Observations on an Unusual "Arrhythmic" Gait in Sengis

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Running has shaped the life of the sengi. Morphological specializations in sengis such as long, slender limbs ending in digitigrade feet, parasagittal motion of the limbs, and elongation of the metatarsals are classic features associated with cursorial locomotion (Polly 2007). In general, sengis do not usually retreat to protective shelters, such as burrows, when faced with predators. Instead, they escape by running along pathways in the undergrowth, which they meticulously maintain. Of the two extant subfamilies of sengis, Macroscelidinae (soft-furred sengis) and Rhynchocyoninae (giant sengis; see Rathbun 2017 for summary of taxonomy), the soft-furred sengis are particularly specialized for cursorial locomotion, with small litters of 1 – 3 precocial young that are able to walk and run within hours of birth. This suite of correlated morphological, behavioral, ecological, and life history characters in sengis has been identified as a microcursorial adaptive syndrome (Rathbun 1979; Lovegrove and Mowoe 2014).

Unusual arrhythmia has been previously reported in the locomotion of a soft-furred sengi, *Macroscelides proboscideus* (Schmidt and Fischer 2007a; Schmidt and Fischer 2007b). Additional observations by GBR on the footfall patterns of other soft-furred sengi species reveal an occasional "skip" in the footfall pattern, when one of the limbs is kept suspended during the gait cycle when it would otherwise be expected to make contact with the ground, based on the preceding strides. This begs some fundamental questions: Under what conditions does skipping occur? Do all sengis skip? And why skip at all?

In our preliminary exploration of these questions, we analyzed film footage of four sengi species from both Macroscelidinae and Rhynchocyoninae subfamilies: *Petrodromus tetradactylus* (Macroscelidinae; footage from GBR), *Elephantulus rufescens* (Macroscelidinae; footage from NHK television series "Darwin's Amazing Animals: Quick and Tidy! – Sengi, Africa"), *Rhynchocyon petersi* (Rhynchocyoninae; footage from Zoo Antwerpen by YouTube user Gilles Delhaye), and *Rhynchocyon chrysopygus* (Rhynchocyoninae; footage from GBR). We analyzed video sequences of uninterrupted locomotion and constructed gait diagrams to illustrate the pattern of footfalls during each frame of the video (*Figure 1*).

