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RESEARCH ARTICLE

Moving in complex environments: a biomechanical analysis of locomotion on inclined and narrow substrates

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ABSTRACT

Characterisation of an organism's performance in different habitats provides insight into the conditions that allow it to survive and reproduce. In recent years, the northern quoll (*Dasyurus hallucatus*) – a medium-sized semi-arboreal marsupial native to northern Australia – has undergone significant population declines within open forest, woodland and riparian habitats, but less so in rocky areas. To help understand this decline, we quantified the biomechanical performance of wild northern quolls as they ran up inclined narrow (13 mm pole) and inclined wide (90 mm platform) substrates. We predicted that quolls may possess biomechanical adaptations to increase stability on narrow surfaces, which are more common in rocky habitats. Our results showed that quolls have some biomechanical characteristics consistent with a stability advantage on narrow surfaces. This includes the coupled use of limb pairs, as indicated via a decrease in footfall time, and an ability to produce corrective torques to counteract the toppling moments commonly encountered during gait on narrow surfaces. However, speed was constrained on narrow surfaces, and quolls did not adopt diagonal sequence gaits, unlike true arboreal specialists such as primates. In comparison with key predators, such as cats and dogs, northern quolls appear inferior in terrestrial environments but have a stability advantage at higher speeds on narrow supports. This may partially explain the heterogeneous declines in northern quoll populations among various habitats on mainland Australia.

KEY WORDS: Performance, Northern quoll, Torque, Substrate reaction force, Kinematics, Kinetics

INTRODUCTION

An ecological niche is the set of environmental conditions that enable a species to grow and reproduce (Schoener, 2009). The fitness of an organism is largely defined by its performance in any environment, which in turn depends upon morphology and physiology (Arnold, 1983; Garland and Losos, 1994). Thus, characterisation of a species' performance across different habitats provides insight into the conditions that allow for an animal to survive and reproduce. All behaviours require movement and the niche that an animal occupies is largely dependent on movement capabilities; for example, if an animal cannot climb trees it cannot fill a niche that is wholly or partially arboreal. Furthermore, an animal's performance will change with respect to environmental conditions that hinder movement. Understanding the locomotor capabilities of a species is key for understanding its niche, which may allow us to quantify the habitat requirements for conservation. One species of conservation significance in Australia is the northern quoll *Dasyurus hallucatus* Gould 1842.

Northern quolls are primarily nocturnal, partially arboreal marsupial carnivores, found in grassy or rocky habitats across northern Australia (Schmitt et al., 1989; Oakwood, 2000). The northern quoll has declined from a broad distribution across northern Australia to several disjunct populations often centred on rocky plateaus with local extinctions primarily occurring in lowland savanna (Braithwaite and Griffiths, 1994; Morris, 1996; Braithwaite and Muller, 1997). Dingoes and feral cats are the main predators of Northern quolls, and both have been historically present across their range for 4000 and over 100 years, respectively (Burbidge et al., 1988; Corbett, 1995). The reason for the recent rapid decline in population is therefore complex; however, it has been hypothesised that habitat loss or fragmentation (due to land clearing, altered fire regimes or grazing by invasive herbivores) can leave smaller mammalian species more vulnerable to predation (Newsome, 1975; Burbidge and McKenzie, 1989; McKenzie et al., 2007). In a study on quoll survival, Oakwood (2000) reported that all northern quolls killed by predators were killed within forest, woodland and riparian habitats, and that no kills occurred in rocky outcrops. Also, females whose home ranges included a larger proportion of rocky habitat, were more likely to survive to a second breeding season. This suggests that the differential survival of quolls may be linked to habitat complexity.

The differential survival of a species across various habitats may be due to changes in their detection by predators or ease of capture after detection. As different environments are likely to impose different limitations on locomotor performance, our study examined how one aspect of variation in habitat – substrate width – influences the kinematics and kinetics of northern quolls. This can contribute to the basis for a mechanistic understanding of predation and its conservation significance among different habitats.

We characterised the biomechanics of northern quolls while they climbed up two different substrates: an inclined wide platform, wider than the hindfoot length, and an inclined narrow pole, narrower than the foot length. We further compare the quolls' biomechanics on these substrates with biomechanical strategies used by arboreal specialists (such as primates, arboreal rats and kinkajous) and terrestrial specialists (such as rats, cats and dogs) to understand the relative performance of quolls to these groups of animals. We hypothesised that on narrow substrates quolls would modify biomechanical characteristics to be more reflective of arboreal species, which would therefore help to explain their increased survival in complex habitats.

