Zoology 117 (2014) 146–159

Contents lists available at ScienceDirect

Zoology

journal homepage: www.elsevier.com/locate/zool

Locomotion in degus on terrestrial substrates varying in orientation – implications for biomechanical constraints and gait selection

André Schmidt*

Department of Biomedical Sciences, Heritage College of Osteopathic Medicine, Ohio University, 120 Life Science Building, Athens, OH 45701, USA

ARTICLE INFO

Article history:
Received 28 February 2013
Received in revised form 27 June 2013
Accepted 26 August 2013
Available online 20 December 2013

Keywords:
Octodon degus
Inclines
Declines
Running gaits
Gait selection

ABSTRACT

To gain new insights into running gaits on sloped terrestrial substrates, metric and selected kinematic parameters of the common degu (*Octodon degus*) were examined. Individuals were filmed at their maximum voluntary running speed using a high-speed camera placed laterally to the terrestrial substrate varying in orientations from −30° to +30°, at 10° increments. Degus used trotting, lateral-sequence (LS) and diagonal-sequence (DS) running gaits at all substrate orientations. Trotting was observed across the whole speed range whereas DS running gaits occurred at significantly higher speeds than LS running gaits. Metric and kinematic changes on sloped substrates in degus paralleled those noted for most other mammals. However, the timing of metric and kinematic locomotor adjustments differed significantly between individual degus. In addition, most of these adjustments took place at 10° rather than 30° inclines and declines, indicating significant biomechanical demands even on slightly sloped terrestrial substrates. The results of this study suggest that DS and LS running gaits may represent an advantage in small to medium-sized mammals for counteracting some level of locomotor instability. Finally, changes in locomotor parameters of the forelimbs rather than the hindlimbs seem to play an important role in gait selection in small to medium-sized mammals.

1. Introduction

Previous studies in small to medium-sized quadrupedal mammals (<2.5 kg) have shown common principles during locomotion on level surfaces (Fischer et al., 2002). Forelimbs and hindlimbs, for example, are strongly flexed ("*z*-configuration") so that both scapular pivot and hip joint have the same vertical distance to the ground (Fischer et al., 2002). Natural habitats of terrestrial small to medium-sized quadrupedal mammals, however, also comprise inclined and declined substrates so that investigations of the locomotion on those substrates are necessary to fully understand the mechanics of movements and how animals utilize their habitats (Lammers et al., 2006). When moving across sloped substrates, the biomechanical demands increase enormously due to the shift of gravitational forces towards the forelimbs on declines and towards the hindlimbs on inclines (Cartmill, 1974, 1985; Preuschoft, 2002).

In response to shallow terrestrial slopes, metric gait parameters change significantly. For example, when moving on shallow terrestrial slopes, gray short-tailed opossums decrease their speed compared to level substrates (Lammers and Biknevicius, 2004; Lammers, 2007). As a consequence, stance durations and stride durations increase on inclines, and decrease on declines (Lammers et al., 2006; Lammers, 2007). Comparable changes in stride cycle characteristics have also been observed for rats during incline and decline locomotion on a treadmill (Gillis and Biewener, 2002). Kinematic gait parameters that are significantly affected on shallow slopes include more strongly retracted hindlimbs on inclines than on declines and more strongly protracted forelimbs on declines than on inclines due to the need for greater propulsion and higher braking forces, respectively (Lammers and Biknevicius, 2004; Lammers et al., 2006; Lammers, 2007). Kinematic adjustments during locomotion on sloped terrestrial substrates also include highly flexed forelimbs on inclines and highly flexed hindlimbs on declines, which reduce the risk of toppling backwards or forwards, respectively (Lammers et al., 2006). Not surprisingly, comparable observations were made for several small to medium-sized mammals during inclined and declined arboreal locomotion (e.g., primates: Prost and Sussman, 1969; Stevens, 2003; Nyakatura et al., 2008; Stevens et al., 2011; gray short-tailed opossum: Lammers and Biknevicius, 2004; Lammers, 2007; sugar glider: Shapiro and Young, 2010; rat and European red squirrel: Schmidt and Fischer, 2010, 2011; Schmidt, 2011).