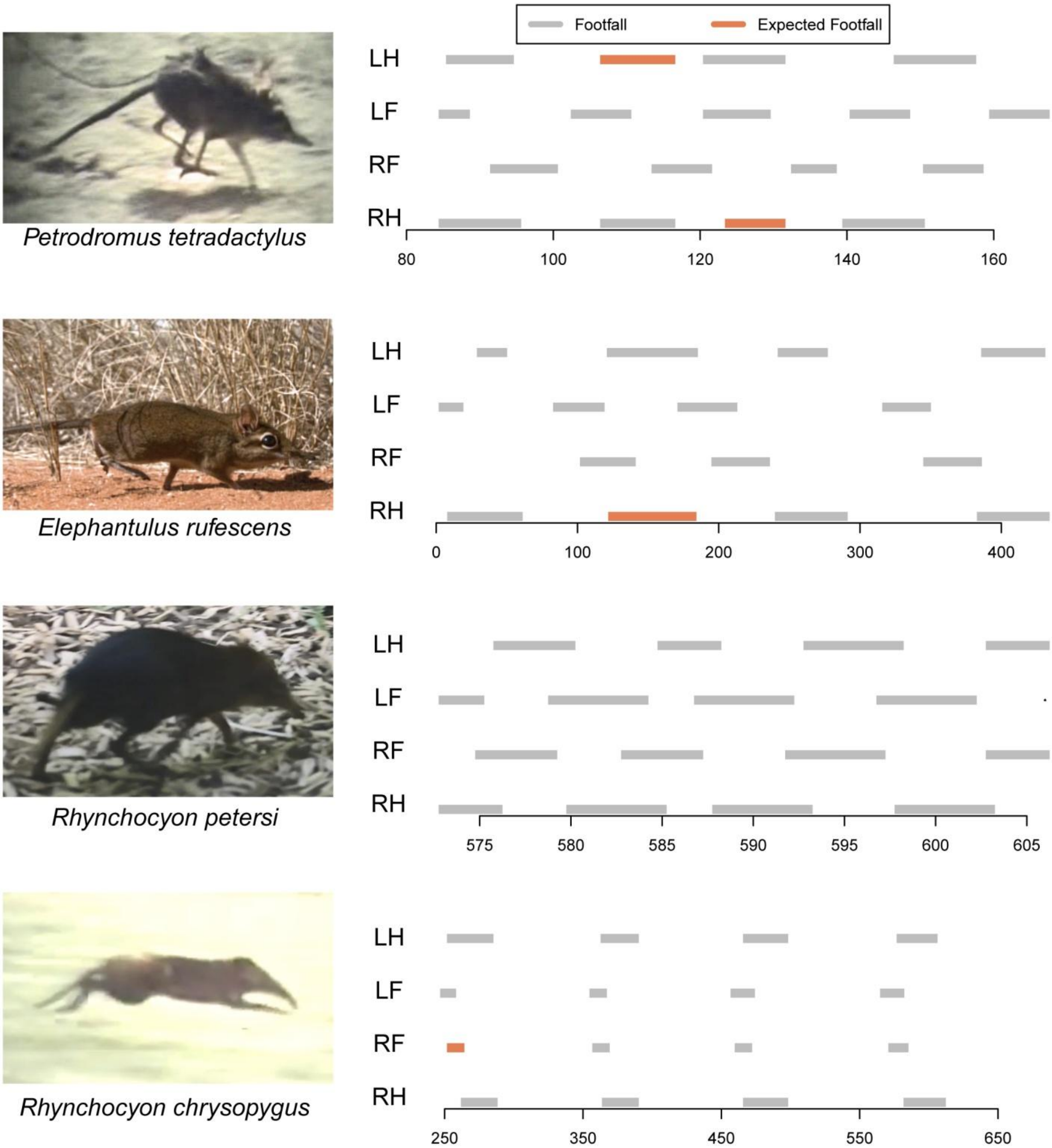

Figure 1. Four species of sengi (left) with corresponding gait diagrams (right). The top two species are in the subfamily Macroscelidinae (soft-furred sengis), the bottom two in Rhynchocyoninae (giant sengis). The gait diagrams show the video frames, labeled on the x-axis, when each foot is in contact with the ground ("footfall" in grey) or when a foot does not make ground contact and is kept suspended in a skip ("suspended expected footfall" in orange). Abbreviations: LH = left hindfoot; LF = left forefoot; RF = right forefoot; RH = right hindfoot. All instances of skipping were seen during the half-bound gait, in which the hindlimbs move together as a synchronous pair. Soft-furred sengis Petrodromus tetradactylus *and* Elephantulus rufescens *employed the half-bound gait at slow and high speeds, respectively, with hindlimb skipping observed in both instances. In contrast, the giant sengi* Rhynchocyon petersi *used a trotting gait at low speeds with no observed skipping and* R. chrysopygus *showed forelimb skipping only during a fast half-bound. Note that all the gait diagrams represent a selected portion of the total analyzed video sequence to show four continuous gait cycles for clarity of comparison.*

The video footage of *P. tetradactylus* is of a wild-caught animal with a leash around its abdomen moving across a flat, mowed grassy substrate (footage from GBR; "Tethered locomotion" on http://www.sengis.org/videographic.php). The sengi moves using a slow half-bound gait in which the right and left forelimbs move with alternating strokes, but the hindlimbs swing together as a generally synchronized pair. This is unlike the half-bound of mustelids, in which forelimbs are synchronized in movement, but the hindlimbs move alternately (Hildebrand 1989). In the approximately 10-second-long sequence, we observed a total of five skips. Most of these skips occurred as consecutive left-right couplets in the following sequence: (1) as the hindlimbs swing forward, only the right hindlimb contacts the ground while the left hindlimb is suspended in the air; (2) the right hindlimb pushes off as the left hindlimb remains flexed; (3) as the hindlimbs swing forward again, only the left hindlimb makes ground contact while the right hindlimb remains suspended. This occurred twice, with a few "normal" gait cycles in between. There does not seem to be a bias towards skipping with one hindlimb or the other. Interestingly, later in the film sequence, the sengi is moving at a faster half-bound and the forelimb alone makes a skip. There appears to be limited spinal flexion at both low and high speeds.

