

RESEARCH ARTICLE

Quantifying koala locomotion strategies: implications for the evolution of arborealism in marsupials

Joshua L. Gaschk, Celine H. Frère and Christofer J. Clemente*

ABSTRACT

The morphology and locomotor performance of a species can determine their inherent fitness within a habitat type. Koalas have an unusual morphology for marsupials, with several key adaptations suggested to increase stability in arboreal environments. We quantified the kinematics of their movement over ground and along narrow arboreal trackways to determine the extent to which their locomotion resembled that of primates, occupying similar niches, or basal marsupials from which they evolved. On the ground, the locomotion of koalas resembled a combination of marsupial behaviours and primate-like mechanics. For example, their fastest strides were bounding type gaits with a top speed of 2.78 m s^{-1} (mean 1.20 m s^{-1}), resembling marsupials, while the relatively longer stride length was reflective of primate locomotion. Speed was increased using equal modification of stride length and frequency. On narrow substrates, koalas took longer but slower strides (mean 0.42 m s^{-1}), adopting diagonally coupled gaits including both lateral and diagonal sequence gaits, the latter being a strategy distinctive among arboreal primates. The use of diagonally coupled gaits in the arboreal environment is likely only possible because of the unique gripping hand morphology of both the fore and hind feet of koalas. These results suggest that during ground locomotion, they use marsupial-like strategies but alternate to primate-like strategies when moving amongst branches, maximising stability in these environments. The locomotion strategies of koalas provide key insights into an independent evolutionary branch for an arboreal specialist, highlighting how locomotor strategies can convergently evolve between distant lineages.

KEY WORDS: Anteroposterior sequence, Morphology, Arboreality, Primate, Stability

INTRODUCTION

The locomotor performance of an individual limits its behaviour, and inherently fitness, within its niche (Irschick and Garland, 2001). The study of locomotor performance thus gives an understanding of both the challenges an animal may encounter within their environment, and the morphology that aids them in overcoming these (Byrnes and Spence, 2011; Clemente et al., 2016; Wynn et al., 2015). Arboreal habitats may represent one of the more challenging environments to animals, as they are typically characterised by compliant, discontinuous substrates, often at significant heights from the ground (Günther et al., 1991; Hyams et al., 2012; Youlatos

et al., 2015), yet a range of phyla use trees for food and shelter (e.g. birds, reptiles, mammals; Clemente et al., 2013; Foster and Higham, 2012; Gálvez-López et al., 2011). To successfully navigate arboreal environments, animals must develop strategies to overcome these challenges, including climbing vertical substrates (Byron et al., 2011) and traversing circular supports of varying inclination and diameter (Clemente et al., 2019; Nasir et al., 2017; Shapiro et al., 2016), often with inconsistencies in the surface (diverging branches, knots, bends, texture) (Lammers and Sufka, 2013), and develop an effective way to cross the gaps between branches or trees (Byrnes and Spence, 2011; Byron et al., 2011). Finally, it is necessary for these strategies to maximise stability, as slips and falls have severe consequences (Wynn et al., 2015; Nasir et al., 2017; Wheatley, et al., 2018).

Locomotor performance in arboreal mammals has been widely documented, resulting in a remarkable diversity of morphologies and behaviours among marsupials, primates, carnivores and rodents (Camargo et al., 2016; Delciellos and Vieira, 2009; Ercoli and Youlatos, 2016; Lammers and Gauntner, 2008; Larson and Demes, 2011; Pontzer et al., 2014; Lemelin and Schmitt, 2007; O'Neill and Schmitt, 2012; Schmitt and Lemelin, 2002; White, 1990). Primates are considered the most derived of these owing to their affiliation with, and fitness within, arboreal niches (Gebo, 2004). Their performance, morphology and behaviours have been considered optimal strategies for the stability that is required for tree-living (Larson et al., 2001; Lemelin and Cartmill, 2010; Sargis, 2001). Much then, has been dedicated to understanding primate locomotion and its evolution (Hildebrand, 1967; Higurashi et al., 2009; Byron et al., 2011; Delciellos and Vieira, 2009; Cartmill et al., 2002, 2007; Shapiro and Raichlen, 2005).

Primates incorporate a diagonally coupled (DC) walk, common in fine branch locomotion, and adjust the timing of footfalls that increases or decreases the moment of diagonal bipedal support (decreased=lateral sequence, LS; increased=diagonal sequence, DS; Byron et al., 2011; Gebo, 2004; Cartmill et al., 2007). DSDC walks are almost exclusive to primates, with most species favouring this gait in arboreal environments, and few instances reported outside of primates (e.g. kinkajou and woolly opossum; Lemelin and Cartmill, 2010; Lemelin and Schmitt, 2007; Wallace and Demes, 2008; Young, 2012; Chadwell and Young, 2015; Nyakatura and Heymann, 2010; O'Neill and Schmitt, 2012; Wunderlich et al., 2014). This gait is thought to increase stability as the body would be balanced over a protracted hindlimb when the forefoot comes down, important when support for the forelimb is unknown (Cartmill et al., 2002, 2007). However, there is much debate on the topic, with some suggesting that LSDC gaits may confer similar benefits (Shapiro and Raichlen, 2005). LSDC walks are reported as the favoured narrow support gait in some opossums, gliders and marmosets, all small arboreal specialists (Chadwell and Young, 2015; Delciellos and Vieira, 2009; Lemelin et al., 2003; Shapiro and Young, 2012; Schmitt, 2003).

School of Science and Engineering, University of the Sunshine Coast, Sippy Downs, QLD 4556, Australia.

*Author for correspondence (cclement@usc.edu.au)

 C.J.C., 0000-0001-8174-3890

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The locomotion of some arboreal marsupials reflects strategies of primates during arboreal locomotion (Lemelin and Schmitt, 2007). The marsupial lineage diverged from placental mammals long before primates were present, meaning any similarities in strategy have developed through convergent evolution (Sears, 2009). Thus, to obtain a clearer picture of the evolution of arboreality in mammals, it would be insightful to understand the locomotion of a specialised arboreal marsupial that possesses a similar morphology to primates.

Koalas, *Phascolarctos cinerus* (Goldfuss 1817), may be a suitable species, with a primate-like morphology and a marsupial life history. They possess relatively long limbs for their body mass, and have powerful grasping hands and feet (Grand and Barboza, 2001). An opposable hallux has developed on the feet (Fig. 1A), a feature present in both marsupial and primate arboreal specialists, suggesting convergent strategies (Byron et al., 2015; Sargis, 2001). Further, koalas have two opposable digits on the hands, termed zygodactyly, which allows them to create a strong grip (Fig. 1A) (Cartmill, 1974; Youlatos, 2010).

