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RESEARCH ARTICLE

Patterns of single limb forces during terrestrial and arboreal locomotion in rosy-faced lovebirds (Psittaciformes: *Agapornis roseicollis*)

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ABSTRACT

The biomechanical demands of arboreal locomotion are generally thought to necessitate specialized kinetic and kinematic gait characteristics. While such data have been widely collected across arboreal quadrupeds, no study has yet explored how arboreal substrates influence the locomotor behavior of birds. Parrots – an ancient arboreal lineage that exhibit numerous anatomical specializations towards life in the trees – represent an ideal model group within which to examine this relationship. Here, we quantify limb loading patterns within the rosy-faced lovebird (*Agapornis roseicollis*) across a range of experimental conditions to define the circumstances under which arboreal gaits are triggered, and how, during arboreal walking, gait patterns change across substrates of varying diameter. In so doing, we address longstanding questions as to how the challenges associated with arboreality affect gait parameters. Arboreal locomotion was associated with the adoption of a sidling gait, which was employed exclusively on the small and medium diameter poles but not terrestrially. When sidling, the hindlimbs are decoupled into a distinct leading limb (which imparts exclusively braking forces) and trailing limb (which generates only propulsive forces). Sidling was also associated with relatively low pitching forces, even on the smallest substrate. Indeed, these forces were significantly lower than mediolateral forces experienced during striding on terrestrial and large diameter substrates. We propose that the adoption of sidling gaits is a consequence of avian foot morphology and represents a novel form of arboreal locomotion where inversion/eversion is impossible. Such movement mechanics is likely widespread among avian taxa and may also typify patterns of arboreal locomotion in humans.

KEY WORDS: Parrots, Biomechanics, Gait, Kinetics, Sidling

INTRODUCTION

Navigating an arboreal environment involves locomotion using substrates of varying diameter, compliance, orientation and continuity (e.g. Grand, 1972; Jenkins, 1974; Cartmill, 1985;

Preuschoft, 2002). Accordingly, animals, regardless of anatomical specialization, are understood to alter their kinetics and kinematics in predictable ways to overcome these challenges (e.g. Cartmill et al., 2002; Lemelin et al., 2003; Fischer et al., 2010; Granatosky et al., 2019, 2021). While many of these rules and trends are considered ‘well established’, it is important to note that most of our understanding of arboreal movement is based on sampling from quadrupedal primates (e.g. Larson, 1998; Schmitt, 1999; Jenkins, 2012; Young, 2012; Granatosky, 2020), with limited inferences from other mammals (e.g. Jenkins, 1974; Lemelin et al., 2003; Lemelin and Cartmill, 2010; Granatosky and Schmitt, 2017; Granatosky et al., 2021) and squamates (e.g. Higham and Jayne, 2004; Fischer et al., 2010). As such, it is unclear whether our understanding of the biomechanics of arboreal locomotion is applicable to all tetrapods in general, quadrupeds, mammals or just primates.

To our knowledge, there has been no study assessing how arboreal substrates influence the locomotor behavior of birds. However, of the ~10,000 extant avian species, most demonstrate at least some arboreal tendencies, and certain lineages have become highly specialized for arboreal movement (del Hoyo et al., 2010; Provini and Höfling, 2020). The parrots (Order: Psittaciformes) are an ancient arboreal lineage (Waterhouse, 2006; Ksepka et al., 2011; Ksepka and Clarke, 2012) characterized by numerous anatomical specializations for a life in the trees, including relatively short tarsometatarsi (Provini and Höfling, 2020), long zygodactylous digits (Carril et al., 2021), distal elongation of the penultimate phalanx accompanied by a shortening of the proximal phalanges (Hopson, 2001; Backus et al., 2015; Struble et al., 2020), and a highly mobile hip joint (Reader et al., 2022). Despite the well-known arboreal tendencies of Psittaciformes, there is limited information about the biomechanics of arboreal locomotion in this lineage. In this study, we begin bridging this gap by exploring how/whether the forces applied by the limb in parrots are altered in response to arboreal substrates. In so doing, we assess both the circumstances under which arboreal locomotion requires parrots to implement changes in gait, and how such changes are manifested in a mechanistic context.

The interplay between limb loading and movement on arboreal substrates has been well studied (e.g. Schmitt, 2003; Schmitt and Hanna, 2004; Granatosky and Schmitt, 2019; Schapker et al., 2022; Wölfer et al., 2021). Such interest is attributable to a general curiosity of how animals maintain balance on thin compliant substrates (e.g. Lammers and Biknevicius, 2004; Lammers and Gauntner, 2008; Lammers and Zurcher, 2011) without breaking the substrate under their own body weight (Schmitt and Hanna, 2004; Schapker et al., 2022). From these studies, there are some general trends in limb loading patterns that appear to be common across

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species. Specifically, compared with terrestrial movement, arboreal locomotion is characterized by a reduction in peak vertical forces and overall resultant force (Schmitt and Hanna, 2004; Schapker et al., 2022). This trend is exaggerated as substrate diameters decrease and is thought to limit potential substrate oscillations (Demes et al., 1990; Schapker et al., 2022) and/or to prevent damage to highly mobile, but weak, limb joints (Schmitt, 1999; Schmitt and Hanna, 2004). There has been considerable investigation exploring the mechanical underpinnings of this pattern, but such analysis is beyond the scope of this paper, and we refer the reader to Schmitt (1999), Raichlen et al. (2009), Larson and Demes (2011), Granatosky et al. (2018) and Dickinson et al. (2022) for further discussion. Mediolateral forces shift from being primarily laterally directed on terrestrial substrates to medially directed on arboreal ones (Schmitt, 2003; Franz et al., 2005). Such a change in limb function has been proposed to allow the opposite limb pairs to ‘grip’ around the substrate, thereby increasing stability (Granatosky and Schmitt, 2017; Granatosky, 2018). Braking/propulsive forces appear to change little in response to arboreal substrates and generally are characterized by a braking force as the limb makes initial contact with substrate, followed by a propulsive force as the limb passes caudally to the center of mass (Franz et al., 2005; Granatosky et al., 2018). However, as outlined above, these general patterns are derived from observations of quadrupedal mammals and squamates, and it is unclear whether these same principles apply to arboreal movement in bipeds. Further, most studies of arboreal versus terrestrial kinetics are usually limited solely to a dichotomous experimental protocol (e.g. pole versus ground; but see Schapker et al., 2022, and Wölfer et al., 2021). As such, it remains largely unknown at what substrate diameter animals need to adjust neuromuscular gait characteristics to counter the challenges of arboreal movement.

