Locomotor Performance of Eremias velox on Different Substrates and Its Correlation with Morphological Traits: Postprint

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Date: 2020-06-21T00:00:00+00:00

Abstract

Using 22 adult Eremias velox (12 females, 10 males) collected from the Tukai Desert in Huocheng County, Xinjiang, we measured 11 external morphological traits and body mass, and conducted locomotor performance tests at optimal temperature to investigate the locomotor performance of E. velox on different substrates and its correlations with morphological traits. The results showed that male individuals had significantly greater snout-vent length than female individuals. On soil substrate, males exhibited significantly greater maximum sprint speed than females, while females demonstrated significantly greater endurance than males. Male snout-vent length showed a significant positive correlation with maximum sprint speed on soil substrate, whereas body mass of both sexes showed a significant negative correlation with maximum sprint speed on sand substrate. Substrate type affected male maximum sprint speed, as evidenced by significantly greater maximum sprint speed and acceleration on soil substrate compared to sand substrate. In contrast, female endurance was influenced by substrate type, showing significantly lower endurance on sand substrate than on other substrates. Thus, there exists a certain degree of trade-off between maximum sprint speed and endurance in E. velox, and the effects of morphological traits and substrate type on locomotor performance differed significantly between sexes.

Full Text

Preamble

The "home field advantage" hypothesis suggests that organisms exhibit optimal performance in their native habitats, while the "jack of all trades and master of none" principle predicts that generalist species may display compromised performance across varying environmental conditions. Previous studies have demon-

strated that substrate type significantly influences locomotor performance in lizards, with morphological traits such as hindlimb length and toe morphology affecting sprint speed and acceleration. However, the relationship between morphology and performance can vary substantially across different substrates, and trade-offs between maximal sprint speed and endurance capacity remain poorly understood in many species.

Eremias velox (the rapid racerunner) is a lacertid lizard endemic to the arid regions of Central Asia, inhabiting diverse substrates including sandy deserts, gravel plains, and clay soils. While previous research has investigated aspects of its thermal biology, reproductive ecology, and morphological variation, the relationship between its locomotor performance and substrate type has not been systematically evaluated. This study addresses three key questions: (1) Does locomotor performance of *E. velox* differ across substrate types? (2) Is there a trade-off between sprint speed and endurance? (3) How do morphological traits correlate with locomotor performance on different substrates?

1 Materials and Methods

1.1 Morphological Measurements

We collected 22 adult *E. velox* specimens (12 males, 10 females) from the field in 2018. Eleven external morphological traits were measured using digital calipers (±0.01 mm): snout-vent length (SVL), head length (HL), head width (HW), head depth (HD), mouth breadth (MB), axilla-groin length (AG), abdominal width (AW), tail base width (TBW), forelimb length (FLL), hindlimb length (HLL), and tail length (TL). Body mass was measured with an electronic balance (±0.01 g). Body condition index was calculated as BMI = body mass (kg) / (SVL (m))^2.

1.2 Sprint Speed Testing

Sprint performance was measured on a 1.2 m racetrack with a sandpaper substrate. Lizards were acclimated at 36.0±0.5°C for 30 minutes prior to testing. Each individual was tested three times with 1-day intervals between trials. Trials were recorded at 240 fps using a high-speed camera, and videos were analyzed with Adobe Premiere CS6. From the recordings, we calculated: (1) maximum sprint speed (Vmax) and acceleration ($a = (V^2 - V^2)/2S$), where S was the distance over the fastest 0.2 s interval.

1.3 Endurance Testing

Endurance was measured by continuously chasing lizards on a 4-5 m track until exhaustion. Each individual was tested three times across three different substrates (sand, soil, and gravel) with 1-day intervals. Exhaustion was defined as the point when lizards no longer responded to stimulation after 10 consecutive attempts. The total distance covered was recorded as the endurance measure.

1.4 Statistical Analysis

Morphological data were tested for normality using Kolmogorov-Smirnov and F-max tests. Sex differences in morphological traits were analyzed using t-tests or ANCOVA with SVL as a covariate. Performance data were analyzed using repeated measures ANOVA with substrate as the within-subject factor and sex as the between-subject factor. Principal component analysis (PCA) was performed on morphological traits. Model selection for performance predictors used Akaike Information Criterion (AIC) in R 3.5.0. Significance level was set at = 0.05.

2 Results

2.1 Morphological Characteristics

Males had significantly greater SVL than females (60.35±1.64 mm vs 54.26±1.28 mm, $P < 0.05$). PCA extracted two principal components explaining 82.32% of the variance: PC1 loaded heavily on SVL, HL, and mass; PC2 loaded on TL and TBW. ANCOVA revealed significant sex differences in forelimb length, hindlimb length, and mass after controlling for SVL ($P < 0.05$).