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MATERIALS AND METHODS

Morphology

Northern quolls were trapped on Groote Eylandt, Northern Territory, Australia, between July and August 2013 using Tomahawk original series cage traps (20×20×60 cm; Tomahawk ID-103, Hazelhurst, WI, USA) baited with canned dog food. Traps were set overnight and checked early in the morning (no later than 07:30 h) to avoid quolls being subjected to warmer parts of the day. A total of 14 individual quolls (9 females, 5 males) were captured throughout the study period. Each quoll was taken to the Anindilyakwa Land and Sea Ranger Research Station for subsequent experiments. All individuals received a microchip (Trovan nano-transponder ID-100, Keysborough, Australia) that was placed subcutaneously between the shoulder blades to ensure identification during any subsequent recaptures. Research methodologies were approved by the University of Queensland animal ethics committee (SBS/541/12/ANINDILYAKWA/ MYBRAINSC) and were conducted under the Northern Territory Parks and Wildlife Commission (permit number: 47603).

Body mass was measured for each individual using an electronic balance (±0.1 g; A&D Company Limited HL200i, Brisbane, Australia) and 11 morphological variables were each measured three times using digital callipers (Whitworth, Brisbane, Australia, ±0.01 mm), with an average used as the overall measure (Wynn et al., 2015). These body dimensions were included as covariates in our initial analysis, but none appeared to have a significant effect on our results and thus were not included in further analysis (Table 1). To minimise long-term stress on the animals, all performance measures and tests were completed within 6 h of capture, after which the animals were released at the exact point of capture.

Kinematics and kinetics

To assess the biomechanics of northern quolls, we filmed each individual as it moved up two different raised trackways. Trackways were suspended within a Perspex box (2600×470×160 mm) with a release and escape box at the start and end, respectively (Fig. 1). Quolls were run along the two trackways (inclined platform, inclined pole) in a random order. The inclined platform was a 90-mm-wide plank of wood, covered in fine sandpaper (P120) to provide traction at a 38 deg angle, and represented a wide surface larger than the length of the hindfoot (see Movie 1). The inclined pole was a 12-mm-diameter wooden dowel running the length of the box at a 38 deg angle, and represented a narrow surface, smaller than the length of the hindfoot (see Movie 2). Both tracks ran the length of the box with a force transducer (Nano-17 titanium, ATI instruments) placed level and centrally with the trackway, with either a 90×90 mm platform or a 90-mm-long doweling attached to it.

Table 1. Mean morphological measurements for mass and body dimensions of northern quolls included in the study

Measurement	Description	Mean	s.e.m.
Body mass (g)		384.3	21.5
Head width (mm)	Widest point of jaw	36.07	0.47
Head length (mm)	Nuchal crest to snout tip	67.22	0.73
Body length (mm)	Nuchal crest to base of tail	179.92	3.32
Right+left fore-limb length (mm)	Radius to ulna	50.91	0.75
Right+left hind-limb length (mm)	Tibia to fibula	63.75	0.79
Right+left hind-foot length (mm)	Heel to claw base	38.49	0.48
Tail width (mm)	Max. tail diameter	14.54	0.43
Tail length (mm)	Base to tip of tail	228.48	4.49

See Wynn et al. (2015) for a diagrammatic description of body dimensions.

Two cameras (Fastec IL-3, Fastec Imaging, 1280×700 pixels, 250 fps) were positioned approximately perpendicular to each other, to capture a ventral–lateral, and lateral–dorsal view. These camera positions were used to ensure footfalls were visible in both camera views, yet allowed enough variation in viewing angle that 3D position information was still accurate. Cameras were synchronised using internal triggers. The cameras were calibrated using a wand-based camera calibration method, implemented in the Argus software in Python v2.1 (Jackson et al., 2016). The MATLAB GUI DLTdv5 (Hedrick, 2008) was then used to track individual feet and a single spot on the back, close to the body centre of mass.

Analysis

We excluded very slow strides where speed was less than 0.75 m s^{-1} and excluded runs that included slips or falls. This resulted in 283 runs from 14 individuals, including 61 runs from 5 individuals on the inclined platform, and 222 runs from 12 individuals on the inclined pole. The median number of runs per individuals was 15, with a maximum of 34 and a minimum of 6.

