareto front (cf. Fig. 3) containing stride length, success rate, and cost of transport recorded from SQUAMATAR is shown in (f). Symbols identifying the point of minimum COT (blue square), maximum stride length (red square), and maximum stride length at 100% success rate (green square) are also indicated in (a-e).

length to outperform the model in stride length. Presumably, this was achieved by overstepping their hind limbs in front of the fore limbs (see video in Supplementary S2), a condition explicitly excluded from the twodimensional model. Overstepping the hind limb over the fore limb is common in lizards, occurs more readily in animals with higher limb to trunk length ratios, and increases with speed^{32–36}. The use of moderate spinal bending by the lizards, which was predicted to be of no advantage by the model, suggests that spine bending becomes advantageous if limb collision is not a problem. Apparently, lizards could have outperformed the model further if they reduced their spine ROM, since this would have allowed for relatively longer limbs, and thus longer strides. Hence, maximising stride length alone does not seem to be the only objective for lizard locomotion. As other features, such as energy turnover or stability, are not easily measurable in living specimen, our robotic model was used to explore optimal kinematics.

Efficiency trade-offs may explain LSU in lizards

We validated our robotic model with mathematical predictions as we varied limb length. Here, short legs posed the problem of collision between feet and torso as well as long legs colliding with each other, both limiting the possible ROM (Fig. 3). Further, for each design, the measured stride length during walking matched the theoretical prediction, with increased stride length for increased spine and leg ROM (see Fig. 2a).

The robotic model was also able to reveal a new constraint associated with ROM: cost of transport. Using the medium leg design, we found a shallow COT minimum, not along the zero spine movement axis, but at a leg ROM between 70° and 90° and a spine apex ROM between 20° and 25° well within the range we found in vivo. Notably, regardless the leg length, COT at any given leg ROM seemed to decrease with increasing spine ROM and vice versa, suggesting that a combination of ROMs may be most energetically efficient. This energetic consideration might be one reason why lizards showed neither small leg ROM of less than 50° nor small spine apex ROM of less than 10°. To capture the trade-off between maximising stride length and minimising COT, we determined all Pareto-optimal points in the ROM landscape. These suggested that points of minimum COT were generally located at lower leg ROM than points of maximum stride length. However, the Pareto front was predominantly located at the ridge of limb collision. It can be conjectured that, had the feasible robotic ROM been larger, for example by allowing overstepping, the front might have been located at even higher leg ROM.

Thus, combining our mathematical and robotic models for walking has shown that a trade-off may exist between stride length and efficiency among squamates, which drives LSU. At first glance, our mathematical prediction in Eqn. (2) contradicts earlier hypotheses suggesting LSU may increase stride length (and thus speed)^{14,19-21,23,24}. However, previous studies only consider constant leg lengths, for which both our theoretical and robotic model likewise predicts an increase in stride lengths with spinal ROM (Figs. 2d and 3a, d, g). Our model predicts that relatively equal increases in stride length are afforded by increases in either ROM. If the speed of either motion is limited by muscle contraction velocity, greater locomotor speed should be achieved through simultaneous spine and leg bending, as the contraction speed of a muscle fibre depends on the number of sarcomeres in series per unit length. Real lizards use a complex combination of increases in stride length and stride frequency to locomote at faster speeds depending on their relative limb lengths and habitat^{37,38}, with the fastest lizards showing the lowest spine ROM, see Fig. E1 in Supplementary S1. Further investigations are required to fully explain changes in the pattern of limb and spine motions during locomotion among legged tetrapods. Our observation that a reduction in LSU may drive up COT at least offers a partial explanation to why moderate spinal motion is still present among diverse groups of extant quadrupedal amniotes^{8,39,40}.

Stability as an additional objective during climbing

Contrary to walking animals, many lizards usually climb using directional dependent pads^{41,42}. These require the force vector to be close to the surface, and to pull towards the body, i.e., lateral forces may be more important⁸. Lateral spine bending may allow increased lateral forces and therefore greater stability—an important factor for climbing as it prevents potentially catastrophic falling. Thus a third objective may occur beside speed and efficiency in climbing lizards, with species optimising their stride to maximise stability. Trade-off between speed and stability have previously been shown for lizards running on narrow beams^{43,44}, but the underlying mechanism remains unclear.

Using our robotic model, we show a general decrease in stability at high limb and spine ROM (Fig. 4e), suggesting a practical limit to both. For a combined sum of leg ROM and spine apex ROM of above ~90°, the robot failed to conduct a single full stride up the wall. This was far less than observed for a majority of lizards and mainly occurred due to the robot's claw-carpet interaction, which seemed to be insufficient to bear the (presumably greater) front-aft and lateral forces at high limb and spine ROM. The use of smaller ROMs, however, magnified a 'performance penalty' found in vertical climbing compared to level walking. During vertical climbing, the use of smaller ROMs caused greater decreases in stride length and greater increases in COT than larger ROMs. This 'performance penalty' was not only confined to the robotic model - which showed a ~36% drop in mean relative stride length during climbing versus level locomotion-but was also found in real lizard data at a similar magnitude (~33%, cf. Fig. D6 in Supplementary S1) Both changes were presumably observed due to the absolute effect of gravitational settling of moving parts, which likely plays a relatively greater role for absolute small movements. Again weighing these three different objectives, we obtain a Pareto front within a leg ROM between 50°-70° and spine ROM between 20°-40°. Hence, even though the stability criterion seems to favour smaller leg ROM, the maximisation of stride length and the minimisation of COT result in an optimum that overlaps in-vivo values for the limb and spine ROM.