2.2 Locomotor Performance

Males exhibited significantly higher maximum sprint speed on soil substrates compared to females ($P < 0.05$), while females demonstrated significantly greater endurance than males ($P < 0.01$). For males, both sprint speed and acceleration were significantly greater on soil than on sand ($P < 0.05$), whereas female performance did not differ significantly between substrates. However, female endurance on sand was significantly lower than on other substrates ($P < 0.01$), while male endurance showed no substrate-related differences.

2.3 Morphological Correlates of Performance

Male sprint speed on soil showed a significant positive correlation with SVL ($r = 0.721$, $P < 0.05$) and a significant negative correlation with body mass ($r = -0.801$, $P < 0.05$). On sand substrates, body mass negatively correlated with sprint speed for both sexes ($r = -0.685$, $P < 0.05$). Endurance was positively correlated with hindlimb length on soil ($r = 0.832$, $P < 0.05$) and with axilla-groin length on gravel ($r = 0.758$, $P < 0.05$).

[Figure 3: see original paper]

3 Discussion

Our results demonstrate that *E. velox* exhibits substrate-dependent locomotor performance with clear sex-specific patterns. The observed trade-off between sprint speed and endurance aligns with the "jack of all trades" hypothesis, where

specialized morphology confers advantages on specific substrates but may compromise performance on others. Males, with longer hindlimbs and larger body size, achieve higher sprint speeds on firm soil, which is crucial for territory defense and mate acquisition. In contrast, females prioritize endurance, which is advantageous for foraging and predator avoidance over extended periods.

The negative correlation between body mass and sprint speed, particularly on sand, suggests that larger individuals experience greater substrate resistance, consistent with previous studies on lacertid lizards. The positive correlation between hindlimb length and endurance indicates that limb morphology influences not only burst speed but also sustained locomotion. These findings highlight the complex interplay between morphology, performance, and habitat structure in shaping the ecological strategies of desert lizards.

The sex differences in performance may reflect different selective pressures related to reproductive strategies. Males likely face strong selection for rapid acceleration during territorial disputes and courtship chases, while females may benefit more from sustained locomotor capacity during gestation and foraging. This divergence illustrates how intraspecific variation in morphology can lead to functional trade-offs that align with sex-specific ecological demands.

Our study underscores the importance of considering substrate heterogeneity when assessing locomotor performance in natural populations. The "home field advantage" may be limited for generalist species like *E. velox* that inhabit multiple substrate types, as morphological specialization for one substrate inevitably compromises performance on others. Future research should investigate the kinematic mechanisms underlying these performance differences and examine how they translate to fitness outcomes in natural habitats.

References

[1] Brandt R, Galvani F, Kohlsdorf T. Sprint performance of a generalist lizard running on different substrates: Grip matters[J]. Journal of Zoology, 2015, 297(1): 15-21.

[2] Irschick DJ, Garland T. Integrating function and ecology in studies of adaptation: Investigations of locomotor capacity as a model system[J]. Annual Review of Ecology and Systematics, 2001, 32(1): 367-396.

[3] Scales JA, Butler MA. Adaptive evolution in locomotor performance: How selective pressures and functional relationships produce diversity[J]. Evolution, 2016, 70(1): 48-61.

[4] Braña F. Morphological correlates of burst speed and field movement patterns: The behavioural adjustment of locomotion in wall lizards (Podarcis muralis)[J]. Biological Journal of the Linnean Society, 2003, 80(1): 135-146.

[5] Robson MA, Miles DB. Locomotor performance and dominance in male tree lizards, Urosaurus ornatus[J]. Functional Ecology, 2000, 14(3): 338-344.

[6] Van Damme R, Vanhooydonck B. Speed versus manoeuvrability: Association between vertebral number and habitat structure in lacertid lizards[J]. Journal of Zoology, 2002, 258(3): 327-334.

[7] Lin Zhihua, Fan Xiaoli, Lei Huanzong, et al. The effects of substrates on locomotor performance of two sympatric lizards, Takydrmus septentrionalis and Ples tiondon chinensis[J]. Acta Ecologica Sinica, 2011, 31(18): 5316-5322.

[8] Tang XL, Yue F, He JZ, et al. Ontogenetic and sexual differences of thermal biology and locomotor performance in a lacertid lizard, Eremias multiocellata[J]. Zoology, 2013, 116(1): 331-335.

[9] Luo LG, Qu YF, Ji X. Thermal dependence of food assimilation and sprint speed in a lacertid lizard Eremias argus from Northern China[J]. Acta Zoologica Sinica, 2006, 52(2): 256-262.

[10] Qualls FJ, Shine R. Geographic variation in 'Costs of Reproduction' in the scincid lizard Lampropholis guichenoti[J]. Functional Ecology, 1997, 11(6): 757-763.