We also used video footage of *E. rufescens* from a nature documentary that filmed animals in their natural surroundings in Kenya. This individual is filmed speeding along its small trail cleared through the leaf litter in a fast half-bound with aerial phases in which none of the feet are in contact with the ground. However, unlike the *P. tetradactylus* that incorporated skips as a regular part of its gait cycle, the *E. rufescens* appears to have kept one of its hindlimbs suspended in order to avoid a small stand of dried grass, suggesting a dynamic adjustment of the gait in response to obstacles. The spine flexes noticeably during the aerial phase.

To compare the two sengi subfamilies, we selected a video of the giant sengi *R. petersi* moving at what appeared to be a similar speed to the skipping *P. tetradactylus*. The captive giant sengi was in a zoo exhibit with a substrate of loose wood chips. Instead of a half-bound gait, this individual moved briskly through its enclosure using a trotting gait, in which contralateral limbs moved synchronously: right forelimb with left hindlimb, and left forelimb with right hindlimb. No skipping was observed.

A video of *R. chrysopygus* in Kenya (footage from GBR; "Tethered locomotion" on http://www.sengis.org/videographic.php) shows a leashed sengi half-bounding across an open sandy ocean beach at high speed (limited to about as fast as GBR could run on sand). In contrast to the predominantly hindlimb skipping observed in the soft-furred sengi video footage, this animal skipped only with its forelimbs. There was a total of three skips – each occurrence separated by several normal gait cycles – with the following limbs suspended: right forelimb, both forelimbs, and left forelimb. The sengi also showed significant spinal flexion while in motion.

Despite the apparent uniformity of cursorial features across the sengi clade, there appear to be differences in the mode of locomotion between the two subfamilies. Both Macroscelidinae in our preliminary observations showed instances of hindlimb skipping during the half-bound gait at different speeds. While the sampled Rhynchocyoninae video footage showed a slower trot gait with no skipping and a high speed half-bound with forelimb skipping.

We hypothesize that the gait alterations employed by the smaller Macroscelidinae sengis are associated with further miniaturization of a microcursor, resulting in allometrically long and overpowered hindlimbs relative to torso length. We suspect that the flexible spine of the relatively longer torso of Rhynchocyoninae helps redirect the force produced by the hindlimbs into forward motion, while increasing stride length, as in quadrupedal rodents (Gasc 2001). In a smaller sengi, the powerful "rear-wheel drive" and decreased torso length may potentially require behavioral adaptations to prevent the animal from pitching forward during each stride. In order to accommodate this anatomical configuration, the Macroscelidinae sengis may adjust the stride frequency by keeping a limb suspended during the gait cycle and/or perhaps even decouple movement of the hindlimbs from the forelimbs to redistribute the force of each bound and smooth their stride, as the decoupled tölt gait does for Icelandic horses (Andersson *et al.* 2012). A greater sampling across body sizes would allow us to determine whether there is a relationship between gait arrhythmia and size in sengis. Furthermore, a comparison to other cursorial clades exhibiting a range of body size would elucidate whether gait arrhythmia is a general consequence of cursorial miniaturization or remains unique to sengis.

We aim to examine these questions about sengi locomotion in greater depth by expanding our research into collaborative partnerships with zoos, field stations, or other institutions. While our preliminary observations were based on a few serendipitous video recordings, without observations and data collection under controlled conditions, it is challenging to fully understand the biomechanical mystery of skipping sengis. Our goal is to collect data on locomotory patterns of different sized sengi species at different speeds using high-speed video cameras, a treadmill, and force plates. Using these non-invasive methods, we hope that our findings will contribute to the understanding of the natural history of sengis and also inform conservation efforts by defining normal behavioral repertoire. For instance, these data can help identify whether or not observed gait patterns in captive animals are pathological. Likewise, this information can be applied towards the design of better enclosures and substrates to enhance the well-being of sengis by allowing for the full range of locomotory performance, something that is a defining element of this unusual evolutionary lineage of microcursors.

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