Sidling gaits

This translation is further complicated by the use of a sidling gait in many arboreal birds, which involves sideways progression along a substrate whereby one foot is moved before the other in a shuffling manner (Dilger, 1960; Brockway, 1964; Ellis, 1966; Skeate, 1985). Such movement has been anecdotally documented during arboreal locomotion in parrots (Dilger, 1960; Brockway, 1964; Skeate, 1985), but the conditions that elicit this gait are entirely unknown. Dilger (1960) proposed the use of sidling in parrots was reserved for slow speed, but Brockway (1966) noted sidling was adopted even at high speeds in budgerigars (*Melopsittacus undulatus*). While no study has yet to report single-limb force profiles of sidling gaits, it is possible to make inferences from the sideways locomotion observed in crabs (Blickhan and Full, 1987). During sideways walking, both the leading and trailing limbs produce braking and propulsive forces. Generally, the leading limb tends to produce a net braking effect, while the trailing limb serves a propulsive function. Occasionally, crabs alter this functional differentiation such that the trailing limb serves to decelerate the animal, while the leading limb is propulsive (i.e. the crab pulls itself with the leading limb). During sideways running, the trailing limb in crabs always produces propulsive forces, while the leading limb produces a net braking force, although with lower magnitude (Blickhan and Full, 1987).

The use of sidling also alters the interpretation of mediolateral forces. Because of the reorientation of the body, mediolateral forces would no longer reflect an inward or outward application of force by the limbs, rather provide information as to whether the animal is pitching forward or backward (relative to the animal’s anatomical axis, not the direction of travel) to balance on the substrate.

Relatively high magnitudes of pitching forces might be expected, especially as substrate size decreases, but currently no reference data have been reported.

Aims and predictions

Herein, we compare limb loading patterns of the rosy-faced lovebird (*Agapornis roseicollis*) across a range of experimental conditions to define under which circumstances arboreal gaits are triggered, and how, during arboreal walking, gait patterns change across substrates of varying diameter. In so doing, we address longstanding questions as to how the challenges associated with navigating an arboreal environment affect gait parameters within Psittaciformes. On the basis of previous biomechanical analyses of arboreal locomotion across other lineages, we outline the following predictions. Prediction 1: following the proposal by Dilger (1960) that the use of sidling is related to slow-speed locomotion, we predict that movement speeds during sidling will be slower than those during striding. Prediction 2: when sidling is adopted, the leading limb will serve a net braking function, while the trailing limb will serve a propulsive function, as typically observed during sideways walking in crabs (Blickhan and Full, 1987). Prediction 3: during sidling, the magnitude of mediolateral (pitching) forces will increase as substrate diameter decreases, reflecting the decreased stability of these smaller substrates. Prediction 4: in other tetrapod lineages, it has been demonstrated that peak vertical forces are greatest on terrestrial substrates and reduced arboreally, particularly on thin diameter substrates (Schmitt and Hanna, 2004; Schapker et al., 2022); thus, we predict that in parrots, peak vertical forces will be greatest on terrestrial substrates and will decrease on arboreal substrates. Prediction 5: unlike peak vertical forces, braking/propulsive forces are reported to remain relatively consistent between terrestrial and arboreal locomotion (Franz et al., 2005; Granatosky et al., 2018). Thus, we predict that substrate condition will not significantly alter the magnitude of these forces.

MATERIALS AND METHODS

Study subjects

Single limb force data were collected from six rosy-faced lovebirds, *Agapornis roseicollis* (Vieillot 1818), at the New York Institute of Technology College of Osteopathic Medicine (Old Westbury, NY, USA). The data were collected following the protocols approved by New York Institute of Technology College of Osteopathic Medicine Institutional Animal Care and Use Committee (IACUC protocol: 2021-MG-03). All animals were adults and were clear of any visible pathologies or gait abnormalities (Table 1).

Kinetic analyses

The experimental procedures described below follow protocols adapted from arboreal gait studies collected in primates (Lemelin and Schmitt, 2004; Schmitt and Lemelin, 2004; Young, 2012; Granatosky and Schmitt, 2019; Granatosky et al., 2019), small

Table 1. Basic morphometric information collected from the six rosy-faced lovebirds (*Agapornis roseicollis*) analyzed in this study

Subject	Body mass (g)	No. of footfalls contributed
Individual 1	49.9	111
Individual 2	48.3	110
Individual 3	44.9	124
Individual 4	46.9	103
Individual 5	49.9	137
Individual 6	53.0	128