Timing parameters and gait

Feet were digitised for the duration of contact with the surface of the calibrated racetrack. A mark near the body centre of mass was used to calculate speed. Footfall sequence and gait parameters were calculated using antero–posterior sequence methods (Abourachid, 2003; Chadwell and Young, 2015). The first forefoot touchdown defined the start of a sequence and its subsequent touchdown defined the end of the sequence. $T_{lag, F}$, $T_{lag, H}$ and $T_{lag, P}$ were calculated as the temporal lag between the mid-stances of the two forefeet, hindfeet and averaged across the ipsilateral feet, respectively. $T_{lag, P}$ is also therefore a measure of diagonality, but the naming convention here follows Abourachid (2003). Speed was calculated for the duration of the sequence, and duty factor was calculated as the average duty factor of feet within a sequence. We examined the effects of, and interaction between, speed and surface for the time lag between footfalls of the forefeet ($T_{lag, F}$), hindfeet ($T_{lag, H}$) and the ipsilateral feet ($T_{lag, P}$) to determine which pairs of limbs may be contributing most to increasing stability on narrow substrates.

Spatial parameters

We further examined the effects of the absolute distance between the left and right forefoot (D_F), the left and right hindfoot (D_H) and the mean distance between the forefoot pair and the hindfoot pair (D_P). Since the lateral distance effects are likely to be constrained on narrow supports we further examined the distance in the fore–aft axis for each variable (fore–aft D_F, D_H and D_P, respectively), making comparisons between wide and narrow platforms more analogous.

Substrate reaction forces

Substrate reaction forces (SRFs) were recorded for each foot individually or for multiple feet simultaneously using an ATI Nano17 6 DOF micro force transducer (ATI instruments). The force transducer was calibrated by the company with estimated error of <0.75% in the x, y and z axes. The force transducer was aligned with the x-axis representing the fore–aft direction, y representing the lateral direction and z representing the vertical direction. The transducer output forces in these three axes along with torques about each axis. Torques about the axes are likely dependent on the position of the footfall relative to the centre of the force transducer and therefore are of limited use, with the exception of the torque about the x-axis on the narrow trackway. In this setup, the narrow pole was less than the length of the foot. Thus, we assume the position of the footfall must
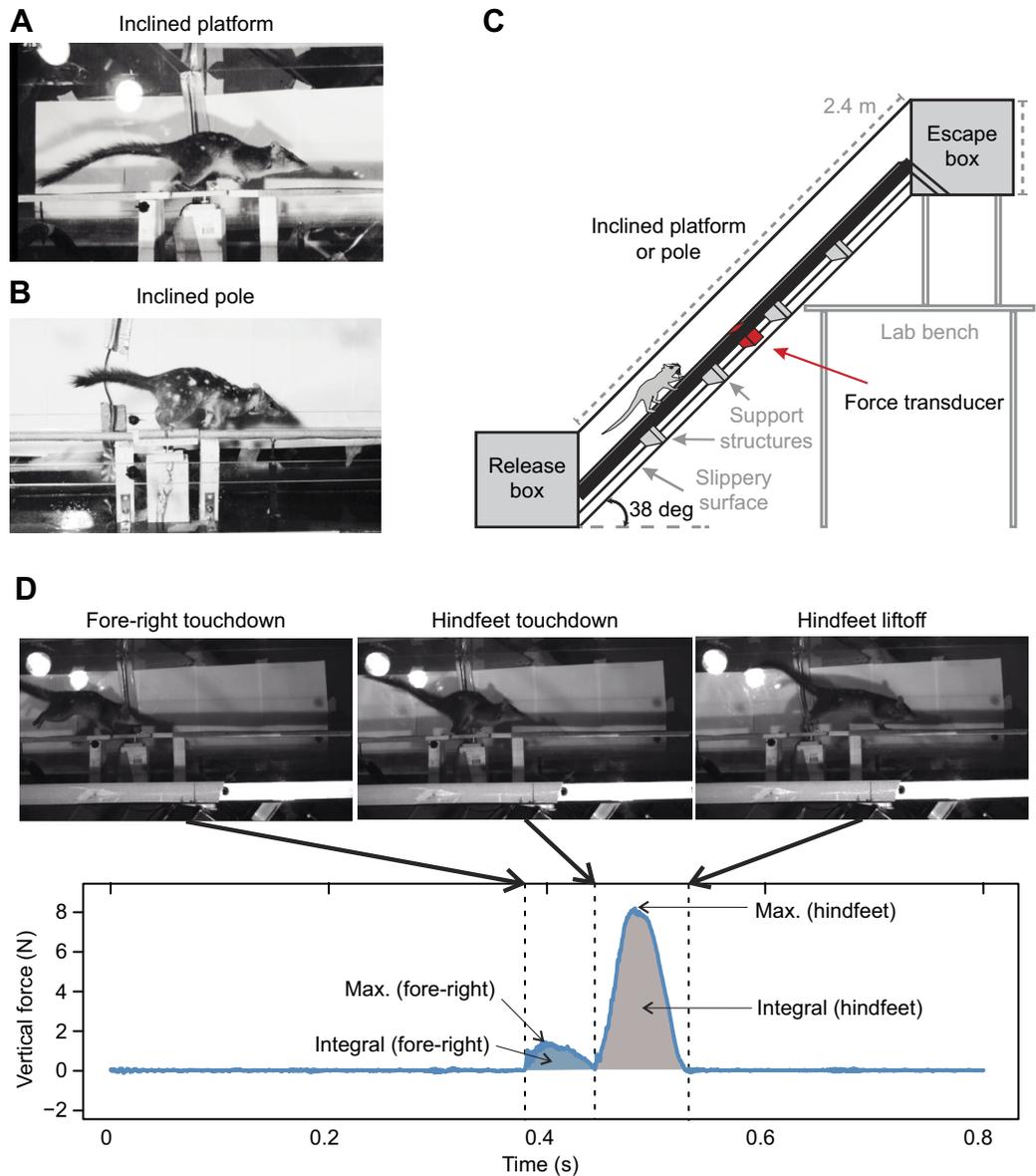
Fig. 1. Experimental setup to analyse biomechanics of locomotion on inclined substrates. (A) Northern quoll (*Dasyurus hallucatus*) running on inclined platform. (B) Quoll running on inclined narrow pole. (C) Schematic of custom-made experimental setup showing location of force transducer. (D) Vertical substrate reaction force trace over time for a single forelimb followed by both hindlimbs with representative images shown above. Shaded regions represent integral with respect to time (impulse) for the fore-right (blue) and hind-left and hind-right combined (grey).