[11] Bi JH, Wang Y, Li SR, et al. Is habitat preference associated with locomotor performance in multiocellated racerunners (Eremias multiocellata) from a desert steppe?[J]. Asian Herpetological Research, 2015, 6(2): 143-149.

[12] Higham TE, Russell AP. Divergence in locomotor performance, ecology, and morphology between two sympatric sister species of desert-dwelling gecko[J]. Biological Journal of the Linnean Society, 2010, 101(4): 860-869.

[13] Tulli MJ, Abdala V, Cruz FB. Relationships among morphology, clinging performance and habitat use in Liolaemini lizards[J]. Journal of Evolutionary Biology, 2011, 24(3): 843-855.

[14] Tucker DB, Mcbrayer LD. Overcoming obstacles: The effect of obstacles on locomotor performance and behaviour[J]. Biological Journal of the Linnean Society, 2012, 107(4): 813-823.

[15] Bergmann PJ, Pettinelli KJ, Crockett ME, et al. It' s just sand between the toes: How particle size and shape variation affect running performance and kinematics in a generalist lizard[J]. Journal of Experimental Biology, 2017, 220(20): 3706-3716.

[16] Vanhooydonck B, Van Damme R. Evolutionary relationships between body shape and habitat use in lacertid lizards[J]. Evolutionary Ecology Research, 1999, 1(7): 785-805.

[17] Tulli MJ, Abdala V, Cruz FB. Effects of different substrates on the sprint performance of lizards[J]. Journal of Experimental Biology, 2012, 215(5): 774-784.

[18] Herrel A, Vanhooydonck B, Porck J, et al. Anatomical basis of differences in locomotor behavior in Anolis lizards: A comparison between two ecomorphs[J]. Bulletin of the Museum of Comparative Zoology, 2008, 159(4): 213-238.

[19] Calsbeek R. An ecological twist on the morphology-performance-fitness axis[J]. Evolutionary Ecology Research, 2008, 10(2): 197-212.

[20] Sathe EA, Husak JF. Sprint sensitivity and locomotor trade-offs in green anole (Anolis carolinensis) lizards[J]. Journal of Experimental Biology, 2015, 218(4): 2174-2179.

[21] Pouyani ER, Noureini SK, Pouyani NR, et al. Molecular phylogeny and intraspecific differentiation of the Eremias velox complex of the Iranian Plateau and Central Asia (Sauria, Lacertidae)[J]. Journal of Zoological Systematics and Evolutionary Research, 2012, 50(3): 220-229.

[22] Zhao Erm, Zhao Kentang, Zhou Kaiya, et al. Fauna Sinica, Reptilia: Vol. 2 (Squamata: Lacertilia)[M]. Beijing: Science Press, 1999: 287-291.

[23] Liu Wei, Jiang Fengqing, Li Xiaolan. Spatiotemporal evolution of adaptive capacity to climate change in Xinjiang[J]. Arid Zone Research, 2017, 34(3): 531-540.

[24] Wang Yong, Han Guang, Yang Lin, et al. Grain size distribution of sand dunes at river banks[J]. Arid Zone Research, 2016, 33(1): 210-214.

[25] Szczerbak NN. Yashchurki Palearktiki (Eremias lizards of the Palearctic)[C]// Kiev: Akademiya Nauk Ukrainskoi SSR. Institut Zoologii. Naukova Dumka (In Russian), 1974: 83-113.

[26] Lisachov AP, Galkina SA, Saifitdinova AF, et al. Identification of sex chromosomes in Eremias velox (Lacertidae, Reptilia) using lampbrush chromosome analysis[J]. Comparative Cytogenetics, 2019, 13(2): 121-132.

[27] Guo Xianguang, Chen Dali, Wan Hongfu, et al. Review of systematics on the racerunner lizard (Lacertidae: Eremias)[J]. Sichuan Journal of Zoology, 2010, 29(4): 665-672.

[28] Dai Xin, Chen Bin, Zhang Zhengwei, et al. The morphological research of eight species of Eremias distributed in China (Lacertidae, Eremias)[J]. Acta Zootaxonomica Sinica, 2006, 31(4): 697-708.

[29] Wang Yang, Zhou Lu, Shi Lei. Scalation variation and subspecies classification status of rapid racerunner (Eremias velox) in Xinjiang[J]. Sichuan Journal of Zoology, 2014, 33(1): 13-18.

[30] Omar Abliz. The experimental studies on the severe tails regeneration of Eremias velox Pallas[J]. Arid Zone Research, 2000, 17(2): 61-64.

[31] Du Weiguo, Lin Chixian, Shou Lu, et al. Morphological correlates of locomotor performance in four species of lizards using different habitats[J]. Zoological Research, 2005, 26(1): 41-46.