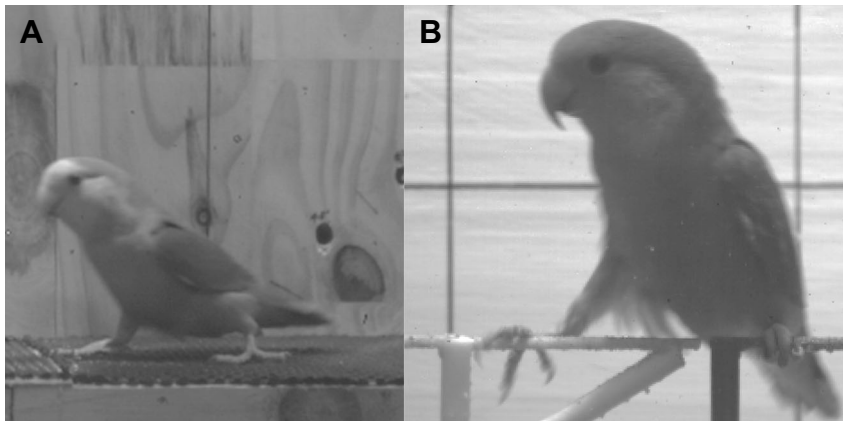


Fig. 1. Gait analysis. Single frame capture of striding on a terrestrial substrate (A) and sidling on small diameter simulated arboreal substrate (B) in the rosy-faced lovebird (*Agapornis roseicollis*).

mammals (Schmitt and Lemelin, 2002; Wölfer et al., 2021) and squamates (Wang et al., 2015). Single limb forces were collected as the birds walked across an instrumented terrestrial and three simulated arboreal runways of varying diameters (Fig. 1). The terrestrial runway consisted of a wooden board (61×18 cm) with shelf-liner adhered to provide grip. The large and medium pole substrates were wooden dowels measuring 61 cm in length and 6.35 and 1.91 cm in diameter, respectively, and wrapped in shelf-liner. The small pole substrate consisted of stainless-steel cable wire coated with epoxy and sand, measuring 0.32 cm in diameter (Fig. 1). The instrumented portion of the runway consisted of a small-load force plate (model HE6X6; Advanced Mechanical Technology, Inc., Watertown, MA, USA) mounted with custom 3D printed platforms to ensure recording of single hindlimb contact (Fig. 2; see Young et al., 2022, for more details). The instrumented portion was secured in the middle of the runway with a small gap at each end separating it from the non-instrumented sections. This created a flush runway utilized to isolate single hindlimb contacts. Each instrumented section was 4.50 cm in length and the same width (with respect to the terrestrial runway) or diameter (with respect to the arboreal runways) as the corresponding non-instrumented substrate. The length of the instrumented section was large enough to accommodate the fore-aft length of the animal's foot, while limiting the potential for overlapping footfalls between left and right limbs (Fig. 2).

Prior to data collection, weights of known mass were placed on the HE6X6 force plate to test the accuracy of force readings and ensure no cross-talk between channels. All trials began by zeroing out the HE6X6 force plate to remove any drift or offsets from previous recordings. The animals were acclimated to the experimental setups and were comfortable as they moved across the length of each runway. In most cases, minimal motivation was required to encourage the animal to begin moving. Such motivation was achieved either through a light tap on the tail or by blowing on the animal. Only trials where the animal moved in a straight continuous path and no visual acceleration or deceleration was observed were considered successful. Of these successful trials, only trials where a clear footfall was observed were saved for subsequent processing and statistical analysis. We aimed to collect ~30 footfalls for each bird on each substrate.

Two high-speed cameras (XC-2; Xcitex Inc., Woburn, MA, USA) were mounted to capture bird movement at 125 Hz from a lateral view and posterior view. Forces (sampled at 1250 Hz) and video data were synchronized using Procapture. A markerless pose estimation program, DeepLabCut (Mathis et al., 2018), was utilized to obtain positional data of a point on the animal's neck in the lateral

view throughout the extent of each trial. Using its machine learning algorithm, ~150–200 frames of this neck point as well as two additional points of a known distance (10 cm) were labeled to train the neural network (see Fig. S1). This known distance was used to calibrate the space by calculating a pixel to world space conversion factor. Custom-written MATLAB (MathWorks, Natick, MA, USA)

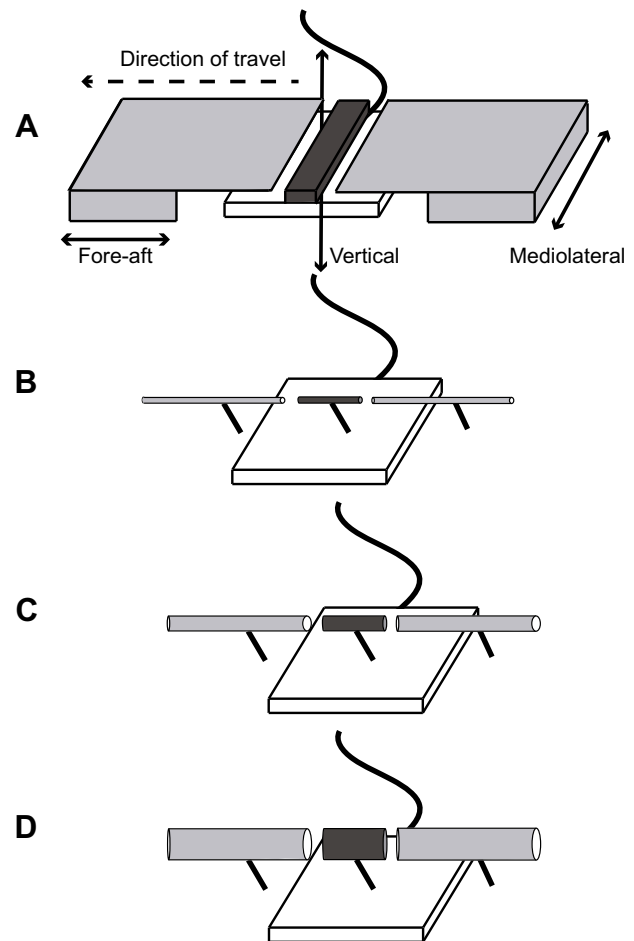


Fig. 2. Schematic diagram depicting instrumented (HE6X6 low-load force plate) ground and pole setups. (A) Terrestrial ground set up, and (B) small, (C) medium and (D) large pole set up. In terms of the forces, propulsive forces are directed along the axis of the fore-aft arrow. Positive forces are termed propulsive and negative forces are termed braking. Vertical forces directed onto the force plates are always positive. Positive forces along the mediolateral axis are termed lateral and negative forces are termed medial.

code allowed velocity to be calculated by dividing the positional data output from DeepLabCut by the time elapsed between the start and end of a stride.