more or less align with the x-axis of the force transducer. We corrected the torque for the diameter of the pole, by subtracting the lateral force multiplied by the outlever of the sensor (in this case the 13 mm pole and the 10.4 mm mounting platform).

Strides where any foot partially stepped on the plate were excluded from further analysis. Forces were synchronised with the video footage to identify each foot as it struck the substrate. For each foot strike, we measured the maximum (maximum positive) and minimum (maximum negative) force, as well as the integral of the force-time profile using the trapezoidal numeration integration function (trapz.m) in MATLAB, for the fore–aft, medial–lateral and dorsal–ventral directed forces. We corrected for the inclined slope in the fore–aft forces, by multiplying fore–aft force by the cosine of the slope (38 deg) and subtracting the sine of the vertical force (Eqn 1). Similarly, we corrected vertical forces by multiplying vertical force by the cosine of the angle and adding the sine of the fore-aft forces

(Eqn 2). This rotated forces such that they were comparable to flat-trackway forces.

$$\text{Corrected } \mathbf{F}_x = \mathbf{F}_x \times \cos(\text{slope}) - \mathbf{F}_z \times \sin(\text{slope}), \quad (1)$$

$$\text{Corrected } \mathbf{F}_z = \mathbf{F}_z \times \cos(\text{slope}) + \mathbf{F}_x \times \sin(\text{slope}). \quad (2)$$

Statistics

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 v3.2.3 (https://CRAN.R-project.org/package=nlme). To examine variation between factors we specified the model with lme.R function, and then used glht.R function from the multcomp package (Hothorn et al., 2008) to perform Tukey *post hoc* tests, correcting the P-values using the Bonferroni adjustment method.

RESULTS

Speed

Quolls with different body lengths did not use significantly different speeds when traversing either of the surfaces ($F_{1,10}$=0.24, P=0.635). However, quolls ran significantly faster on the wide platform than on the narrow pole ($F_{1,181}$=22.8, P<0.001) (Fig. 2).