Koalas are arboreal specialists that feed on the leaves of eucalypt trees in the woodlands and forests of eastern Australia (Grand and Barboza, 2001). A solely eucalypt diet is low in energy, thus they are mostly inactive (Krockenberger and Hume, 2007; Melzer et al., 2014; Ryan et al., 2013), remaining in trees unless searching for mates, moving to new eucalypt patches or searching for water (Ellis et al., 1995; Gordon et al., 2006; Phillips and Callaghan, 2000). They are also of conservation significance, as much of their habitat is being cleared owing to urbanisation, compounding the effect of diseases and causing a decline in many koala populations (Ellis et al., 2013,

2002; Ryan et al., 2013). Habitat clearance also means koalas must travel longer distances between remnant patches, which is not only energetically costly given their diet, but also increases the probability of encountering risks, such as vehicle collisions and dog attacks (Grand and Barboza, 2001; Gordon et al., 2006; Melzer et al., 2014).

Despite the koala's unique morphology and life history, their locomotion is yet to be explored in detail. We analysed 198 strides from six subjects, across four terrain types, including over ground locomotion, and horizontal, inclined and declined narrow supports. Data collection was designed specifically for comparison with a range of other arboreal specialists in the class Mammalia. We further compared these strategies with those of primates, marsupials and various other mammals. We hypothesise that their primate-like morphology is also reflected in convergent strategies for arboreal locomotion.

MATERIALS AND METHODS

Koalas and substrates

The koalas used during this study were housed and cared for by the Queensland Zoo (Wildlife HQ). Six koalas [age=6.8±4.1 years, mass=5.35±0.70 kg, length (head to tail)=39.67±2.07 cm, sex ratio F:M=5:1] were filmed in their enclosure traversing substrate similar to that present in their natural habitat, between January and February 2017. Ethics for the project were approved via the Animal Ethics Committee at the University of the Sunshine Coast (AN/S/16/45). To encourage movement, film was collected just prior to and after eucalypt leaves were replaced for feeding. Arboreal locomotion was filmed while moving along natural branches with a mean (±s.d.) diameter of 9.23±1.33 cm (see Fig. S1). Three arboreal cases were

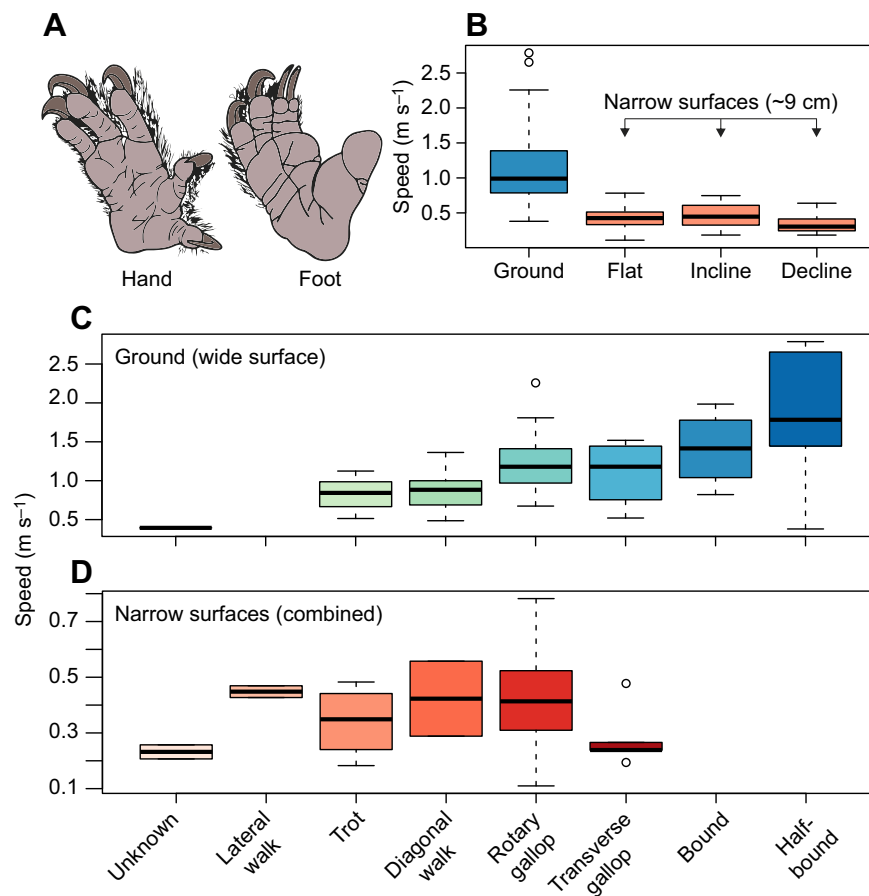


Fig. 1. The effect of substrate and gait on speed (m s^{-1}) in six koalas. (A) The hands and feet of koalas. (B) Boxplot of the speed (m s^{-1}) of strides ($n=198$), from six koalas over the different surface conditions of ground, flat (narrow), inclined (narrow) and declined (narrow). (C, D) Boxplots of the speed progression of gait patterns defined by Abourachid (2003) during (C) ground locomotion ($n=47$) and (D) narrow surface locomotion ($n=151$). Mixed-effects linear models showed strides over ground were significantly faster than other substrates ($F_{1,184}=135$, $P<0.001$), and half-bounds were significantly faster than other strides ($F_{6,35}=3.95$, $P=0.004$). No significant difference in speed was recorded across gait patterns on narrow surfaces.

identified: inclined, declined and flat. All the substrates measured for horizontal locomotion had a mean height above the ground of 155 ± 24.2 cm and mean angle of 5.0 ± 2.7 deg. The inclined and declined cases had a mean height of 185 ± 59.7 cm and angle of 26.6 ± 4.0 deg, with koalas moving upwards for inclined movements and downwards for declined movements. To film locomotion along the ground, keepers placed koalas 1–2 m away from the closest climbing point. The ground was a flat sandy soil with no obstructions. During filming dates, one of the koalas was pregnant (Ariel), and another had a joey at foot (Maple); this was compensated for with nested analyses detailed below.

Cameras and video analysis

Cameras were paired in model types (Hero3+ Black, 720 pixels $120 \text{ frames s}^{-1}$, narrow field of view; Hero4 Silver, 960 pixels, $100 \text{ frames s}^{-1}$, wide field of view) and placed on tripods perpendicular to each other. Pairs were synchronised via Wi-Fi to GoPro Smart Remotes. Once the cameras were set up, a calibration wand with two points separated by 24 cm was waved through the space. Recordings were started as the koalas began to locomote across the substrates and stopped when the koalas paused or reached the other end, to reduce the lengths of the videos. Approximately 40 min of footage across 204 videos was collected. Videos were analysed using the Argus script (version 2.1) within the Python environment (version 2.7.12) (argus.web.unc.edu, January 2017), including camera intrinsics for each model to remove any lens distortion.