Using a custom-written MATLAB script, forces were corrected to reflect direction of travel, orientation and whether the contacting limb was right or left. Only trials in which there was a clear separation between subsequent hindlimb footfalls were analyzed (Table 1). Force signs were standardized to reflect the forces applied to the animal, such that vertical forces toward the force plate reflected positive values, fore-aft forces were split into negative braking and positive propulsive forces, and for mediolateral forces, medially oriented forces were negative while lateral forces were positive. Once standardized, all forces were filtered through a low-pass Fourier filter at 15 Hz (Mateo and Fernández-Caballero, 2009). Peak fore-aft, vertical and mediolateral forces were extracted from each hindlimb single limb footfall. All peak force data were normalized using the animal's body weight (% BW) to allow statistical comparison between individuals (see below). Additionally, we measured the area under the horizontal component of the force–time curve to generate a braking, propulsive and net horizontal impulse. The net fore-aft force impulse provides a means for differentiating the overall braking or propulsive role of the limb during particular locomotor behaviors (Granatosky et al., 2018). The net fore-aft force impulse for each limb was calculated by subtracting the braking impulse from the propulsive impulse. Positive values indicate a net propulsive limb, while negative values indicate a net braking limb. Values approximating zero represent single limb contact forces wherein braking and propulsive impulses are approximately equal. Impulse data were normalized to percentage body weight seconds (% BW s) to allow statistical comparison between individuals (see below).

To test Dilger's (1960) hypothesis about sidling gaits being influenced by speed, we conducted a logistic ordinal regression. We also used a χ^2 -test to assess whether the likelihood of adopting a sidling gait was influenced by substrate diameter. Shapiro–Wilk and Levene's tests were used to determine normality of datasets (Sokal and Rohlf, 2012). All data were rank transformed to satisfy assumptions of subsequent statistical analyses. Speed, which is well known to influence the magnitude of force data [see Granatosky et al. (2020) for statistical discussion], was included in all ANCOVA used to assess differences in variables of interest. We ran a series of ANCOVA comparing the magnitude of propulsive to braking impulses between the gait types within each substrate size to assess the extent to which the animals were moving at steady state.

As peak vertical forces did not change in orientation or semantic meaning as the birds transitioned from striding to sidling, our first set of ANCOVA used the entire dataset to assess the effect of substrate size (flat ground, and large, medium and small pole) and gait type on peak vertical forces. Then, we subset our data by gait type (sidling or striding). Within the striding dataset, we conducted another series of ANCOVA, assessing the effect of substrate size on peak fore-aft and mediolateral forces, and fore-aft impulses. Within

the sidling dataset, we first created ANCOVA models to assess the effect of substrate size on peak mediolateral or pitching forces. As the parrots underwent a complete functional separation of limbs whilst adopting a sidling gait, the sidling dataset was further subset into a leading limb data frame (peak braking force and impulse) and a trailing limb data frame (peak propulsive force and impulse). Within each data frame, we assessed how peak braking force and impulse (leading limb) and peak propulsive force and impulse (trailing limb) were affected by substrate size (large, medium and small pole). All statistical analyses were conducted using R (<http://www.R-project.org/>) using the packages ARTool and multcomp. Raw data used in analyses are presented in Table S1.

RESULTS

Gait preferences across substrates

Sidling gaits were observed on all arboreal substrates and were employed exclusively when traversing the medium and small diameter substrates. Accordingly, the incidence of sidling was significantly influenced by substrate size ($\chi^2=533.91$; $P<0.001$). On the large pole substrate, wherein the two gaits were directly comparable, sidling gaits were significantly slower than striding gaits (0.17 ± 0.031 versus 0.33 ± 0.12 m s⁻¹, $P<0.005$). Similarly, significant differences in contact time (0.17 ± 0.03 versus 0.33 ± 0.12 s, $P<0.001$), duty factor ($64.8\pm5.70\%$ versus $61.3\pm6.40\%$, $P<0.001$) and stride frequency (4.23 ± 0.67 versus 3.84 ± 0.75 Hz, $P=0.038$) were observed between sidling and striding gaits, respectively (see Fig. S2). Within a sidling gait, contact times were equivalent between large and medium poles ($P=0.568$), but both differed significantly from those for the small pole ($P<0.001$ in each instance). Duty factor was significantly different between large and medium and large and small poles ($P<0.001$), but equivalent on small and medium poles. Stride frequency was significantly different between all substrate combinations ($P<0.009$).

Peak vertical forces

Peak vertical forces associated with striding did not differ between the flat ground substrate ($123.00\pm22.70\%$ BW) and the large arboreal substrate ($127.00\pm18.10\%$ BW; $P=0.224$; Table 2 and Fig. 3A). Within a sidling gait, substrate size had a variable impact on peak vertical forces (Table 3, Fig. 3A). Peak vertical forces were significantly different for large ($121.00\pm18.9\%$ BW) versus small ($110\pm11.7\%$ BW, $P<0.001$) and large versus medium ($108\pm10.7\%$ BW, $P<0.001$) poles, but no differences were observed between small and medium poles ($P=0.942$; Table 3 and Fig. 3A). Sidling peak vertical forces were significantly lower than those during striding ($P<0.001$).