Speed also varied significantly with gait. For the inclined surfaces, speeds varied between gaits on the narrow pole ($F_{4,206}$=3.68, P=0.006), but not on the platform ($F_{4,52}$=1.87, P=0.130). On the narrow pole, transverse gallops were slower than bounds (z=3.49, P=0.004) and half bounds (z=3.44, P=0.005), but speeds during other gaits were not significantly different.

Stride characteristics

Duty factor varied with both speed ($F_{1,266}$=238.39, P<0.001) and surface ($F_{1,266}$=224.71, P<0.001), although there was no significant interaction between speed and surface ($F_{1,266}$=1.39, P=0.238). Duty factor was highest on the inclined pole, reflecting the lower speeds on this surface. After removing the interaction term, surface still had a significant effect on the relationship between speed and duty factor, suggesting a significant difference in the intercept between the surfaces (Fig. 3A). Thus, quolls are able to move along the pole at similar speeds to the inclined platform, but do so using a higher duty factor. At any given speed, stride duration tends to be shorter for strides on the inclined pole when compared with the inclined platforms (surface, $F_{1,267}$=6.72, P=0.010; speed, $F_{1,267}$=291.52, P<0.001; Fig. 3B). Given that stride durations are shorter on the pole than the platform, this implies that, at any given speed, stride lengths must be longer on the pole than the platform. We confirmed this for data for which stride length was available; stride length was significantly influenced by both surface ($F_{1,81}$=41.94, P<0.001) and speed ($F_{1,81}$=83.33, P<0.001).

Timing between footfalls

Differences in footfall timing between the forefeet ($T_{lag, F}$) was associated with speed, surface and the interaction between the two (speed, $F_{1,263}$=20.98, P<0.001; surface, $F_{1,263}$=10.16, P=0.002; speed×surface, $F_{1,263}$=4.59, P=0.033). Removing the interaction

term affected the model fit, suggesting significant differences in the slope and intercept between the surfaces (L ratio=4.55, P=0.033). $T_{lag, F}$ decreased rapidly with speed on the inclined platform (Fig. 4A). This effect was reduced on the inclined pole, with shorter $T_{lag, F}$ being preferred across speeds, indicating that the forefeet are acting in unison on narrow poles (Fig. 4A). Overall, this suggests that there is a tendency to decrease the temporal separation between the forefeet at higher speeds, but this is greatly constrained on narrower surfaces.

Conversely, the time difference between footfalls of the hindfeet ($T_{lag, H}$) was not significantly affected by speed or surface (square root transformed $T_{lag, H}$: speed, $F_{1,266}$=0.05, P=0.825; surface, $F_{1,266}$=0.22, P=0.636; Fig. 4B). Overall, hindfeet tend to be used simultaneously (indicated by short time lags) at all speeds on both surfaces.

Time lag between the mean forefeet and hindfeet footfalls ($T_{lag, P}$) was significantly correlated with speed ($F_{1,266}$=18.75, P<0.001; Fig. 4C), but not with surface ($F_{2,266}$=1.89, P=0.169), while the interaction between surface and speed was close to statistical significance ($F_{1,266}$=3.63, P=0.057). When analysing each surface separately, there was no significant effect of speed on $T_{lag, P}$ for the inclined platform ($F_{1,59}$=0.09, P=0.758), but a significant effect of speed was found on the inclined pole ($F_{1,220}$=34.5, P<0.001). On this latter surface, higher speeds were associated with a reduction in the temporal separation between the fore and hindfeet (Fig. 4C).