[32] Madsen T, Shine R. The adjustment of reproductive threshold to prey abundance in a capital breeder[J]. Journal of Animal Ecology, 1999, 68(3): 571-580.

[33] Madsen T, Shine R. Short and chubby or long and slim? Food intake, growth and body condition in free-ranging pythons[J]. Austral Ecology, 2002, 27(6): 672-680.

[34] Li C, Lian X, Bi J, et al. Effects of sand grain size and morphological traits on running speed of toad-headed lizard Phrynocephalus frontalis[J]. Journal of Arid Environments, 2011, 75(11): 1038-1042.

[35] Vanhooydonck B, Androne cu A, Herrel A, et al. Effects of substrate structure on speed and acceleration capacity in climbing geckos[J]. Biological Journal of the Linnean Society, 2005, 85(3): 385-393.

[36] Vanhooydonck B, Measey J, Edwards S, et al. The effects of substrate on locomotor performance in lacertid lizards[J]. Biological Journal of the Linnean Society, 2015, 115(4): 869-881.

[37] Liu Ningna, Chu Hongjun, Zhang Junyong, et al. Behavioral differences and synchronization on males and females of Ovis ammon darwini in Kalamaili Mountains, Xinjiang[J]. Arid Zone Research, 2016, 33(1): 197-203.

[38] Cromie GL, Chapple DG. Impact of tail loss on the behaviour and locomotor performance of two sympatric Lampropholis skink species[J]. Plos One, 2012, 7(4): e34732.

[39] McElroy EJ, Bergmann PJ. Tail autotomy, tail size, and locomotor performance in lizards[J]. Physiological and Biochemical Zoology, 2013, 86(6): 669-679.

[40] Argaez V, Solano-Zavaleta I, Zúñiga-Vega JJ. Another potential cost of tail autotomy: Tail loss may result in high ectoparasite loads in Sceloporus lizards[J]. Amphibia Reptilia, 2018, 39(2): 191-198.

[41] Zamora-Camacho FJ, Reguera S, Rubiño-Hispán M, et al. Effects of limb length, body mass, gender, gravity, and elevation on escape speed in the lizard Psammodromus algirus[J]. Evolutionary Biology, 2014, 41(4): 509-517.

[42] Liang Tao, Li Ye, Zheng Peng, et al. Sexual dimorphism and female reproduction of Eremias arguta[J]. Arid Zone Research, 2018, 35(5): 1160-1166.

[43] Lowie A, Gillet E, Vanhooydonck B, et al. Do the relationships between hindlimb anatomy and sprint speed variation differ between sexes in Anolis lizards?[J]. Journal of Experimental Biology, 2019, 222: jeb.188805.

[44] Alexander RM. Principles of Animal Locomotion[M]. Princeton: Princeton University Press, 2003.

[45] Tsuji JS, Huey RB, Van Berkum FH, et al. Locomotor performance of hatchling fence lizards (Sceloporus occidentalis): Quantitative genetics and morphometric correlates[J]. Evolutionary Ecology, 1989, 3(3): 240-252.

[46] Vanhooydonck B, Herrel A, Irschick DJ. Out on a limb: The differential effect of substrate diameter on acceleration capacity in Anolis lizards[J]. Journal

of Experimental Biology, 2006, 209(22): 4515-4523.

[47] Arnold SJ. Morphology, performance and fitness[J]. American Zoologist, 1983, 23(2): 347-361.

[48] Garland T. Physiological correlates of locomotor performance in a lizard: An allometric approach[J]. American Journal of Physiology, 1984, 247(2): 806-815.

[49] Le Galliard JF, Paquet M, Cisel M, et al. Personality and the pace-of-life syndrome: Variation and selection on exploration, metabolism and locomotor performances[J]. Functional Ecology, 2013, 27(1): 136-144.

[50] Van Damme R, Aerts P, Vanhooydonck B. Variation in morphology, gait characteristics and speed of locomotion in two populations of lizards[J]. Biological Journal of the Linnean Society, 1998, 63(3): 409-427.

[51] Vanhooydonck B, Van Damme R, Aerts P. Speed and stamina trade-off in lacertid lizards[J]. Evolution, 2001, 55(5): 1040-1048.

[52] Jia Wenru, Li Shengyu, Ma Xuexi, et al. Spatial variation of compaction on transverse dune surface in hinterland of the Taklimakan Desert[J]. Arid Zone Research, 2016, 33(3): 664-671.

[53] Lejeune TM, Willems PA, Heglund NC. Mechanics and energetics of human locomotion on sand[J]. Journal of Experimental Biology, 1998, 201(13): 2071-2080.

[54] Wainwright PC, Alfaro ME, Bolnick DI, et al. Many-to-one mapping of form to function: A general principle in organismal design?[J]. Integrative and Comparative Biology, 2005, 45(2): 256-262.

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