Mediolateral forces

During striding, medial forces between terrestrial ($-20.60\pm14.30\%$ BW) and large pole ($-17.20\pm9.54\%$ BW) substrates were comparable ($P=0.596$; Table 2 and Fig. 3C),

Table 2. Peak forces and impulses collected from six rosy-faced lovebirds (*A. roseicollis*) during striding

Substrate	<i>n</i>	Peak braking force (% BW)	Braking impulse (% BW s)	Peak propulsive force (% BW)	Propulsive impulse (% BW s)	Net fore-aft impulse (% BW s)	Peak vertical force (% BW)	Peak medial force (% BW)	Peak lateral force (% BW)
Ground	87	-30.70 ± 11.7	-1.33 ± 0.67	23.70 ± 9.19	1.59 ± 1.13	0.25 ± 1.52	123.00 ± 22.70	-20.60 ± 14.30	10.00 ± 9.89
Large pole	29	-40.30 ± 19.6	-2.62 ± 1.51	27.70 ± 7.90	2.00 ± 1.31	-0.62 ± 1.91	127.00 ± 18.10	-17.20 ± 9.54	16.90 ± 11.10

% BW, percentage body weight; % BW s, percentage body weight seconds; *n*, number of footfalls. Data are means \pm s.d.

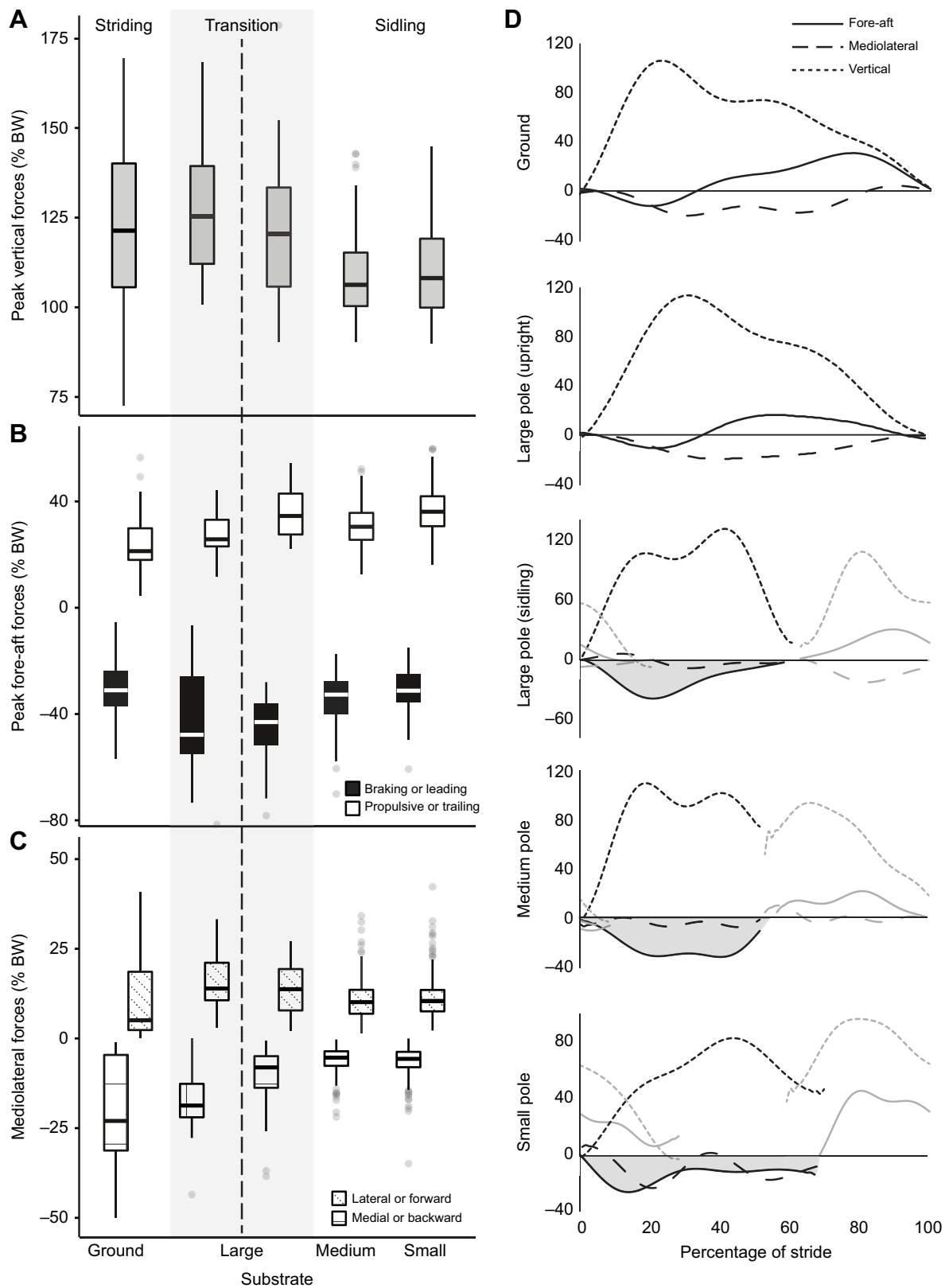


Fig. 3. Peak forces for terrestrial and arboreal locomotion. (A) Vertical, (B) fore-aft and (C) mediolateral forces presented as box and whiskers plots, as well as (D) representative force traces from a single stride across a range of substrates in the rosy-faced lovebird. All forces are expressed as a percentage of body weight (% BW). Box plots show median, upper and lower quartiles and $1.5 \times$ the interquartile range; circles are outliers. The gray shading in A–C indicates a gait transition from striding to sidling that exists on large diameter substrates. In B and C, all bars indicate leading or trailing (B) and forward or backward (C) after the dashed vertical line. The black lines in D for large pole (sidling), medium pole and small pole indicate the leading limb and the light gray lines indicate the lagging limb. The shaded areas under the curves in D indicate the fore-aft leading limb force.