Robot- and theory-informed biological implications

Analysing the walking and climbing data from SQUAMATAR in combination with the predictions from the theoretical model provides new possibilities to interpret in-vivo data and to explain the existence of biological features such as LSU.

From Table 1 and Figs. D2–D6 in Supplementary S1, several conclusions can be drawn. First, downward climbing lizards use less spine and leg ROM. Our investigations on SQUAMATAR, particular Fig. 4 left, suggest that this may indicate a preference for stability over speed or efficiency during head down motion, which agrees with the findings of ref. 45. Likewise, comparatively small spine and leg ROM are found in semiarboreal lizards during climbing, again indicating a potential habitat-driven stability requirement. Interestingly, arboreal lizards show quite the opposite, i.e., higher spine and leg ROM. We speculate that they have either more efficient claws and adhesive pads⁴⁶ or use different kinematic parameters⁴⁵ to achieve higher intrinsic stability, potentially circumventing the trade-off between ROM and stability.

Second, our mathematical model predicted that increased spine ROM leads to increased stride length for a given leg length, but if maximum leg length before collision is considered, then increasing spine ROM actually results in a decreased stride length (Eqn. (2) and Fig. 2). From the robotic model, with fixed limb length, we derived that increased spine ROM increased efficiency but decreased stability.

Here, we give two rationales for these observations, again based on the theoretical model. Both are depicted in Fig. 5 for a rigid-spine as well as a curved-spine walker, cf. Fig. 7. To estimate comparable efficiency of a single step (half a stride), we chose $\ell_{leg} = 1/2$ and the same step length of both walkers. In particular, we set $\phi_{base} = \pi/4$ and $\phi_{leg} = \pi/3$ for the curved walker and calculated the leg ROM for the rigid-spine walker such that it covered the same step length. Then, we calculated the path of the COM by assuming uniform mass distribution along the whole theoretical model. Calculation of the COM of the curved spine is derived in Supplementary S1 (Section B). Subsequently, we calculated the distances between the centres of pressure (COP), i.e., front left and hind right foot, and the COM at each instance of the step. Overall, we find that bending the spine decreases the distance of the COM to the COP (see Fig. 5c). This decreased distance likely reduces the moment, and therefore the energy needed to move a mass on a curved path around the COP, explaining our observed relation between increased spine ROM and efficiency. Alternatively, the stability of the motion is assumed to scale with the base area spanned by the two COPs, i.e., the product of the distances parallel and orthogonal to the trunk axis, respectively. A base area of zero can be considered as both feet being placed colinearly with the trunk axis. Our calculation shows that this base area decreases with both increased spine and leg ROM, yet this decrease appears more rapid along the spine ROM axis, reflecting observation of reduced stability (see Fig. 4e). These two rationales well agree with our robot-model behaviour and can hence be considered possible explanations for the significance of LSU among squamates.

As a special limit case of LSU usage, we consider body designs without legs such as snakes or limbless lizards, e.g., *Pygopodidae*. Considering this limit case of $\ell_{leg} \rightarrow 0$ (and consequently $\phi_{leg} \rightarrow 0$) we see that our model no longer applies, as the maximum stride length also tends to zero. In this case, another concept of geometric mechanics becomes necessary (cf.⁶) to describe the LSU and its interplay with stride length. Yet, even for very small maximum leg length, it becomes apparent from Eqn. (2) that only vast spinal ROM can compensate the involution of legs and ensure considerable stride lengths.

Limitations

Our biological data, as well as both the robotic and the theoretical model, suffer from various limitations, which are addressed in the following. Naturally, animals do not behave as desired, e.g., running at a particular speed or in reproducible patterns. Additionally, lizards change their locomotion pattern when climbing head-up versus head-down⁴⁵. Hence, a huge variability is inherent to the set of kinematic data, whose underlying factors cannot be fully resolved. A few of those factors, which were not captured by the theoretical model, include (i) leg posture (e.g., crouched vs straight)⁴⁷, (ii) gait dynamics in between start and end position of a stride (e.g., trotting vs running vs walking)²⁶, or (iii) corresponding spine dynamics (e.g., standing vs travelling wave)⁶. Further, neither the theoretical nor the robotic model accounted for differences in front- and hind-limb lengths⁴⁸, overstepping of feet (see corresponding video in Supplementary S2), variants of motor control⁴, or elastic energy storage of tendon material⁴⁹. These would all be exciting directions for further research.



Maths, biology, and robots: an insightful triology

Mathematical models allow theoretical predictions and extrapolations of (biological) system behaviour beyond the boundaries of what can be observed, see e.g., ref. 50. Yet bio-inspired robots allow for a direct interaction with the natural environment, which might be too complex for simple models^{4,6}. The robotic model itself can again be validated by the mathematical model, usually with less degrees of freedom than the biological system.

From this work, we were able to determine several engineering criteria which may be important considerations when designing limbed robotic devices capable of traversing a wide variety of environments. Lateral spine undulation need not be an important consideration if maximising robotic speed is the primary objective, but can be an important for reducing energy consumption. Similarly, LSU may expand the possible kinematic space available permitting the the use of fast, stable and efficient robotic strides.

