

# MULTI-FUNCTIONAL USE OF THE ELONGATE HIND FOOT OF THE ZEBRA-TAILED LIZARD DURING RUNNING ON DIFFERENT SUBSTRATES

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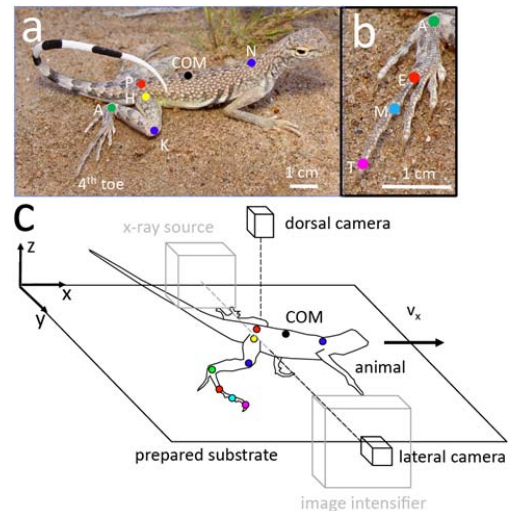
## INTRODUCTION

In many organisms, the kinematics and dynamics measured during running on level, rigid, non-slip ground (such as tracks and treadmills) [1] can be represented by the SLIP model [2]. The mechanics by which cursorial animals run over diverse terrain is less understood. To discover how organisms control their movement in more complex environments (such as sand, rubble, and debris), we must understand how feet interact with such terrain. This is a challenge in part due to difficulty observing and modeling foot-ground interaction.

The zebra-tailed lizard, *Callisaurus draconoides* (~ 10 cm, ~ 10 g, Fig. 1a), is a desert generalist and runs rapidly across a diversity of substrates ranging from hard ground to loose sand [3]. Compared to its close relatives, it has the most elongate hind foot (Fig. 1b) and runs the fastest (~ 5 m/s) [4]. Elongation of distal limb segments is thought to enhance running capacity, but the mechanism is not known. In this study, we examine the mechanics of foot-ground interaction in the zebra-tailed lizard during running on hard ground and loose sand to reveal principles of multi-functional foot use which contributes to high locomotor performance.

## METHODS

To mimic a hard substrate, we used a wood board bonded with sandpaper. Our granular substrate was glass beads with properties comparable to dry desert sand (~ 0.3 mm,  $\rho = 2.5 \times 10^3 \text{ kg/m}^3$ ) as a granular substrate. A fluidized bed trackway [5] prepared sand into loosely packed, repeatable initial states. Two high speed cameras obtained dorsal and lateral views at 500 frame/s (Fig. 1c, black setup). High-contrast markers were placed on the joints including neck, center of mass (COM), pelvis, hip, knee, ankle, end, middle, and tip of toe. Kinematics from 2-D videos were reconstructed into 3-D by direct



**Figure 1:** Subject animal and experimental setup.

linear transformation. To capture subsurface foot interaction with sand, we used x-ray high speed video (Fig. 1c, black and gray setup). Due to high absorption of x-ray by glass beads, poppy seeds (~ 1 mm,  $\rho = 1.0 \times 10^3 \text{ kg/m}^3$ ) were used, since they have similar penetration resistance as glass beads (~  $10^5 \text{ N/m}^3$ ). We verified that this caused no significant change to our major findings. Opaque markers were bonded to the joints for enhanced contrast. We dissected the hindlimb of a specimen to reveal foot anatomy, and studied the granular physics relevant to the foot-ground interaction using simple intruders like plates and disks.

## RESULTS AND DISCUSSION

For the animals tested, the body length (SVL) is  $6.9 \pm 2.0 \text{ cm}$ , body weight  $9.7 \pm 1.8 \text{ g}$ . The lizards display similar whole body kinematics (*t*-test,  $P > 0.05$ ) during running both hard ground and sand: at similar velocity ( $1.51 \pm 0.23 \text{ m/s}$  vs.  $1.42 \pm 0.27 \text{ m/s}$ ), they use similar stride frequency ( $9.0 \pm 1.3 \text{ Hz}$  vs.  $9.3 \pm 1.8 \text{ Hz}$ ) and duty factor ( $0.42 \pm 0.06$  vs.  $0.37 \pm 0.04$ ). On both substrates, the center of mass falls during landing and rises during push off, in accord with the SLIP model [2].