Table 3. Peak mediolateral and vertical forces collected from six rosy-faced lovebirds (*A. roseicollis*) during sidling on simulated arboreal substrates

Substrate	<i>n</i>	Vertical (% BW)	Medial (% BW)	Lateral (% BW)
Large pole	37	121.00±18.90	−11.10±9.20	13.40±6.69
Medium pole	241	108.00±10.70	−5.65±3.52	10.80±5.50
Small pole	250	110.00±11.70	−6.54±4.15	11.20±5.72

Medial forces were backward pitching; lateral forces were forward pitching. *n*, number of footfalls. Data are means±s.d.

though parrots generated significantly greater laterally directed forces on the arboreal substrate (16.90±11.10% BW) compared with the flat substrate (10.00±9.89% BW, $P<0.001$; Table 3). Whilst sidling, the mediolateral forces produced by the parrots are essentially anteroposterior movements, pitching them forward ('lateral') and backward ('medial') on the arboreal substrates. Pitching forces were generally low in magnitude (Table 3, Fig. 3C), with broadly equivalent 'medial' (i.e. backward pitching) and 'lateral' (i.e. forward pitching) peak forces. 'Medial' (i.e. backward pitching) forces were greater on the large substrate (−11.10±9.20% BW) than on either the medium (−5.65±3.52% BW, $P<0.001$) or small (−6.54±4.15% BW, $P=0.010$; Table 3) substrate, but no differences were observed between small and medium poles ($P=0.183$). 'Lateral' (i.e. forward pitching) forces were universally equivalent between substrate sizes ($P=0.108$ – 0.988 ; Table 3 and Fig. 3C).

Braking and propulsive forces

Other than for the medium pole substrate ($P<0.005$), our ANCOVA assessing the magnitudes of braking and propulsive impulses across the various substrates were insignificant, demonstrating steady-state locomotion for the most part (all $P>0.050$). In striding parrots, significantly greater fore-aft peak braking forces ($P=0.015$) were observed on the arboreal substrate (−40.30±19.6% BW; Table 2 and Fig. 3B) compared with the terrestrial substrate (−30.70±11.7% BW; Table 2 and Fig. 3B), though differences in propulsive forces ($P=0.076$) did not reach statistical significance. Significant differences between propulsive and braking impulses between the flat and large pole substrate were also observed (both $P<0.007$; Table 2).

When sidling, the parrots produce fore-aft forces from what were mediolateral movements in striding as a result of their positioning on the arboreal substrate. Rather than an individual limb undergoing a braking-to-propulsive transition as seen in striding, parrots completely divide the function of their two hindlimbs into a leading and trailing limb when sidling. The leading limb imparts exclusively braking peak forces and impulses, while the trailing limb generates exclusively propulsive peak forces and impulses (Table 4, Fig. 3D). A significant decline in the peak braking force of

leading limbs was observed as the birds traversed substrates of descending diameter (Table 4 and Fig. 3B, $P<0.007$ in all cases). Meanwhile, propulsive peak forces produced by the trailing limbs were significantly different between the small and medium pole (Table 4 and Fig. 3B, $P<0.001$), but not between small and large pole ($P=0.767$) or between the medium and large pole ($P=0.245$). The braking (leading limb) and propulsive (trailing limb) impulses follow a similar trend – increasing in magnitude as substrate size decreases (Table 4 and Fig. 3B). All combinations of substrate types besides medium and large pole (both $P>0.599$) in both the braking (leading limb) and propulsive (trailing limb) impulses were significant (all $P<0.001$).

DISCUSSION

Summary of results

This study provides, to our knowledge, the first analysis of limb loading patterns during arboreal locomotion in a bird. Across four different substrate conditions, rosy-faced lovebirds dramatically alter both gross locomotor behavior and the limb loading patterns within these behaviors. Most notable is the adoption of sidling. As a consequence of the reorientation of the body during sidling, limb loading patterns varied not only in magnitude in response to arboreal movement but also in kind.

General characteristics of sidling

Rosy-faced lovebirds solely used striding gaits on the terrestrial substrate, while sidling was observed on all arboreal substrate conditions, and became ubiquitous on medium and small diameter substrates. In accordance with Dilger (1960), the tendency for rosy-faced lovebirds to adopt sidling was influenced by speed (supporting prediction 1), but a more marked shift was dependent on substrate diameter. Based on this finding, we propose the use of sidling represents a solution to an anatomical constraint. Compared with most tetrapod lineages, birds have greatly reduced the number of tarsal and metatarsal bones into a singular tarsometatarsus. Further, articular surfaces with the knee proximally and phalanges distally are characterized with noticeable deep trochleae (Zelenkov, 2016; Carril et al., 2021), while the projecting pelvic antitrochanter limits abduction of the femur to around 60 deg, which is further constrained by ligaments and soft tissues to just ~30 deg (Hutchinson and Gatesy, 2000). In spite of this theoretically limited mobility, recent studies have demonstrated the ability of birds to reorient the hindlimb via long-axis rotation of the femur and tibiotarsus, and thus modulate foot position in 3D space (Kambic et al., 2014; 2015). Nevertheless, sidling may represent an easy mechanism through which birds may keep their grasping feet perpendicular to the long axis of the substrate, thus ensuring grasping abilities on thin arboreal substrates.