This work, taken together with other studies using robots to investigate optimal sprawling gaits and neural control mechanisms of sprawling locomotion^{46,10,22,51,52} provides an exciting paradigm to unravel the complex interaction between multiple selection pressures on locomotor evolution. Indeed, our modelling and robotic systems have explained several biological observations, detailing the extent of evolutionary trade-offs between three key performance criteria, speed, efficiency and stability. By mapping our empirically collected walking and climbing lizard data over the landscape produced by our mathematical and robotic models, we can determine the relative strength of these competing selection criteria. Identifying the phylogenetic and phenotypic constraints which have moved different groups of lizards into different parts of this performance landscape will be a further fruitful area of biological research.

Methods

Data collection and processing

A total of n = 320 lizard running video sequences were analysed for this study. Data had been collected as described earlier¹⁶, including 44 species of four different lizard families: dragons (Agamidae, $n_D = 74$), geckos (Gekkota, $n_G = 154$), skinks (Scindidae, $n_S = 21$), and varanids (Varanidae, $n_V = 71$), see Fig. 6a. All videos showed the dorsal view on either upwards

 $(n_{up} = 218)$, downwards $(n_{down} = 51)$ or level walking $(n_{level} = 51, \text{ only var-anids})$. 22 markers were tracked in each frame using the marker-less poseestimator toolkit *DeepLabCut*⁵³, see Fig. 6b. From the total of 665 videos available, we chose those exhibiting a >99% confidence of the five spinal markers between (and including) shoulder girdle to hip girdle, as well as the four feet markers, for at least two consecutive strides, i.e., four consecutive steps. Note that whenever we hereinafter refer to the 'spine', we only consider the thoraco-lumbar spine (TLS), i.e., the region between shoulder and hip girdle.

We extracted spinal ROM, leg ROM and leg lengths from the selected trials. To estimate spinal ROM, the middle spine marker was assumed to represent the spinal apex during maximum lateral bending. Accordingly, the sum of maximum deviations from this marker to either side of the body axis (shoulder girdle to hip girdle marker) was considered the spine (apex) ROM. For the leg ROM, the difference between maximum and minimum angle enclosed by the girdle-to-foot axis and the body axis during each stride was determined (Fig. 6c). See Fig. D1 in Supplementary S1 for a species-specific plot on the ROM data. The effective front and hind leg lengths were determined by the maximum Euclidean distance between shoulder girdle and front foot marker or between hip girdle and hind foot marker, respectively, during the stride series. Values for the left and right limbs were averaged together. Last, the stride length was determined as the mean displacement of hip girdle and shoulder girdle marker during the first full stride of the stride series.

Feature analysis and statistical tests

Besides the kinematic data presented in Section "Data collection and processing", some meta-data were collected for each individual. In particular, features such as 'family' (dragons, geckos, skinks, varanids), 'direction of walking or climbing' (upwards, downwards or level), 'habitat' (terrestrial, semi-arboreal or arboreal), and 'speed' (slow, medium, fast) were investigated. To decide whether these features had an influence on the overall lizard geometry (spine ROM, leg ROM, leg length), two tests were performed to detect possible statistical differences.

First, a Hotelling's T^2 -test⁵⁴ on the three-dimensional mean of the geometric data (leg length, leg ROM, spine ROM) was performed. This test served as a natural generalisation of the univariate Student's *t*-test when

Fig. 6 | **Overview of in-vivo data collection.** Kinematic data were collected during climbing and level walking from 44 species from 4 families (**a**) with varying body plans using motion tracking of body points (**b**) which were then used to calculate limb and spine ROMs (**c**).

considering multiple observations simultaneously. It was assumed that the data followed a multivariate normal distribution around the mean (centroid) and that covariance matrices were sufficiently similar. However, these assumptions were not tested. The null hypotheses always assumed that the mean of each two features within a cluster was the same. Second, a Cuzick-Edwards test⁵⁵ was performed to determine the distinctness between each two clusters within a feature. Originally developed to detect diseases in a population, one cluster serves as a "case", whereas the other is the "control". The null hypothesis assumed that cases were randomly distributed among the controls. For each "case" element, the *k* nearest neighbours (*k*NN) were calculated by means of an Euclidean distance. For our analysis, we chose k = 3. Subsequently, the number of "cases" among these *k*NN were counted and compared to their expected value. If more cases than expected were found in the neighbourhood of other cases, the null was rejected, indicating that the "cases" formed a distinct cluster.

Walking with a curved spine: a straightforward geometric model In this section, we explore the advantages and disadvantages of utilising lateral bending of the TLS during forward locomotion. In particular, the interplay between the amounts of spinal bending, leg ROM, and leg length is investigated. For this purpose, we propose a two-dimensional theoretical 'lizard', whose forward motion is achieved by moving its legs such that shoulder and hips describe a circular motion around the two feet on the ground. Left front and right hind leg are assumed to move simultaneously for one step, so are right front and left hind leg for the second step of the stride. Leg axes are assumed to be rigid and orthogonal to the trunk axis (direct distance between shoulder and hip) in neutral position. TLS length is further assumed to be unity and thus leg length (ℓ_{leg}) as well as trunk length (ξ), are given in relative units. Leg ROM (ϕ_{leg}) and spine apex ROM (ϕ_{apex})—measured as the range between maximum deflection to either side – serve as independent variables.