One common phenomenon on inclined and declined terrestrial and arboreal substrates is a change in gait preferences. Primates tend to use more diagonal-sequence gaits (DS; each hindlimb touchdown is followed by the diagonally opposite forelimb touchdown) on inclined substrates but lateral-sequence gaits (LS; each hindlimb touchdown is followed by the ipsilateral forelimb

* Tel.: +1 740 593 0487.
E-mail address: schmidta@ohio.edu

0944-2006/$ – see front matter © 2013 Elsevier GmbH. All rights reserved.
http://dx.doi.org/10.1016/j.zool.2013.08.009

touchdown) on declines, regardless of whether this gait is classified as a run or a walk (e.g., Prost and Sussman, 1969; Vilensky et al., 1994; Stevens, 2003; Nyakatura et al., 2008; Nyakatura and Heymann, 2010). In small to medium-sized non-primates, the use of LS gaits on sloped substrates was observed for sugar gliders walking on poles (Shapiro and Young, 2010) and for gray short-tailed opossums running on a declined terrestrial trackway (Lammers et al., 2006). However, as hypothesized by Hildebrand (1976) and shown for rats and several marsupials (cf. Parchman et al., 2003), running trots and DS gaits occur more frequently than LS gaits during terrestrial level locomotion at higher speeds (White, 1990; Pridmore, 1992; Biknevicius et al., 2012). Thus, previous assumptions that the predominant occurrence of DS gaits is a unique feature of primates remain questionable (for detailed information see, e.g., Stevens, 2006; Nyakatura and Heymann, 2010; Schmitt, 2011). Biomechanical explanations for the predominant use of DS gaits in primates during inclined locomotion include, for example, the distribution of body weight, the possession of prehensile extremities, center of mass mechanics, and the increase in stability (e.g., Cartmill et al., 2002; Lemelin et al., 2003; Shapiro and Raichlen, 2005; Stevens, 2006; Nyakatura et al., 2008; Lemelin and Cartmill, 2010; Young, 2012). However, it is still unknown what distinguishes LS and DS gaits in primates aside from footfall sequences (Wallace and Demes, 2008; Carlson and Demes, 2010), and the exact mechanisms that primates use for interchanging among gait sequence patterns remain unresolved (Stevens, 2006). Gait shifts can result from either changes in stance duration, changes in swing duration (e.g., relatively earlier touchdown) or from a combination of both as observed for slender loris walking on moving branches (mixed strategy; Stevens, 2006). On branches, as compared to walking on a fixed support, slender loris' forelimbs touch the support earlier whereas hindlimbs liftoff later. This mixed strategy results in a switch from DS walking gaits on fixed supports to LS walking gaits on moving supports. So far, primary information about footfall sequences relative to substrate orientation in small to medium-sized non-primate mammals other than the gray short-tailed opossum (*Monodelphis domestica*) is missing (Lammers and Biknevicius, 2004; Lammers et al., 2006; Lammers, 2007). The gray short-tailed opossum uses LS running gaits on declined terrestrial substrates but trots on level and inclined terrestrial substrates. *Monodelphis* also demonstrates a higher adjustability in forelimb than in hindlimb locomotor parameters when confronted with changes in substrate orientation. It is unknown, however, how closely substrate orientation, gait selection and forelimb adjustability in *Monodelphis* are linked to each other.