Kinematic variables

During locomotion, koalas' initial contact with the substrate was commonly midfoot, heel or palm first and the toes were the last point of contact at the end of stance phase. Thus, these instances were indicators for the touchdowns and lift-offs for our footfalls, respectively. The right forefoot was used as a reference foot for the stride events. The majority of strides were during steady-state locomotion and were only used if the right foot touchdowns initiating the stride and concluding the stride were unimpeded. Strides were not used if the koala's feet slipped off the substrate, though these instances were recorded. Cycle duration (s) was the time between consecutive footfalls of the reference limb. Stride length (m) was the distance between the footfalls of the same limb. Swing and stance durations of the feet corresponded to the time the feet were moving through the air and grounded, respectively (s). Stride frequency (Hz) was the number of strides per unit of time. Speed (m s^{-1}) was calculated using the average distance between footfalls of a cycle and the duration of the cycle.

Temporal coordination variables

The anteroposterior sequence (APS) approach was used to analyse the temporal coordination variables; the cut-off values used to describe gaits are represented in Table 1 (Abourachid, 2003; Gálvez-López et al., 2011). APS uses the same variables to compare the kinematic and temporal coordination of all gait types (asymmetrical and symmetrical), including transitioning gaits (see Abourachid, 2003) (Fig. 2E–L). $T_{\text{lag,H}}$ and $T_{\text{lag,F}}$ represent the time lag between the footfalls within the hind and forelimb pairs, respectively. $T_{\text{lag,P}}$ represents the difference between the ipsilateral, or same-side, pair. For this study, we averaged the $T_{\text{lag,P}}$ of both sides of the koalas.

Spatial coordination variables

To understand the positioning of the footfalls within a cycle, we also calculated the spatial distances (m) of these lag variables. $D_{\text{fore-aft,H}}$

Table 1. The frequency (%) of gait patterns of six koalas as they moved across different substrates: ground and narrow (flat, incline and decline)

Gait ($T_{\text{lag,P}}$, $T_{\text{lag,H}}$, $T_{\text{lag,F}}$)	Ground	Narrow		
		Flat	Incline	Decline
Bound (–, 0, 0)	4 (8.5)	–	–	–
Diagonal walk (<0.5, 0.5, 0.5)	10 (21.3)	3 (3.4)	5 (17.2)	–
Half bound (–, 0, 0.5)	6 (12.8)	–	–	–
Lateral walk (>0.5, 0.5, 0.5)	–	5 (5.6)	1 (3.5)	3 (9.1)
Rotary gallop (–, <0.5, <0.0)	11 (23.4)	16 (18.0)	6 (20.7)	5 (15.1)
Transverse gallop (–, <0.5, <0.0)	4 (8.5)	8 (9.0)	3 (10.3)	6 (18.2)
Trot (0.5, 0.5, 0.5)	11 (23.4)	55 (61.8)	14 (48.3)	19 (57.6)
Unknown (unclassified)	1 (2.1)	2 (2.2)	–	–
Sum	47	89	29	33

The values in brackets for each gait pattern represent the proportion of the T_{lag} of pair, hind and forelimbs, respectively, as defined by Abourachid (2003). Speed-dependent lags are represented by two dashes (–). Unknown gaits were those that did not match the lag variables of any defined gait.

$D_{\text{fore-aft,F}}$ and $D_{\text{fore-aft,P}}$ all correspond to the fore–aft distances between touchdowns of the hind, fore and ipsilateral pair feet, respectively. $D_{\text{med-lat,H}}$, $D_{\text{med-lat,F}}$ and $D_{\text{med-lat,P}}$ represent the mediolateral (left–right) distances (m) between the same touchdowns.

Data analysis

Before analysis, data were tested for normality, and log transformed where appropriate. For all analyses, a within-subject design was used, including subject as random factor using the lme.R function from the nlme package in R (version 3.2.3, <https://CRAN.R-project.org/package=nlme>). To examine variation between factors, we specified the model with lme.R function, and then used the glht.R function from the multcomp package to perform Tukey *post hoc* tests, correcting the *P*-values using the Bonferroni adjustment method (Hothorn et al., 2008). Models with and without interaction terms were compared using Akaike's information criterion (AIC) to determine model structure. Means are given \pm s.d. unless otherwise indicated.

RESULTS

Speed and surface

A total of 198 strides were recorded from six (five females, 1 male) subjects, sub-divided into 47 ground, 89 horizontal–narrow, 33 declined–narrow and 29 inclined–narrow substrates. A total of two slips were recorded whilst koalas were locomoting on narrow substrates. Substrate type had a significant effect on speed ($F_{3,182}=47.5$, $P<0.001$). The maximum speed for a koala running on the ground was 2.78 m s^{-1} (10.01 km h^{-1}), with a mean speed for all runs of $1.13 \pm 0.55 \text{ m s}^{-1}$. A Tukey *post hoc* test reported that speeds were significantly lower on horizontal, declined and inclined narrow surfaces when compared with strides on the ground, but no other comparison was significant (Fig. 1B). The maximum speed for movement on narrow surfaces was 0.78 m s^{-1} , with the mean speed being $0.41 \pm 0.14 \text{ m s}^{-1}$, less than half the mean speed on the ground. Body mass had no significant effect on speed ($F_{1,4}=0.14$, $P=0.72$).

Gait, surface and speed

Body mass also showed no effect on gait choices in koalas ($F_{7,185}=1.83$, $P=0.08$). Along the ground, gait significantly changed with speed ($F_{6,35}=3.97$, $P=0.004$), with slower strides tending to be trots or DC walks, medium strides tending to be gallops, and the fastest strides being bounds and half-bounds (Fig. 1C). A Tukey *post hoc* test revealed the only comparisons between gaits that were significant were half-bounds with DS walks, lateral walks, gallops