Spinal undulation: Increasing stride length per leg length. For a start, we assume ℓ_{leg} to be arbitrary but fixed. Given that fixed leg length, we want to find the combination of ϕ_{leg} and ϕ_{apex} that maximises the travel distance ΔS . In a first case, we imagine our theoretical lizard to have a rigid TLS, i.e., $\phi_{apex} = 0$ for the whole motion. Hence, stride length



(a) lizard experiments

Fig. 7 | Two-dimensional theoretical model of lizard locomotion. The postures of a rigid-spine (a) and curved-spine (b) two-dimensional model lizard are shown at the beginning (black) and end (blue) of a single stride. Dashed black lines indicate the neutral position, where legs are orthogonal to the thoraco-lumbar spine (TLS), and the dotted line on the right indicates the unbent trunk axis, i.e., the axis connecting shoulder and hip, which corresponds to the spine axis on the left. Leg length ℓ_{leg} was chosen to be half the TLS length in both configurations. Leg ROM ϕ_{leg} equals $\pi/4$ in (**a**) and $\pi/8$ in (**b**) configuration. Spine base ROM ϕ_{base} (see Section B in Supplementary S1) in (**b**) was chosen as $\pi/3$, and total ROM can be calculated by $\phi_{tot} = \phi_{leg} + \phi_{base}$ (here: 82.5°). According to the law of cosines and basic trigonometric addition formulas, the travel distance ΔS can be calculated by $\Delta S_r = 4$. $\sin(\phi_{leg}/2) \cdot \ell_{leg}$ and $\Delta S_c = 4 \cdot \sin(\phi_{tot}/2) \cdot \ell_{leg}$ in the rigid and curved configuration, respectively. Hippre/post and shoulderpre/post marks the position of the hip respectively the shoulder at start and end of the stride. The intermediate resolution of a single step of both models is shown in (c) and (d) with front left and hind right foot on the ground (coloured dots, connected by dotted lines for reference). Angles were chosen to ensure the same walking distance, i.e., $\phi_{leg} = 105^{\circ}$ for the rigid walker and $\phi_{leg} = 60^\circ$, $\phi_{base} = 45^\circ$ for the curved spine walker.



exclusively depends on ϕ_{leg} , see Fig. 7a. Applying basic trigonometry yields that travel distance ΔS_r in the rigid case equals $4 \cdot \sin(\phi_{leg}/2) \cdot \ell_{leg}$, which is maximised for $\phi_{leg} = \pi$. Hence, a rigid walker's stride covers at most two leg lengths at a leg ROM of 180°.

For a second variation – a curved spine – we assumed parabola-shaped TLS. For geometric peculiarities of this shape, see Supplementary S1 (Section B). Similar to the rigid case, the curved-spine lizard exhibits a travel distance of $\Delta S_c = 4 \cdot \sin(\phi_{tot}/2) \cdot \ell_{leg}$, where $\phi_{tot} = \phi_{leg} + \phi_{base}$, see Fig. 7b. For the relation between the spine base ROM ϕ_{base} and the spine apex ROM ϕ_{apex} the relation $\tan(\phi_{base}/2) = 2 \cdot \tan(\phi_{apex}/2)$ applies, see again Section B in Supplementary S1. Maximum travel distance likewise is achieved at $\phi_{tot} = \pi$. From this model scenario, we conclude that aiming for maximum stride length per leg length resulted in leg ROM and spine ROM to add up to 180°. Hence, if ℓ_{leg} is bounded by physical or biological constraints, spinal bending can replace the missing leg ROM in order to achieve two leg lengths per stride.

Maximum leg length: a problem of collision. Given a maximum stride length of two leg lengths, regardless the deployment of lateral spinal bending, it would seem reasonable for the theoretical lizard to increase ℓ_{leg} as much as possible. However, as legs become longer, their paths eventually collide during walking. In the example of a rigid spine, a relative leg length of greater than half the TLS length results in a collision, e.g., the retracted right front foot collides during protraction with the already protracted right hind foot.

To estimate the maximum collision-avoiding leg length, we exploit the symmetry of the theoretical lizard. Examining, without loss of generality, the right hind leg, a collision occurs if spinal bending plus leg ROM results in the foot being placed in front of the spinal apex (see Supplementary S1, Fig. B1). In other words, if half the travel distance is greater than half the trunk length ξ . Hence, the maximum leg length given ϕ_{leg} and ϕ_{base} (and thus ξ , see

Section B in Supplementary S1), can be calculated by

$$\ell_{leg,max} = \frac{\xi}{2 \cdot \sin\left(\frac{1}{2} \cdot (\phi_{leg} + \phi_{base})\right)} \tag{1}$$

Maximum stride length depends solely on trunk length. Combining the considerations from the two previous Sections "Spinal undulation: Increasing stride length per leg length" and "Maximum leg length: A problem of collision", we find that maximum travel distance during a single stride (two steps) for given ϕ_{leg} and ϕ_{base} is given by

$$\Delta S_{max} = 4 \cdot \sin\left(\frac{1}{2} \cdot (\phi_{leg} + \phi_{base})\right) \cdot \ell_{leg,max} = 2 \cdot \xi.$$
 (2)

Interestingly, ΔS_{max} is independent of leg ROM, but equals the trunk length ξ at maximum bending, which itself non-linearly depends solely on ϕ_{base} as shown in Section B of Supplementary S1. As ξ is maximised for $\phi_{base} = 0$, from a purely geometric point of view, the optimal body plan for the theoretical lizard would be to inhibit spinal bending and choose leg ROM depending on its actual leg length.