Information about the timing of significant locomotor adjustments (e.g., statistically significant changes in locomotor parameters) and individual differences in locomotor parameters due to substrate orientation are limited as well. For example, relative forelimb protraction in cotton-top tamarins did not change between level, −8°, and −16° branch orientations but increased significantly between −16° and −28° (Nyakatura et al., 2008). On inclines the most significant change was observed between level and +8° branch orientation (Nyakatura et al., 2008). However, the high variability among tamarins used in the study prevents general conclusions about the timing of significant locomotor adjustments on sloped substrates. Individual differences in locomotor parameters as observed in cotton-top tamarins on sloped substrates have also been described for rats and European red squirrels (Schmidt, 2011; Schmidt and Fischer, 2011), and for several primate species such as squirrel monkeys, aye-ayes and lemurids (Vilensky et al., 1994; Krakauer et al., 2002; Stevens, 2003; Nyakatura et al., 2008; Kivell et al., 2010). It appears that differences in locomotor speed between individuals were greater on sloped substrates than during level locomotion. However, it is unknown how often significant locomotor adjustments occur if substrate orientation incrementally

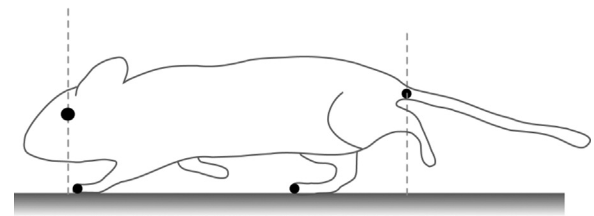

Fig. 1. Landmarks in running degus used for digitization. Note that touchdown or liftoff positions in front of the eye (forelimbs) or the tail base (hindlimbs) result in positive values for relative limb protraction and retraction (and vice versa for negative values). Touchdown position is defined as the moment when the entire foot has substrate contact. Liftoff is defined as the moment of last substrate contact (not shown).

increases and whether a significant locomotor adjustment is more closely related to locomotor speed than to substrate orientation.

All in all, the impact of moderate surface grades on mammal locomotion is somewhat obscure due to the limited amount of standardized experiments and comparable data sets (Gillis and Biewener, 2002). To increase our knowledge of how mammals behaviorally adapt to travel on sloped terrestrial substrates and to get a more complete understanding of running gaits in general, key metric and kinematic gait parameters of the common degu (*Octodon degus*, Molina 1782) were examined as animals moved at different substrate orientations. The common degu is a small caviomorph rodent that inhabits semi-arid scrub areas in Chile (Woods and Boraker, 1975; Meserve et al., 1984; Ebensperger and Bozinovic, 2000). Degus construct and inhabit burrows but spend a large amount of time overground for foraging activities during which they also climb on lower branches of small trees and shrubs (Woods and Boraker, 1975; Ebensperger and Bozinovic, 2000). Despite that, degus do not have prehensile extremities, a feature that might be linked to the predominant use of DS gaits in primates (e.g., Lemelin et al., 2003). The degu's tail is moderately long and is kept elevated during running (Fig. 1; Woods and Boraker, 1975). The present study focused exclusively on symmetrical running gaits (duty factor <50%) since degus rarely use walking gaits on sloped substrates (A.S., personal observation).

The following predictions were tested: (i) degus will use all running gaits (LS, DS, trot) during locomotion across all substrates orientations but will prefer lateral-sequence running gaits on declined terrestrial substrates. (ii) Degus will show comparable locomotor adjustments on moderate terrestrial inclines (+30°) and declines (−30°) as observed previously for small to medium-sized mammals, but significant locomotor adjustments will be apparent even on shallow inclines (+10°) and/or declines (−10°). (iii) Forelimbs will demonstrate a higher variability in locomotor parameters than hindlimbs with changes in substrate orientation. Therefore, changes among gait sequence patterns (e.g., between trot and LS running gaits) will mainly result from locomotor parameter adjustments of the forelimbs.

2. Materials and methods

2.1. Experimental subjects and protocol

Metric (spatio-temporal) and kinematic data were obtained from four male adult subjects (body mass 250–280 g) of the common degu (*O. degus*). The degus were housed individually with food and water ad libitum. Animals were encouraged by sound and hand movements to run as fast as possible across a 1.45 m-slong terrestrial trackway. The trackway was covered with cork, which degus were able to penetrate with their claws, enclosed with Plexiglass and adjustable to several substrate orientations in 10° increments (−30°, −20°, −10°, level, +10°, +20°, +30°). At least 20 trials were