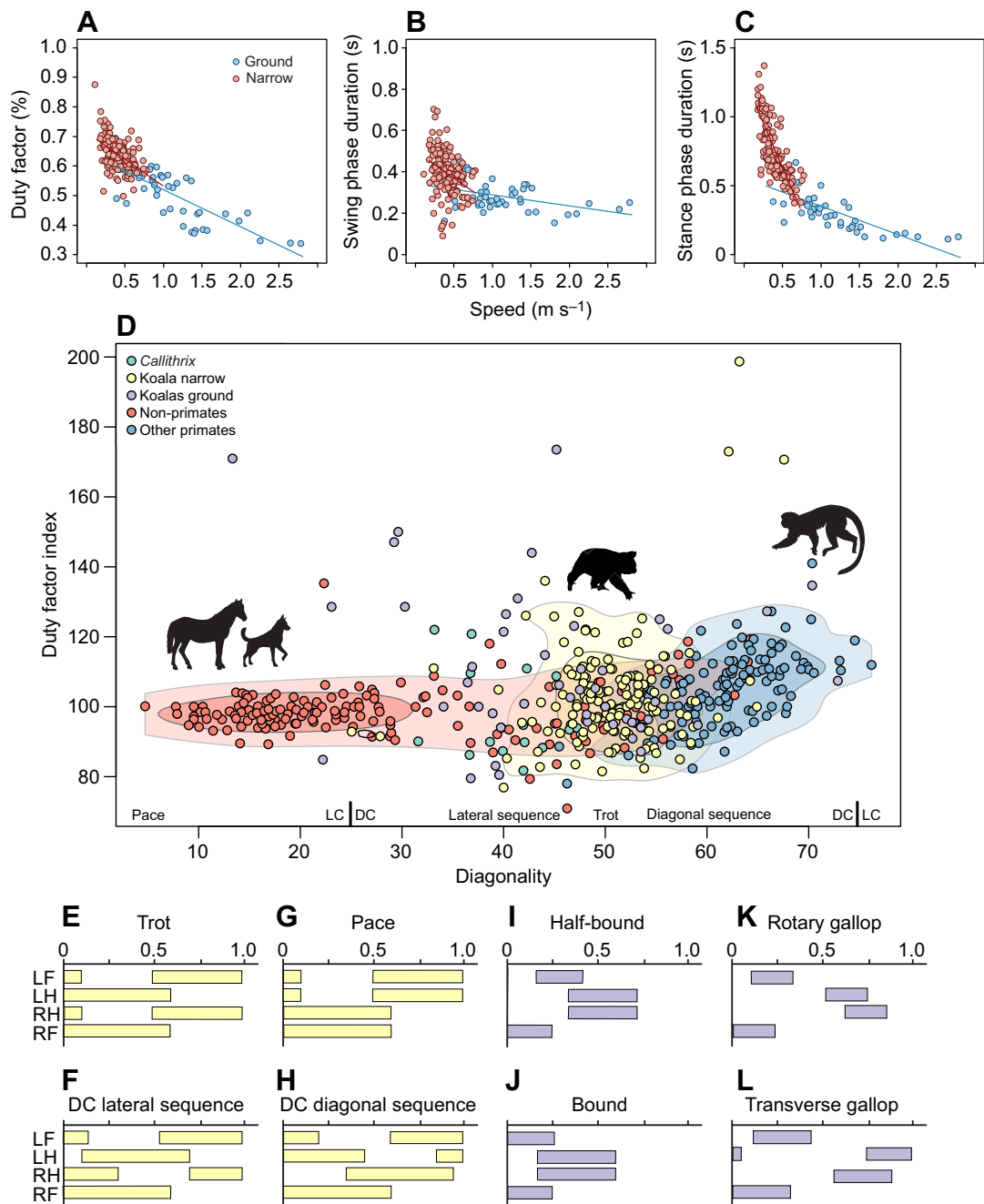


Fig. 2. The stride mechanics and associated gaits of terrestrial and arboreal locomotion in koalas compared with other species. (A–C) The effects of speed ($m s^{-1}$) on (A) duty factor (%), (B) swing phase duration (s) and (C) stance phase duration (s). (D) Comparison of koala gait patterns using data reported in Cartmill et al. (2002). Regression lines are shown for A–C. Contour plots in D represent 50% and 90% of maximal kernel density. Yellow represents koala strides on narrow surfaces, blue represents different primate species, and red represents non-primate species. (E–L) Locomotion diagrams of (E) trots, (F) lateral sequence–diagonally coupled (LSDC), (G) pace, (H) diagonal sequence–diagonally coupled (DSDC), (I) half-bound, (J) bound, (K) rotary gallop and (L) transverse gallop; yellow bars represent symmetrical gaits and purple bars represent asymmetrical gaits.

and trots, and bounds from DS walks and trots, suggesting the gait transition to bounding is the most strongly speed dependent.

On narrow surfaces, half-bounds and bounds, which were the fastest strides on the ground, were completely absent. Gait had little effect on speed over narrow surfaces, with *post hoc* tests supporting a significant difference only between trots and unknown (unclassified) gaits. Koalas primarily utilised a trot or DC walk across the narrow substrate types ($n=96$ of 151; Fig. 1D). Gallops were recorded on narrow substrates based on the coordination variables; however, no aerial phases were seen whilst traversing

narrow substrates. These gallops are not functionally equivalent to the gallops along the ground and are likely akin to asymmetrical walks. For example, when comparing individual feet, the right forefoot and left forefoot were coupled with their diagonal hindfoot 72.1% and 96.1% of the time, respectively. This inconsistency highlights the difficulty of using these defined gait patterns for species that must continually make slight changes during locomotion (Abourachid, 2003).

Although gait transition speeds have been widely used in the literature to understand movement (Hildebrand, 1976; White,

1990), the present study focused on how gait changes favour stability on narrow structures, and further, whether this change is reflected in other arboreal species. Given that the effects between the narrow surfaces were much smaller than effects between the ground and each narrow surface, and to simplify our analysis, we grouped all narrow surfaces together to focus on the effect of stability on gait variables. To do this, we examined the gait of koalas, measuring stride length and frequency, swing and stance phase durations, temporal variables ($T_{\text{lag,P}}$, $T_{\text{lag,F}}$, $T_{\text{lag,H}}$) and spatial variables ($D_{\text{fore-aft}}$, $D_{\text{med-lat}}$).

Stride length and stride frequency

Stride length represents the distance moved during a single stride cycle and is an important contributor of speed. There was a significant effect of both speed and surface on stride length (speed, $F_{1,190}=330$, $P<0.001$; surface, $F_{1,190}=14.4$, $P<0.001$; Fig. 3A). The interaction term was not significant, and the model was updated to remove it. The mean stride length used over ground was higher (0.61 ± 0.17 m) than stride length used on narrow supports (0.44 ± 0.10 m); however, the intercept for narrow supports was greater, indicating longer stride lengths at any given speed. The rate of change of stride length with respect to speed was similar across the two substrates (ground, 0.47, 95% CI 0.33–0.61; narrow, 0.49, 95% CI 0.42–0.55).

Along with stride length, stride frequency is used to moderate speeds; it indicates the number of strides taken over a period of time.

Speed and surface showed a significant effect on stride frequency (speed, $F_{1,190}=772$, $P<0.001$; surface, $F_{1,190}=11.28$, $P<0.001$). This suggests that there is a similar rate of change in frequency on both narrow and ground surfaces (ground, 0.53, 95% CI 0.39–0.67; narrow, 0.51, 95% CI 0.45–0.58). Locomoting on both substrates, koalas modulated frequency and stride length evenly to achieve a speed increase. The significant effect of surface suggests that higher frequencies were used on the ground when compared with narrow substrates (Fig. 3B). By examining the stance and swing phases, we can better understand how frequency is modulated.

Stance and swing phase duration

Stance phase duration is the time in seconds that the feet remain on the ground, which is an important factor in how much time is available to correct imbalances. Speed, surface and the interaction between them had a significant effect on stance phase (speed, $F_{1,189}=1116$, $P<0.001$; surface, $F_{1,189}=18.28$, $P<0.001$; speed \times surface, $F_{1,189}=6.45$, $P=0.012$). This suggests that stance phase is affected by the speed of locomotion across both substrates, but they share different rates of change. When on the ground, the mean stance duration was 0.32 ± 0.15 s and decreased with a steep slope, while on the narrow surfaces the mean stance duration was 0.74 ± 0.26 s and decreased with a shallower slope (ground, -0.86 , 95% CI -1.03 to -0.70 ; narrow, -0.66 , 95% CI -0.74 to -0.58 ; Fig. 3C). This may indicate the priority of koalas locomoting on narrow supports to extend feet contact time with the substrate.