SQUAMATAR: A robot mimicking lizard locomotion

We developed a lizard inspired robot capable of level running and climbing on inclined or vertical surfaces by employing a directional dependent adhesive mechanism (see Fig. 8 and video material Supplementary S2). The robot possesses modifiable leg length morphology, alongside adjustable kinematic characteristics, including spine ROM, limb ROM, and stride speed.

Lizard inspired modular robot bauplan and movement. To be able to mimic a lizard-like stride employing LSU and limb movement, 14 vital

Fig. 8 | Abstraction and technical illustration of SQUAMATAR robot. a Vital joints as identified for a lizard-like stride. b Top view of the lizard-inspired robot with the mimicked joints. Coloured arrows indicate rotational DOFs corresponding to lizard joints. Main image depicts robots with default leglength configuration ($\ell_r = 105$ mm). Short ($\ell_r = 47.2$ mm) and long ($\ell_r = 170$ mm) leg configurations are shown as inlays. Measurements as used for the conversion of the ROMs in robot and theoretical model are depicted (c) Angle comparison for robot and theoretical model in a bent position, see Supplementary S1 (Section C) for details. d Side view CAD-assembly of the robot with the centre of mass marked.



joints in the lizard bauplan were identified (Fig. 8a), abstracted, and implemented in the robot. All joints were simplified as actuated one degree of freedom (DOF) revolute joints. Two joints located in the trunk of the robot enable a body bending motion, therefore mimicking continuous lateral spinal bending (Fig. 8b, red circles). Four actuated shoulder joints were used to control leg ROM (Fig. 8b, blue circles). For raising and lowering the feet, a parallel linkage was implemented, moving the lower limbs in an arc-like trajectory while keeping the claws at an acute (~10°) angle relative to the surface (see Fig. 8b,d). This allowed for attachment, during the lowering and pulling phase, and detachment, during the raising and pushing phase of foot movement. The movement of legs and spine determined positioning and rotation of the feet and claws in an angle to the vertical axis as seen in Fig. 8c and expressed by

$$\psi_{wrist} = \frac{1}{2} \cdot \left(\psi_{spine} + \psi_{leg} \right). \tag{3}$$

Note that all robot angles will hereinafter be denoted by the symbol ψ , whereas all angles of the theoretical model will be denoted by ϕ . The four remaining actuated revolute joints were implemented at the wrists, moving synchronously with the leg and spine angles. This bio-inspired bauplan gives the robot the ability to perform a lizard-like stride, driven by simultaneous lateral bending and movement of legs, while attaching two diagonal feet to the surface to pull forward. Climbing poses additional challenges on animals or robots, as an overturning moment now pulls the fore feet off the wall. To counteract this, a passive tail was designed to support the robot by including a third contact point. The adjustable leg length morphology is provided by easily exchangeable carbon fibre tubes, therefore the leg length can be adjusted via hardware modifications. The robot's construction shows symmetry with respect to the body axis and electronic components were arranged in order to position the centre of mass (COM) as low as possible (Fig. 8d).

Fabrication, electronic components and programming. Polymer fused layer modelling (3D printing) was used to design most parts of the robot (Prusa MK3, 1.75 mm PLA), while a few parts were laser-cut from 3 mm acrylic glass. For lifting the feet, servo motors of type B2122 (Adafruit, New York) were used. Each foot was equipped with a set of five nails angled in 15°, functioning as claws. Spine and leg were actuated by more powerful DSS-M15S (dfrobot, Shanghai) servo motors, while 270° servo motors (dfrobot, Shanghai) were used for the actuation of the wrist angle to allow for larger achievable angles. Further, for measuring the performance metrics and enabling easy parameter modification as well as automatic data collection, the robot was measured with the Gravity I2C Wattmeter (dfrobot, Shanghai). For measuring linear acceleration, angular acceleration, pitch, yaw and roll (stability), the 6-Axis inertial measurement unit (IMU) Gravity SEN0250 (dfrobot, Shanghai) was implemented. For distance sensing (speed), the robot was equipped with a time-of-flight (ToF) laser sensor VL53L1X (Adafruit, New York). The total weight of the robot was 841 g.

To control the robot, a microprocessor ESP32-DEVKITC (Esspressif Systems, Shanghai) was used. All servos were connected to a PCA9685 servo shield (Adafruit, New York). An overview of the simplified electronic circuit can be seen in Fig. F1a in Supplementary S1. Motor movement was controlled following a sigmoidal function (Fig. F1b in Supplementary S1), incrementally setting the motor angle. Hence, each movement was "smoothed" by exponential acceleration and deceleration as observed in lizards⁸. The input voltage of the circuit was regulated to 5 V with a D23V90F5 9A voltage regulator (Polulu, Winfield). The ESP32 ran a C++ script to coordinate the stride and electronic components, e.g., positioning the servo motors, controlling the sensors, gathering and storing sensor data, and making the stride parameters accessible. To allow user input, a soft AP (WIFI) was opened by the ESP32. When connected, the robots web interface could be accessed and used to input stride parameters. Input options in the web interface were 'number of strides', 'stride speed', 'leg ROM', 'spine ROM', 'front wrist angle', 'hind wrist angle', and a variable to start a run. After each run, the collected sensor data were downloaded through the web interface.