Sidling in general is slower than striding and, unintuitively, is associated with short contact times, but increased duty factor and

Table 4. Peak braking and propulsive forces and impulses collected from six rosy-faced lovebirds (*A. roseicollis*) during sidling on simulated arboreal substrates

Substrate	<i>n</i>	Leading limb		Trailing limb	
		Braking peak force (% BW)	Braking impulse (% BW s)	Propulsive peak force (% BW)	Propulsive impulse (% BW s)
Large pole	37	−45.20±14.00	−3.14±0.76	36.00±9.57	2.77±0.97
Medium pole	241	−34.60±10.20	−3.38±0.97	30.90±8.07	2.98±0.98
Small pole	250	−30.70±7.78	−3.72±1.44	36.50±8.59	3.68±1.30

Sidling was associated with a functional decoupling of the limbs such that the leading limb imparted only braking forces, while the trailing limb imparted only propulsive forces (see Introduction, 'Sidling gaits'). Therefore, net propulsive impulses are equivalent to each respective braking or propulsive force. *n*, number of footfalls. Data are means±s.d.

stride frequency. Little is known about sidling in any animal, but imposed sideways walking in humans demonstrates high metabolic costs associated with this gait (Handford and Srinivasan, 2014), with 1 m s^{-1} sideways walking having the same gross metabolic rate as running at 2.3 m s^{-1} . These costs are attributed to repeated starting and stopping of the center of mass (COM), which precludes significant energy recovery between strides. However, the anatomy of the human hip differs greatly from that of birds, which have functionally replaced hip abduction and adduction with hindlimb long-axis rotation, resulting in a loss of hip abductor musculature and the co-option of these muscles to control long-axis rotation of the femur (Hutchinson and Gatesy, 2000). Thus, it is unclear whether sidling birds face similarly increased energetic demands – though the short steps associated with relatively slow speeds certainly hint at such costs (Heglund and Taylor, 1988; Reilly et al., 2007) – and a mechanical and metabolic analysis of parrot sidling is required to assess parallels with sideways walking in humans.

Limb loading patterns in an arboreal biped

Observations of bipedal gaits on arboreal substrates are exceedingly rare in non-avian tetrapods. Indeed, only a handful of studies have documented such behaviors, primarily in orangutans (Thorpe et al., 2007) and gibbons (Fleagle, 1976; Fan et al., 2013), and in these cases, bipedalism is limited to quite short of distances and often requiring a supportive overhead substrate. Tree-dwelling birds capable of asynchronous (i.e. left/right alternating) gaits (Provini and Höfling, 2020) typically utilize bipedalism when moving on horizontally oriented arboreal substrates. Accordingly, these species serve as ideal models for understanding the mechanics of moving bipedally in trees broadly. In the sections below, we discuss how limb loading patterns change with regards to bipedalism on arboreal substrates generally, but also aim to determine at what substrate diameter animals need to alter neuromuscular gait characteristics in response to the challenges of arboreal movement.

Peak vertical forces

Of the kinetic variables of interest, only peak vertical forces could be analyzed across the entire sample regardless of gait type. We observed a decrease in peak vertical force from terrestrial and large diameter substrates to medium and small diameter substrates (Tables 2 and 3), in line with prediction 4. This reduction is solely attributable to substrate size, as variation in speed was accounted for in statistical testing. This finding is in accordance with other studies (Schmitt and Hanna, 2004; Schapker et al., 2022) that note a similar reduction in peak vertical forces when traversing thin arboreal substrates. This is thought to be a strategy to reduce potential oscillations between the body and the substrate, and in mammals has been attributed to limb compliance that limits vertical displacement of the COM. It should be noted, however, that recent empirical studies (Young et al., 2016; Schapker et al., 2022) in primates did not observe a proposed reduction in COM displacement in response to arboreal substrates. Therefore, it remains unknown how COM displacement varies during the arboreal movement of parrots, or any other taxon of bird.

Other means by which peak vertical forces could be reduced across substrates include increasing the relative amount of time the limb is in contact with the substrate (McMahon et al., 1987; Schmitt, 1999). While this hypothesis has had some support in quadrupedal mammals (Schmitt and Hanna, 2004; Young, 2012), our data demonstrate that sidling gaits are associated with a decrease in contact time compared with striding on the ground and large diameter pole, refuting this paradigm. While contact time decreased,

the birds began taking more frequent steps, resulting in an increased duty factor. As increased duty factors are well known to correlate with decreases in peak vertical force for similar reasons to contact time [see McMahon et al. (1987) and Schmitt (1999) for discussion of mechanism], this is an additional consideration for the observed reduction in peak vertical forces as the parrots transitioned from striding to sidling (see Fig. S3). It is also possible that the abducted hindlimb observed during sidling (Fig. 1) may serve to decrease peak vertical forces by positioning hip adductors in a more advantageous position to absorb kinetic energy during the stride (Podrąza and White, 2010), though the reduced hip adductor muscles found in birds (Hutchinson and Gatesy, 2000) may limit the utility of such a mechanism.

Mediolateral forces

Within parrots, mediolateral forces were generally low on all arboreal substrates, regardless of gait type (Fig. 3C), contrary to prediction 3. This is in contrast to patterns generally observed in arboreal mammals (Schmitt, 2003; Lammers and Biknevicius, 2004; Franz et al., 2005; Lammers and Gauntner, 2008; Schmidt and Fischer, 2010; Granatosky and Schmitt, 2017; Granatosky, 2018). For these species, mediolateral forces tend to increase either as a strategy to correct for side-to-side toppling torques on thin arboreal branches (Lammers and Biknevicius, 2004; Lammers and Gauntner, 2008; Schmidt and Fischer, 2010) or as a means to produce counteracting ‘gripping’ forces to increase balance. The parrots in this study overcame toppling concerns on thin arboreal substrates by adopting sidling gaits. As sidling involves a reorientation of the body, mediolateral forces no longer reflect an inward or outward application of force by the limbs, but instead provide information as to whether the animal is pitching forward or backward to balance on the substrate. Yet, even on the smallest diameter substrate, mediolateral forces were relatively low. This finding suggests that the zygodactylous feet provide sufficient grasping force to counteract potential toppling torques associated with arboreal movement (Cartmill, 1985; Lammers and Gauntner, 2008). Thus, parrots do not require consistent swaying on top of the branch to maintain stability. Presumably, sidling gaits should be present in many other arboreal avian lineages, and future studies should explore whether variation in avian foot morphology influences patterns of mediolateral forces.