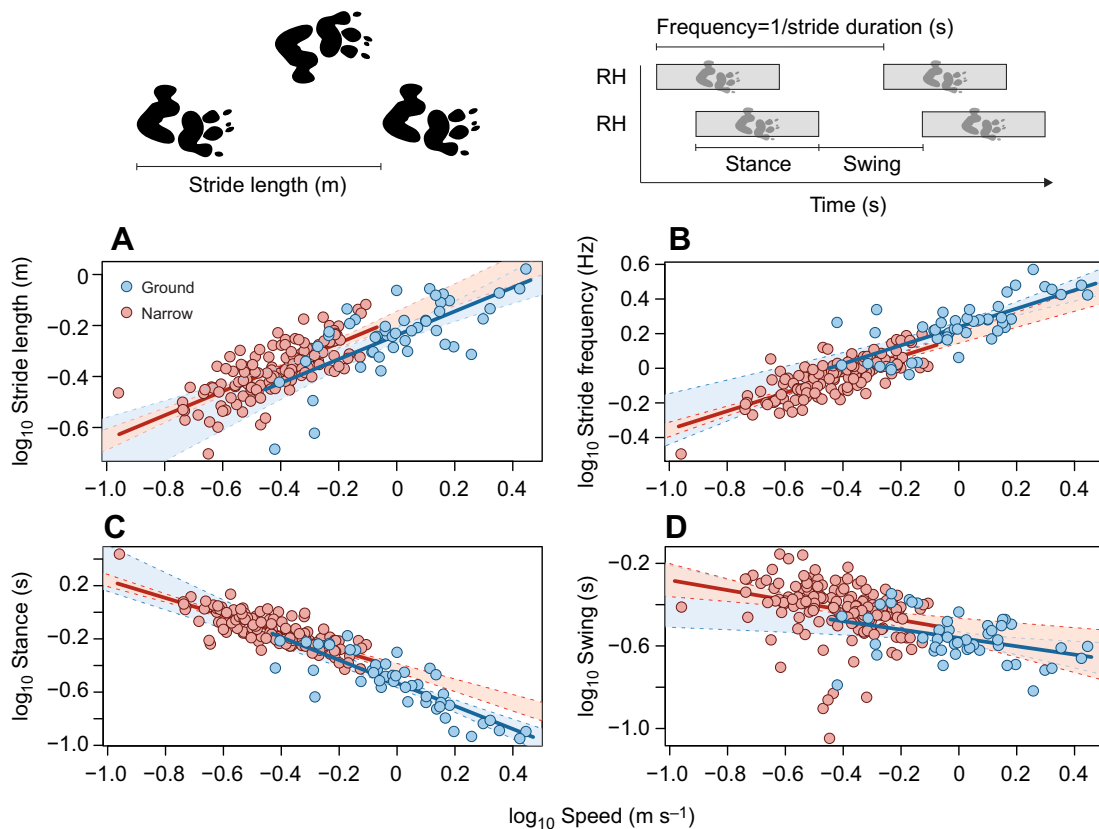


Fig. 3. Log:log plots showing the effects of speed (m s^{-1}) on the stride mechanics of six koalas during locomotion over ground (blue; $n=47$) and narrow surfaces (red; $n=151$). A mixed-effects linear model showed (A) stride length (m) and (B) stride frequency (Hz) had significantly different intercepts over the ground and narrow surfaces (stride length, $F_{1,189}=14.3$, $P<0.001$; stride frequency, $F_{1,190}=764$, $P<0.001$). (C) Stance phase (s) was significantly affected by speed ($F_{1,189}=1116$, $P<0.001$), and showed significantly different intercepts between surfaces ($F_{1,189}=18.28$, $P<0.001$). (D) Swing phase (s) was only significantly affected by speed ($F_{1,189}=60$, $P<0.001$). Regression lines and 95% confidence intervals for each variable are shown. The panels at the top of the figure show the measurements that were used in the figures. All measurements are shown on the right hind (RH) foot.

Swing phase duration represents the time that the limb is moving from lift-off to the next footfall; this, combined with stance phase, shares an inverse relationship with stride frequency (Gálvez-López et al., 2011). Swing phase was significantly affected by speed and surface (speed, $F_{1,189}=60$, $P<0.001$; surface, $F_{1,189}=4.09$, $P=0.045$), but the interaction showed no significant effect (speed×surface, $F_{1,189}=0.52$, $P=0.474$), suggesting a similar rate of change across ground and narrow substrates (ground, -0.20 , 95% CI -0.34 to -0.06 ; narrow, -0.18 , 95% CI -0.3 to -0.05 ; Fig. 3D). The slope suggests swing phase contributed much less to the change in stride frequency than stance phase. This was also reflected in duty factor (stance phase as a proportion of the stride), which was higher on narrow supports with a much shallower slope (surface, $F_{1,188}=17.6$, $P<0.001$; speed×surface, $F_{1,188}=11.8$, $P<0.001$; Fig. 2A–C).

Temporal coordination

Temporal spacing of the footfalls within a stride explains how the limbs function together to maintain stability ($T_{lag,F}$, $T_{lag,H}$, $T_{lag,P}$). Speed had a significant effect on all temporal variables, $T_{lag,F}$, $T_{lag,H}$ and $T_{lag,P}$ (speed: $T_{lag,F}$, $F_{1,186}=187$, $P<0.001$; $T_{lag,H}$, $F_{1,189}=91$, $P<0.001$; $T_{lag,P}$, $F_{1,187}=9.51$, $P=0.002$). Only $T_{lag,P}$ was significantly affected by a change in surface, with koalas taking longer to place their feet on narrow surfaces (surface, $F_{1,187}=12.4$, $P<0.001$; Fig. 4A). $T_{lag,F}$ and $T_{lag,H}$ were also significantly affected by the interaction between speed and surface (speed×surface: $T_{lag,F}$, $F_{1,186}=14.5$, $P<0.001$; $T_{lag,H}$, $F_{1,189}=9.39$, $P<0.001$), showing a negative rate change when on the ground (Fig. 4B,C).

During ground locomotion, koalas changed their gait patterns when speed was increased (Fig. 1C,D). $T_{lag,H}$, $T_{lag,F}$ and $T_{lag,P}$ had a temporal lag of 0.46 ± 0.08 , 0.45 ± 0.04 and 0.51 ± 0.06 , respectively (Fig. 4). These stride proportions signify diagonally coupled walks (Table S1). When moving along the ground, the stride proportions of both $T_{lag,H}$ and $T_{lag,F}$ had negative slopes, with reduced means and increased variability (0.33 ± 0.22 and 0.34 ± 0.17 , respectively; Fig. 4B,C). Further, the proportional lag between the limb pairs was lower on the ground (0.44 ± 0.12), but showed no significant difference in slope from narrow substrates.