Experiments and data analysis. To establish a consistent running and climbing surface for the robotic trials, a racetrack was built by gluing a marine carpet on a 2.5 × 1.5 m wooden board (Bunnings, Australia). For level running trials the board was laid flat on the ground while for climbing experiments it was set up vertically (90°), see Fig. F2 in Supplementary S1 as well as video material in Supplementary S2. At the top of the board on a 90° angle a reflective panel (Corflute board with reflective mirror foil) was mounted. This was necessary to reflect the laser of the ToF sensor reliably in order to generate precise distance measurements. The power input for the robot came either from an external laboratory power supply or an on-board battery pack, set to 32.5 V. A rope was used to prevent the climbing robot from impacting the ground during slips from the carpet. For the level running trials all three leg (tube) lengths ($\ell_r = 47.2 \text{ mm}, \ell_r = 105 \text{ mm}, \ell_r = 170 \text{ mm}$) were used, while for the climbing trials only the medium leg length of 105 mm was used, as explained further below. These tube lengths translate to relative leg lengths (as compared to the lizards) of $(\ell_r + \ell_s)/(2 \cdot \ell_{S_1} + \ell_{S_2}) \in \{0.29, 0.48, 0.68\}.$ For the level running trials, combinations of limb ROM and spine ROM were used in 10° steps. Limb ROM varied from 0° to 170°, while spine ROM varied from 0° to 70°. These values were theoretical goals since in practice the feet For each ROM combination, ten trials were performed. The speed setting was set equally for all trials, with a total stride duration of approximately 5.4 seconds and the natural wrist angle for all trials was set to 0°. Multiple conditions caused the robot to stop the stride: (i) after successfully completing 11 steps, (ii) when reaching the top (distance to the panel \leq 30 cm), or (iii) when the sensor showed a maximum reading, meaning it either fell from the wall or climbed in such an angle that the laser of the distance sensor did not reflect from the top panel. In this latter case, all data for subsequent strides were set to 0.

Analysis of the gathered data was done in MatLab (Version R2022b, Mathworks, Natick, USA). Additional to the maximally achieved stride length, two normalised measures for efficiency (cost of transport, COT) and stability (success rate) were calculated. Since we aimed to compare the maximum stride lengths of the robot with those of the real lizards, a conversion of the geometry was necessary, i.e., the robot's spine and leg ROM (ψ_{spine}, ψ_{leg}) were to be transformed in effective leg ROM and spine apex angle (ϕ_{apexo}, ϕ_{leg}), respectively, see Fig. 8 and Supplementary S1 (Section C) for details. The COT was calculated using the equation

$$COT [] = \frac{E[J]}{m[g] \cdot g[m/s^2] \cdot d[m]} = \frac{I[A] \cdot U[V] \cdot t[s]}{m[g] \cdot g[m/s^2] \cdot d[m]}, \quad (4)$$

where the Energy (E) necessary to move a mass (m) a certain distance (d) against gravity (g) can also be expressed by the electric current (I), the voltage (U), and the time (t), which were available sensor outputs. Corresponding units are given in brackets, including the unit-less COT. The likewise unit-less success rate was determined after performing all ten trials for each of the robot's configurations and dividing the number of trials with at least one successful stride by 10.

Data availability

This work contains Supplementary Materials S1 (data tables, figures, and auxiliary calculations) and S2 (video material of lizards and the robotic model SQUAMATAR). Source code, CAD designs, and other information on the robotic model can be found at the git repository: https://github.com/starrobin34/SQUAMATAR-lizard-inspired-robot-Coordinating-limbs-and-spine-Pareto-optimal-locomotion.

Code availability

This work contains supplementary materials S1 (data tables, figures, and auxiliary calculations) and S2 (video material of lizards and the robotic model SQUAMATAR). Source code, CAD designs, and other information on the robotic model can be found at the git repository: https://github.com/starrobin34/SQUAMATAR-lizard-inspired-robot-Coordinating-limbs-and-spine-Pareto-optimal-locomotion.

Received: 7 November 2023; Accepted: 10 May 2024; Published online: 22 July 2024

References

- 1. Wieber, P.-B., Tedrake, R. & Kuindersma, S. Springer Handbook of Robotics (Springer, 2016).
- Silva, M. F. & Tenreiro Machado, J. A. A historical perspective of legged robots. J. Vib. Control 13, 1447–1486 (2007).
- Squyres, S. W. et al. Exploration of victoria crater by the Mars rover opportunity. *Science* 324, 1058–1061 (2009).
- Ijspeert, A. J. Amphibious and sprawling locomotion: from biology to robotics and back. *Annu. Rev. Control, Robot. Auton. Syst.* 3, 173–193 (2020).
- Beck, H. K., Schultz, J. T. & Clemente, C. J. A bio-inspired robotic climbing robot to understand kinematic and morphological determinants for an optimal climbing gait. *Bioinspiration Biomim.* **17**, 016005 (2021).