It should be noted that compared with fore-aft and vertical forces, mediolateral forces were highly variable (see Tables 2 and 3, and Fig. 3C, to appreciate relative standard deviation of mean differences) across strides. This appears to be a common feature of locomotion in birds (Bishop et al., 2018) and tetrapods generally (Granatosky et al., 2020). The reason for such variability was best articulated by Bishop et al. (2018), who posited that rather than mediolateral forces being thought of as a predetermined motor pattern, these forces should be considered as essential to step-to-step stabilization. As similarly high variability in mediolateral forces was observed regardless of gait type and/or substrate (Tables 2 and 3, and Fig. 3C), it seems reasonable that Bishop and colleagues’ (2018) predictions about the functional role of mediolateral forces is valid outside typical locomotor modes or ecological situations.

Braking and propulsive forces

Patterns of braking and propulsive forces changed dramatically between typical striding and sidling, contrary to prediction 5. During striding on the ground and the large diameter substrate, all strides started with a braking force during the first portion of stance phase, then transitioned to a propulsive force as the limb

moved posteriorly to the COM (Granatosky et al., 2018). Consistent with findings in most bipeds (Bishop et al., 2018), braking and propulsive impulse are generally equal within a limb (i.e. the hindlimb experiences both braking and propulsive forces). This is in sharp contrast to what we observed during sidling. Here, the leading limb served a solely braking role (see Fig. 3D), while the trailing limb only produced propulsive forces (Blickhan and Full, 1987), supporting prediction 2. This complete functional separation occurred because the short steps did not show any overstriding past each other. Thus, the posterior position of the leading limb was consistently limited by the anterior placement of the trailing limb. Unlike sideways walking in crabs (Blickhan and Full, 1987), we observed no strides in which the leading limb was propulsive and the trailing limb was braking. Thus, the parrots are not pulling themselves along the arboreal substrate. The use of hindlimb abduction as a means of forward progression on thin substrates would likely require significant neuromuscular alterations within these muscles, and future work exploring how muscle activation patterns of the hindlimb musculature change between striding and sidling would be of great interest for our general understanding of neuromuscular flexibility during locomotion.

Although peak braking and propulsive magnitudes tended to vary between the leading and trailing limbs, analyses of fore-aft impulse demonstrated sidling gaits of parrots were relatively ‘steady state’, apart from movement on the medium diameter substrate (Fig. S2). The relatively larger peak braking forces compared with propulsive peaks could be attributable to kinematic parameters or to relative variation in contact time (Fig. S2). The mechanisms underscoring these patterns are beyond the scope of this study, and future work is required to elucidate the reason for this disparity.

Conclusion

This study sought to explore whether the well-established patterns of single limb forces observed during arboreal locomotion in quadrupedal mammals and squamates are consistent in parrots. We employed an experimental design spanning several substrate diameters, rather than simply a terrestrial versus arboreal substrate – though other variables (e.g. substrate compliance, inclination and friction) were not assessed herein and require consideration in future studies.

Overall, the kinetic analysis within reveals that the limb loading mechanics of bipedal locomotion in parrots is not conserved when moving from terrestrial to arboreal substrates or when moving on substrates of varying diameter. Further, arboreal movement in parrots involved a radical shift in gait type to sidling that became ubiquitous when the substrate diameter was smaller than the dorsoventral height of the animals’ body. Consequently, attributing kinetic adjustments to arboreal movement versus sidling proved difficult with the current sample, but some generalizations can be inferred. Specifically, regardless of gait type, peak vertical forces dropped considerably in magnitude when moving on relatively small diameter substrates. This may serve to limit oscillations of the underlying branch which could reduce stability, and thus represents a mechanical goal for all arboreal animals regardless of taxonomy or gait type.

Sidling in turn drastically alters both fore-aft and mediolateral forces, reorienting the body such that mediolateral forces no longer reflect an inward or outward application of force by the limbs, but instead provide information as to whether the animal is pitching forward or backward to balance on the substrate. Unexpectedly, these mediolateral forces were significantly lower compared with forces during striding on terrestrial and large diameter substrates.

Taken together, our findings indicate that sidling represents an entirely different gait pattern to striding. While similar patterns of movement are energetically expensive in humans, it is possible that the highly derived hip osteology and musculature of birds may contribute to reductions in metabolic costs, such that sidling in parrots, and by extension other arboreal avian lineages, is relatively metabolically cheaper than striding. Future work is required to assess this claim. It is also possible that many of the kinetic adjustments adopted by arboreal parrots may also typify strategies of humans moving on thin arboreal substrates, as both humans and birds lack the ability to invert the ankle to any significant degree. While professional gymnasts are trained to move with their body axis oriented parallel to the substrate, novice human movement in trees resembles sidling and often involves the forelimbs as an additional support. While studies of such movements are severely lacking, the kinetic strategies observed in bipedal sidling parrots may prove useful in future discussion of possible scenarios of human evolution (Thorpe et al., 2007).

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Competing interests

The authors declare no competing or financial interests.

Author contributions

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