Spatial coordination

$D_{fore-aft}$ and $D_{med-lat}$ variables are the distances between the placement of the feet in the plane that is parallel to the ground. The $D_{fore-aft}$ variables represent the fore–aft direction of movement whilst the $D_{med-lat}$ variables are mediolateral distances. Where the lag variables show the timing within a stride, $D_{fore-aft}$ and $D_{med-lat}$ variables show the spatial placement of hind, fore and limb pairs relative to one another within a stride. This may highlight the potential constraints between substrate and gait choice. $D_{fore-aft,H}$ and $D_{fore-aft,F}$ were significantly affected by speed ($D_{fore-aft,H}$, $F_{1,177}=26.4$, $P<0.001$; $D_{fore-aft,F}$, $F_{1,177}=16.1$, $P<0.001$), and $D_{fore-aft,P}$ was significantly affected by the substrate ($D_{fore-aft,P}$, $F_{1,177}=36.1$, $P<0.001$). All three showed a significant effect from the interaction of speed and surface ($D_{fore-aft,P}$, $F_{1,177}=22.8$, $P<0.001$; $D_{fore-aft,H}$, $F_{1,177}=51.7$, $P<0.001$; $D_{fore-aft,F}$, $F_{1,177}=17.8$, $P<0.001$). $D_{fore-aft,H}$ and $D_{fore-aft,F}$ both shared similar slopes over narrow supports ($D_{fore-aft,F}$, 0.23, 95% CI 0.18–0.28; $D_{fore-aft,H}$, 0.19, 95% CI 0.14–0.24). As speed increases, koalas change the distance within their limb pairs such that over narrow substrates this distance increases, and on the ground, it decreases or remains steady (Fig. 5A,C,E). This agrees with the bounding gait patterns defined by the temporal variables whilst on the ground and supports the increased stride length and uniform patterns while on narrow supports.

All $D_{med-lat}$ variables were affected by speed ($D_{med-lat,P}$, $F_{1,177}=92.1$, $P<0.001$, $D_{med-lat,H}$, $F_{1,178}=123$, $P<0.001$, $D_{med-lat,F}$, $F_{1,177}=14.2$, $P<0.001$). Surface was also significant across the mediolateral distances ($D_{med-lat,P}$, $F_{1,177}=58.7$, $P<0.001$, $D_{med-lat,H}$, $F_{1,178}=15.4$, $P<0.001$, $D_{med-lat,F}$, $F_{1,177}=8.04$, $P=0.003$). The interaction between speed and surface was not significant across all variables and produced a better model when removed from $D_{med-lat,H}$ ($D_{med-lat,P}$, $F_{1,177}=2.89$, $P=0.091$; $D_{med-lat,H}$, $F_{1,177}=0.66$, $P=0.42$; $D_{med-lat,F}$, $F_{1,177}=2.68$, $P=0.103$). As expected, the mediolateral distances were reduced on narrowing substrates, as there is limited width (Fig. 5B,D,F). The effect of speed on the $D_{med-lat}$ suggests koalas showed a slight trend in widening their hind feet on both substrate types as they increased speed, yet this was more prominent on the ground (Fig. 5B,D,F).

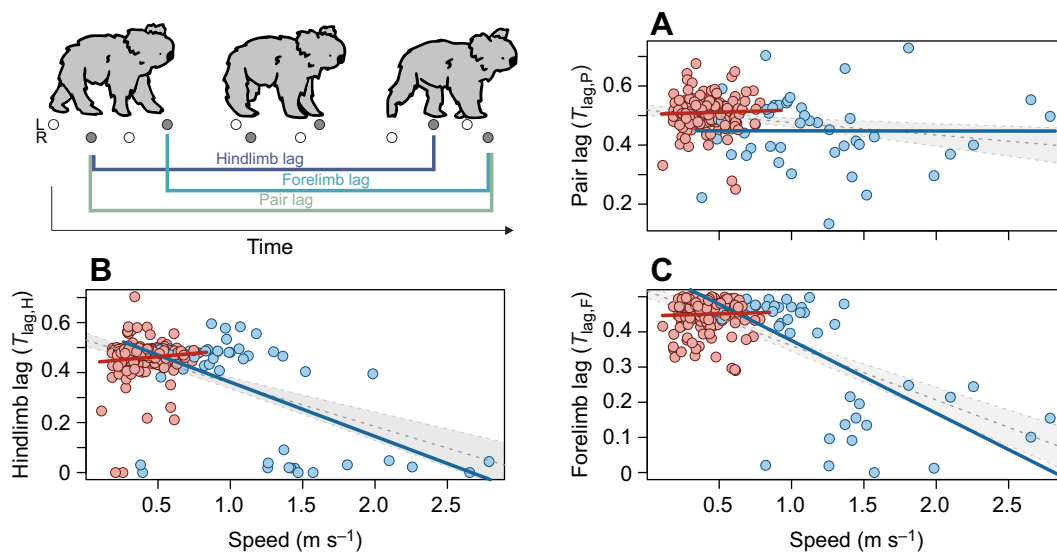


Fig. 4. The effects of speed (m s^{-1}) on the temporal lag of the footfalls of six koalas during locomotion over ground (blue; $n=47$) and narrow surfaces (red; $n=151$). Temporal variables represent the proportional lag between the ipsilateral (A; $T_{lag,P}$), hind (B; $T_{lag,H}$) and fore (C; $T_{lag,F}$) pairs of feet. A lag of 0.5 in both hind and fore feet show a symmetrical gait pattern. A pair lag of 0.5 shows a trot-like gait when hind and fore pairs are also 0.5. A negative hind lag shows a rotary gallop. A hind lag of close to 0, and a fore lag between 0 and 0.5 show bounds and half-bound gait patterns. Regression lines are shown for all data. The grey shaded area represents the regression line and confidence intervals of the combined data.