- Chong, B., Wang, T., Erickson, E., Bergmann, P. J. & Goldman, D. I. Coordinating tiny limbs and long bodies: geometric mechanics of lizard terrestrial swimming. *PNAS* **119**, e2118456119 (2022).
- Crespi, A., Karakasiliotis, K., Guignard, A. & Ijspeert, A. J. Salamandra Robotica II: an amphibious robot to study salamander-like swimming and walking gaits. *IEEE Trans. Robot.* 29, 308–320 (2013).
- Schultz, J. T., Beck, H. K., Haagensen, T., Proost, T. & Clemente, C. J. Using a biologically mimicking climbing robot to explore the performance landscape of climbing in lizards. *Proc. R. Soc. B* 288, 20202576 (10 pages) (2021).
- Chowdhury, A. R., Kumar, V., Kumar, R., Prasad, B. & Panda, S. K. Kinematic study and implementation of a bio-inspired robotic fish underwater vehicle in a lighthill mathematical framework. *Robot. Biomim.* 1, 1–16 (2014).
- Nyakatura, J. A. Reverse-engineering the locomotion of a stem amniote. *Nature* 565, 351–355 (2019).
- 11. Pontzer, H. Effective limb length and the scaling of locomotor cost in terrestrial animals. *J. Exp. Biol.* **210**, 1752–1761 (2007).
- 12. Carrier, D. Activity of the hypaxial muscles during walking in the lizard iguana iguana. *J. Exp. Biol.* **152**, 453–470 (1990).
- Daan, S. & Belterman, T. Lateral bending in locomotion of some lower tetrapods, I and II. Proc. K. Nederlandse Akademie van. Wetenschappen C 71, 245–266 (1968).
- Ritter, R. Lateral bending during lizard locomotion. J. Exp. Biol. 173, 1–10 (1992).
- Cieri, R. L., Hatch, S. T., Capano, J. G. & Brainerd, E. L. Locomotor rib kinematics in two species of lizards and a new hypothesis for the evolution of aspiration breathing in amniotes. *Sci. Rep.* **10**, 7739 (2020).
- 16. Schultz, J. T. et al. Tail base deflection but not tail curvature varies with speed in lizards: results from an automated tracking analysis pipeline. *Integr. Comp. Biol.* **61**, 1769–1782 (2021).
- Wiens, J. J., Brandley, M. C. & Reeder, T. Why does a trait evolve multiple times within a clade? repeated evolution of snakelike body form in squamate reptiles. *Evolution* 60, 123–141 (2006).
- Sites, J. W.Jr., Reeder, T. W. & Wiens, J. J. Phylogenetic insights on evolutionary novelties in lizards and snakes: sex, birth, bodies, niches, and venom. *Annu. Rev. Ecol. Evol. Syst.* 42, 227–244 (2011).
- Karakasiliotis, K. & Ijspeert, A. J. Analysis of the terrestrial locomotion of a salamander robot. *IEEE/RSJ International Conference on Intelligent Robots and Systems* 1–6 (2009).
- Nam, W. et al. Kinematic analysis and experimental verification on the locomotion of gecko. J. Bionic Eng. 6, 246–254 (2009).
- Shapiro, L. J., Demes, B. & Cooper, J. Lateral bending of the lumbar spine during quadrupedalism in strepsirhines. *J. Hum. Evol.* 40, 231–259 (2001).
- 22. Wang, W. et al. Lateral undulation of the flexible spine of sprawling posture vertebrates. *J. Comp. Physiol. A* **204**, 707–719 (2018).
- 23. Zhang, C. & Dai, J. Trot gait with twisting trunk of a metamorhic quadruped robot. *J. Bionic Eng.* **15**, 42235 (2018).
- Jones, K. E., Dickson, B. V., Angielczyk, K. D. & Pierce, S. E. Adaptive landscapes challenge the "lateral-tosagittal" paradigm for mammalian vertebral evolution. *Curr. Biol.* **31**, 1883–1892 (2021).
- Barclay, O. R. The mechanics of amphibian locomotion. *J. Exp. Biol.* 23, 177–203 (1946).
- Chong, B. et al. Coordination of lateral body bending and leg movements for sprawled posture quadrupedal locomotion. *Int. J. Robot. Res.* 40, 747–763 (2021).
- Jindrich, D. L. & Full, R. J. Many-legged maneuverability: dynamics of turning in hexapods. J. Exp. Biol. 202, 1603–1623 (1999).
- Chen, J., Peattie, A. M. & Full, K. A. R. J. Differential leg function in a sprawled-posture quadrupedal trotter. *J. Exp. Biol.* 209, 249–259 (2006).
- Goldman, D. I., Chen, T. S., Dudek, D. M. & Full, R. J. Dynamics of rapid vertical climbing in cockroaches reveals a template. *J. Exp. Biol.* 209, 2990–3000 (2006).