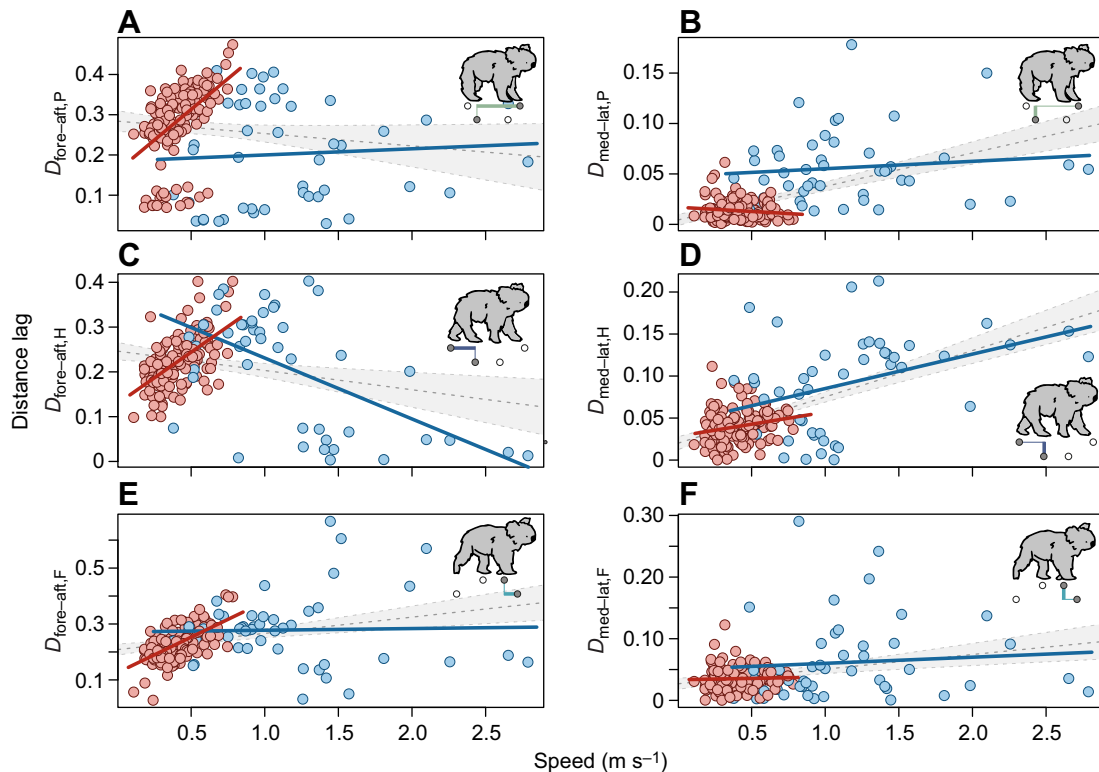


Fig. 5. The effects of speed (m s^{-1}) on fore–aft and mediolateral distances (m) of six koalas whilst locomoting over narrow surfaces (red; $n=151$) and the ground (blue; $n=47$). Fore–aft distances between pairs, hind and fore limbs are represented by (A,C,E), respectively, and (B,D,F) are the mediolateral distance between the pairs, hind and fore limbs, respectively. There was a significant difference in the slopes of all fore–aft pair variables ($D_{\text{fore-aft,P}}$, $F_{1,177}=22.8$, $P<0.001$; $D_{\text{fore-aft,H}}$, $F_{1,177}=51.7$, $P<0.001$; $D_{\text{fore-aft,F}}$, $F_{1,177}=17.8$, $P<0.001$). The mediolateral distances were all affected significantly by both speed and surface (speed, $D_{\text{med-lat,P}}$, $F_{1,177}=92.1$, $P<0.001$; $D_{\text{med-lat,H}}$, $F_{1,178}=123$, $P<0.001$; $D_{\text{med-lat,F}}$, $F_{1,177}=14.2$, $P<0.001$; surface, $D_{\text{med-lat,P}}$, $F_{1,177}=58.7$, $P<0.001$; $D_{\text{med-lat,H}}$, $F_{1,178}=15.4$, $P<0.001$; $D_{\text{med-lat,F}}$, $F_{1,177}=8.04$, $P=0.003$). Regression lines for each are shown by the grey dotted line and the shaded area represents the regression line for the combined surfaces and 95% confidence intervals.

DISCUSSION

Understanding the locomotory ability of a species is important to estimate their inherent fitness within a particular habitat type. Koalas move extensively within an arboreal environment and their morphology shares similarities with other canopy-dwelling specialists such as primates; thus, we hypothesised that their locomotory strategies would be convergent with these species (Sustaita et al., 2013; Grand and Barboza, 2001). Yet, koalas must also traverse the ground, albeit less frequently – for example, to move between eucalypt patches, to obtain access to water and to find mates – thus overground locomotion may also contribute to the inclusive fitness of this species (Ellis et al., 2002; Reilly et al., 2007). We compared koala locomotion in both arboreal and terrestrial environments, to understand how locomotory strategies change between habitat types, and further determine whether this difference resembles that observed in other arboreal specialists.

The top ground speed of koalas in this study was 2.78 m s^{-1} (10.01 km h^{-1}). The fastest strides were primarily bounds or half-bounds. Koalas were relatively slow given their body mass, similar to the top speeds reported for opossums, *Didelphis marsupialis* (Garland, 1983) (Fig. 6B). These bounds or half-bounds were mostly deliberate actions to return to their arboreal refuges, resembling the intermittent locomotion of smaller mammals during predator avoidance (Kramer and McLaughlin, 2001; Clemente et al., 2019; Jenkins, 1974). The objective of this study was not to assess maximum speeds and it is likely the speeds recorded here are slower than what is capable by koalas. Although

bounding gaits are very common in small arboreal specialists, they are not the preferred gait patterns in larger primates (Arms et al., 2002; Delciellos and Vieira, 2009; Hildebrand, 1967; Lammers, 2007; Nyakatura et al., 2008; White, 1990). At slower paces, these primates choose DC gaits similar to that seen in koalas (trots and diagonal walks; Fig. 1C). Thus, the natural progression of gait for larger primates, as speed increases, is walking gaits < canters/ambles < gallops, whereas in most marsupials it is DC gaits (i.e. trots, walks) < gallops < half bounds < bounds (Arms et al., 2002; Hildebrand, 1967; Nyakatura et al., 2008; White, 1990). Gallops in many primates are used at top speeds; however, in koalas, like other marsupials, it appears to be a transitional gait between walks and bounds (White, 1990).

Over narrow supports, koalas were much slower, resulting in a different repertoire of gaits (DC walks). Although koalas mainly used trots (58.3%), their gait sequence was adjusted to both lateral (6.0%) and diagonal (5.3%; Fig. 2D). As hypothesised in primates, the reliance on diagonally coupled feet during arboreal locomotion may reduce the toppling moment that is created by the koala's elongated limbs and erect posture (Cartmill et al., 2007; Reilly et al., 2007). It has further been reported that koala forelimb and hindlimb excursions are similar to those of primates (i.e. their extended forelimb reaching would be supported by a protracted hindlimb; Larson et al., 2001). Despite similar kinematics, koalas did not show an exclusive preference for diagonal sequence gaits as seen in primates. Instead, they used lateral sequences with similar frequency, comparable to the short-tailed opossum (*Monodelphis domestica*) on flat surfaces

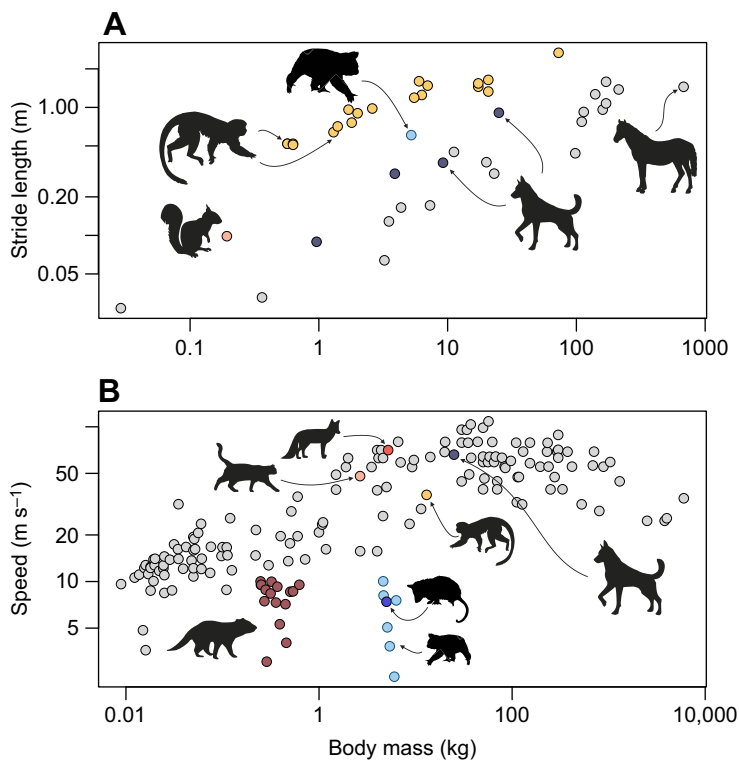


Fig. 6. The effect of body mass (kg) on stride length (m) and speed (m s^{-1}) for the ground locomotion of six koalas compared with various mammals. Log:log relationship of (A) stride length (m), compiled from Reynolds (1987) (primates: yellow), Strang and Steudel (1990) and Heglund and Taylor (1988), and (B) speed (m s^{-1}) from Garland, 1983, Clemente et al. (2016) (echidna) and Clemente et al. (2019) (northern quolls: maroon dots), over body mass (kg). Koalas are represented by light blue dots. Other species of significance are represented by different colours and silhouettes.

(Lemelin et al., 2003). The indifference in sequence shown by koalas may be a result of the relative width of the narrow substrates used. Kinkajous (*Potos flavus*), a non-primate arboreal specialist, were shown to use more diagonal sequence gaits as substrate width decreased (Lemelin and Cartmill, 2010). Among koalas, footfall width between the forelimbs and hindlimbs were smaller on the narrower substrates compared with the ground (Fig. 5E,F), suggesting some effect of spatial footfall placement to substrate width. Yet the extent to which DSDC becomes more prominent in koalas on finer (narrower) branch locomotion remains to be explored.

Koalas modulated stride length and frequency equally to increase speed on both ground and narrow substrates (Fig. 3A,B). This equal modulation was not reflected in the semi-arboreal marsupial *M. domestica*, which predominantly modulated stride frequency (Lammers and Biknevicius, 2004), nor in primates, which showed increased modulation of stride length with speed (Alexander and Maloiy, 1984). Terrestrial species also vary in patterns of stride length and frequency modulation, with cats showing greater increases in stride frequency with speed, but dogs primarily increasing stride length (Gálvez-López et al., 2011). Yet, although slopes were similar among koalas, the intercepts of stride frequency and length were different between surfaces.

Koalas took longer but slower steps on narrow supports at any given speed, resembling other arboreal specialists (e.g. Simiiformes, Alexander and Maloiy, 1984; *Caluromys philander*, Delciellos and Vieira, 2009) (Fig. 3A,B). This reliance on increased stride length is hypothesised to reduce peak forces on narrow substrates, which can lead to destabilising or toppling moments (Larson et al., 2000; Daley and Usherwood, 2010). Alternatively, longer strides may reduce the angular momentum and limb interference on arboreal substrates, particularly when DC gaits are used (Chadwell and Young, 2015; Larson et al., 2001). Conversely, the koala's use of higher stride frequencies along the ground may reflect a relaxation of this constraint, as there is a reduced requirement to reduce

peak forces on solid substrates (Chadwell and Young, 2015; Demes et al., 1990).

Both swing and stance phase influenced stride frequency in koalas, but the slope of stance phase decreased to a greater extent across both substrates (Fig. 3C,D). Despite this decrease, stance phase was much longer than swing phase. The longer stance phase gives koalas adequate time to apply corrective torques using their grasping appendages (Cartmill, 1974). Among primates, stance phase modulation is the prominent factor for variation in stride frequency, with some species showing near-invariant swing phase time with speed (*Saguinus oedipus*, *Saimiri boliviensis*, Arms et al., 2002; *Pan troglodytes*, *Macaca mulatta*, *Sapajus apella*, *Lemur catta*, Kimura, 1992; *Cercopithecus aethiops*, Vilensky and Gankiewicz, 1986). Like primates, speed in koalas is less reliant on swing phase compared with stance phase (Fig. 3D). This suggests a minimum limit of required time to place their footfalls with precision. The need for meticulous foot placement on narrow surfaces is evident by the placement of footfalls within a stride, similarly, observed in common marmosets and opossums (Chadwell and Young, 2015; Lammers and Biknevicius, 2004) (Fig. 5). This increased reliance of precision in foot placement is likely related to the evolution of grasping appendages in koalas and may be a significant adaptation for their survival in arboreal habitats.

Koalas possess contrasting strategies for locomotion: whilst their ground locomotion seems to combine both marsupial and primate-like strategies, their methods along narrow substrates converge on primate strategies. When moving in terrestrial environments, bounding gaits are used for quick retreats to safety, though their slower ground speeds may leave them vulnerable (Fig. 6B). Their terrestrial walking gaits and elongated limbs could provide koalas with a mechanism to optimise efficiency (Biewener, 1990; Reilly et al., 2007). However, it remains to be determined how habitat loss and increasing distance between foraging patches reduces their inclusive fitness given their low-energy diet.

The locomotion of the koala seems highly adapted for life in trees, which is not surprising given that they spend a significant amount of time locomoting in eucalypt canopies (Ryan et al., 2013). Their locomotory strategy likely results from their elongated limbs and strong grasping appendages shared with primates. Combined, these results provide strong evidence for morphological, behavioural and mechanical convergence on similar strategies from both marsupials and primates. While this research supports convergent strategies, there are many other arboreal or semi-arboreal marsupials yet to be considered in such depth. Using similar methods to study the gait of such species provides greater insight into the evolution of climbing in mammals.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: C.H.F., C.J.C.; Methodology: J.L.G., C.J.C.; Software: J.L.G., C.J.C.; Validation: C.J.C.; Formal analysis: J.L.G., C.J.C.; Investigation: J.L.G., C.J.C.; Resources: C.J.C.; Data curation: J.L.G., C.J.C.; Writing - original draft: J.L.G.; Writing - review & editing: C.H.F., C.J.C.; Visualization: C.H.F., C.J.C.; Supervision: C.H.F., C.J.C.; Project administration: C.H.F., C.J.C.; Funding acquisition: C.J.C.

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Data availability

Data are available from Figshare: <https://doi.org/10.6084/m9.figshare.8157980.v1>.

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.207506.supplemental>

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