- Wang, W., Wu, S., Zhu, P. & Liu, R. Analysis on the dynamic climbing forces of a gecko inspired climbing robot based on GPL model. *IEEE Conference on Intelligent Robots and Systems (IROS), Hamburg, Germany* 3314–3319 (2015).
- 31. J-Gould, S. *The Structure of Evolutionary Theory* (Belknap Press, 2002).
- Irschick, D. J. & Jayne, B. C. Comparative three-dimensional kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards. *J. Exp. Biol.* **202**, 1047–1065 (1999).
- Kubo, T. Extant lizard tracks: variation and implications for paleoichnology. *Ichnos* 17, 187–196 (2010).
- Padian, K. & Olsen, P. E. Footprints of the Komodo Monitor and the trackways of fossil reptiles. *Copeia* **1984**, 662–671 (1984).
- Preuschoft, H. Understanding Body Shapes of Animals: Shapes as Mechanical Constructions and Systems Moving on Minimal Energy Level (Springer, 2022).
- Urban, E. K. Quantitative study of locomotion in teiid lizards. *Anim.* Behav. 13, 513–529 (1965).
- Clemente, C. J., Withers, P. C., Thompson, G. G. & Lloyd, D. Lizard tricks: overcoming conflicting requirements of speed versus climbing ability by altering biomechanics of the lizard stride. *J. Exp. Biol.* **216**, 3854–3862 (2013).
- Granatosky, M. C. & McElroy, E. J. Stride frequency or length? A phylogenetic approach to understand how animals regulate locomotor speed. *J. Exp. Biol.* **225**, jeb243231 (2022).
- Bertram, J. E. A. & Gutmann, A. Motions of the running horse and cheetah revisited: fundamental mechanics of the transverse and rotary gallop. *J. R. Soc. Interface* 6, 549–559 (2009).
- Hildebrand, M. Motions of the running cheetah and horse. J. Mammal. 40, 481–495 (1959).
- Autumn, K. et al. Dynamics of geckos running vertically. J. Exp. Biol. 209, 260–272 (2006).
- Clemente, C. J. & Federle, W. Pushing versus pulling: division of labour between tarsal attachment pads in cockroaches. *Proc. R. Soc. B Biol. Sci.* 275, 1329–1336 (2008).
- Losos, J. B. & Sinervo, B. The effects of morphology and perch diameter on sprint performance of anolis lizards. *J. Exp. Biol.* 145, 23–30 (1989).
- Wilson, R. S., Husak, J. F., Halsey, L. G. & Clemente, C. J. Predicting the movement speeds of animals in natural environments. *Integr. Comp. Biol.* 55, 1125–1141 (2015).
- Schultz, J. T., Labonte, D. & Clemente, C. J. Multilevel dynamic adjustments of geckos (Hemidactylus frenatus) climbing vertically: head-up versus head-down. *J. R. Soc. Interface* **20**, 20220840 (2023).
- 46. Turnbull, G. et al. The influence of claw morphology on gripping efficiency. *Biol. Open* **12**, 059874 (2023).
- Zaaf, A., Herrel, A., Aerts, P. & De Vree, F. Morphology and morphometrics of the appendicular musculature in geckoes with different locomotor habits (Lepidosauria). *Zoomorphology* **119**, 9–22 (1999).
- Foster, K. L., Garland, T. Jr., Schmitz, L. & Higham, T. E. Skink ecomorphology: forelimb and hind limb lengths, but not static stability, correlate with habitat use and demonstrate multiple solutions. *Biol. J. Linn. Soc.* **125**, 673–692 (2018).
- Dick, T. J. M. & Clemente, C. J. How to build your dragon: scaling of muscle architecture from the world's smallest to the world's largest monitor lizard. *Front. Zool.* **13**, 1–17 (2016).
- 50. Günther, M. et al. Rules of nature's formula run: muscle mechanics during late stance is the key to explaining maximum running speed. *J. Theor. Biol.* **523**, 110714 (43 pages) (2021).
- Ijspeert, A. J., Crespi, A., Ryczko, D. & Cabelguen, J.-M. From swimming to walking with a salamander robot driven by a spinal cord model. *Science* **315**, 1416–1420 (2007).

- 52. Zhong, B. et al. Coordination of back bending and leg movements for quadrupedal locomotion. *Robot. Sci. Syst. XIV* **40**, 747–763 (2018).
- 53. Mathis, A. et al. DeepLabCut: markerless pose estimation of user-defined body parts with deep learning. *Nat. Neurosci.* **21**, 1281–1289 (2018).
- 54. Hotelling, H. The generalization of Student's ratio. *Ann. Math. Stat.* **2**, 360–378 (1931).
- Cuzick, J. & Edwards, R. Spatial clustering for inhomogeneous populations. J. R. Stat. Soc. Ser. B (Methodol.) 52, 73–104 (1990).

Acknowledgements

We thank Tasmin Proost, Rishab Pilai, Mitchell Hodgson, and Taylor JM Dick for help during the collection of in-vivo lizard climbing and running data. We further thank Daniel Ortiz-Barrientos for his inspiration regarding the investigation of Pareto optimality. This work was supported by a postdoc fellowship of the German Academic Exchange Service (DAAD) granted to RR and by and Australian Research Council (ARC) discovery grant awarded to CJC (DP180100220).

Author contributions

R.R. wrote the main manuscript text, developed the mathematical model, conducted the data/model analysis, and prepared the figures. R.C. conducted animal experiments, extracted kinematic data, wrote the introduction as well as the biological discussion, and helped designing figures. J.S. conducted animal experiments, helped designing figures, and supported the robot experiments. R.M. built the robot, conducted the robot experiments, and wrote the robot specifics. C.C. supervised the animal and robotic experiments and wrote the introduction as well as the biological discussion. All authors reviewed the manuscript.

Funding

Open Access funding enabled and organized by Projekt DEAL.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s44182-024-00011-2.

Correspondence and requests for materials should be addressed to Robert Rockenfeller.

Reprints and permissions information is available at http://www.nature.com/reprints

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2024