Distance between footfalls

The hindfeet were generally kept much closer together (0.033± 0.002 m; mean±s.e.m. for all trials) than the forefeet (0.040± 0.002 m). The absolute total distance between the forefeet (total D_F) was significantly larger on the inclined platform than the inclined pole ($F_{1,78}$=151.17, P<0.001; Fig. 5A), but was not affected by speed ($F_{1,78}$=0.98, P=0.323), nor by the interaction between speed and surface ($F_{1,78}$=0.74, P=0.394). When examining footfall distance in only the fore–aft axis, D_F decreased with speed ($F_{1,78}$=6.36, P=0.014) and was greater on the inclined platform than the inclined pole ($F_{1,78}$=8.51, P=0.005; Fig. 5A). Similarly, the interaction between speed and surface did not affect fore–aft D_F.
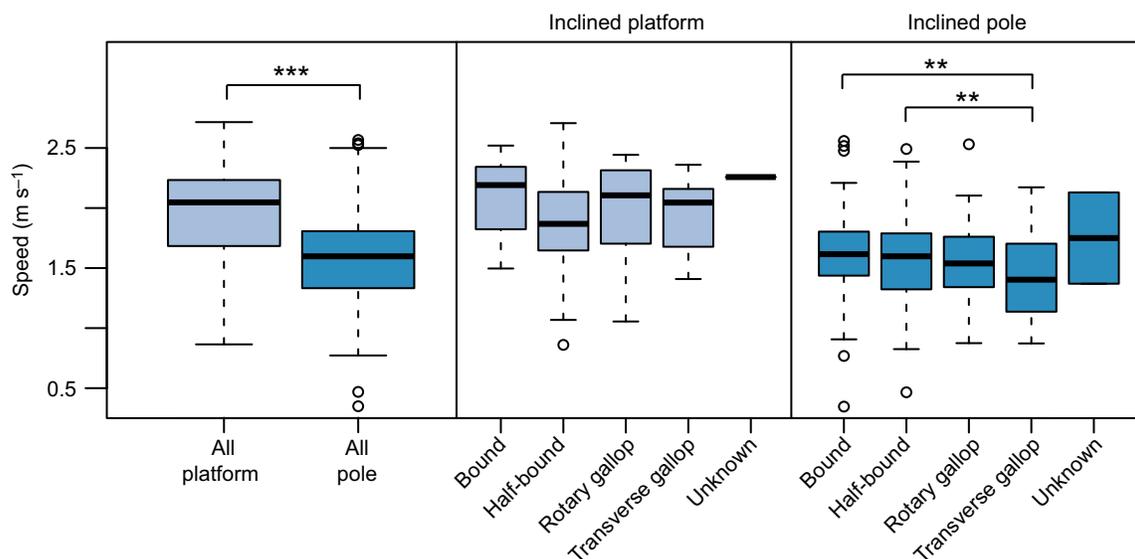

Fig. 2. Variation in speed with surface and gait in the northern quoll (*Dasyurus hallucatus*). Speed varies significantly between the two surfaces and with gait choice on the inclined pole. Unknown indicates gait that could not be classified based upon descriptions in Abourachid (2003). ***P<0.001, **P<0.01, based on linear mixed-effects models. Boxes represent the median, with hinges representing the first and third quartiles; whiskers represent the 95% CIs, and dots represent outliers.
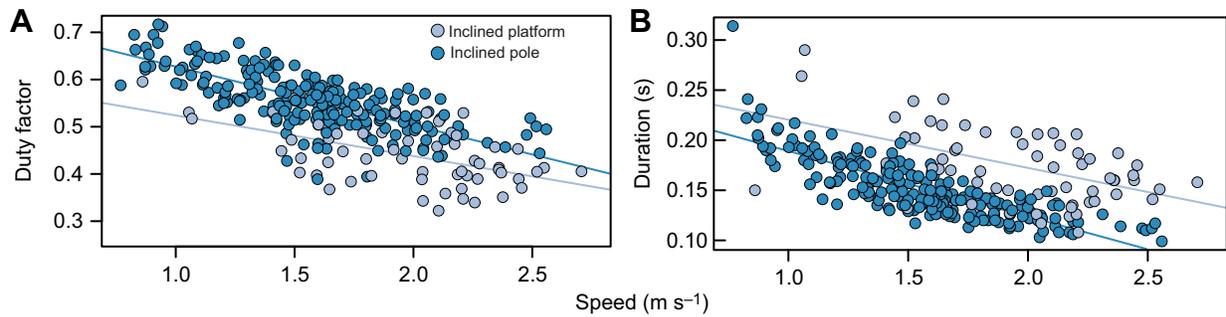
Fig. 3. Duty factor and swing time as a function of speed for quolls running on inclined surfaces. (A) Duty factor and (B) swing time for northern quoll running on an inclined platform or pole. Solid lines indicate linear regression model for each condition.

The total distance between the hindfeet (total D_H) was significantly smaller on the inclined pole than the inclined platform ($F_{1,76}=2.05.97$, $P<0.001$; Fig. 5B). However, unlike the forefeet, the total D_H increased significantly with speed ($F_{1,76}=16.12$, $P<0.001$; Fig. 5A), with no significant interaction between surface and speed ($F_{1,76}=0.49$, $P=0.483$). Compared with
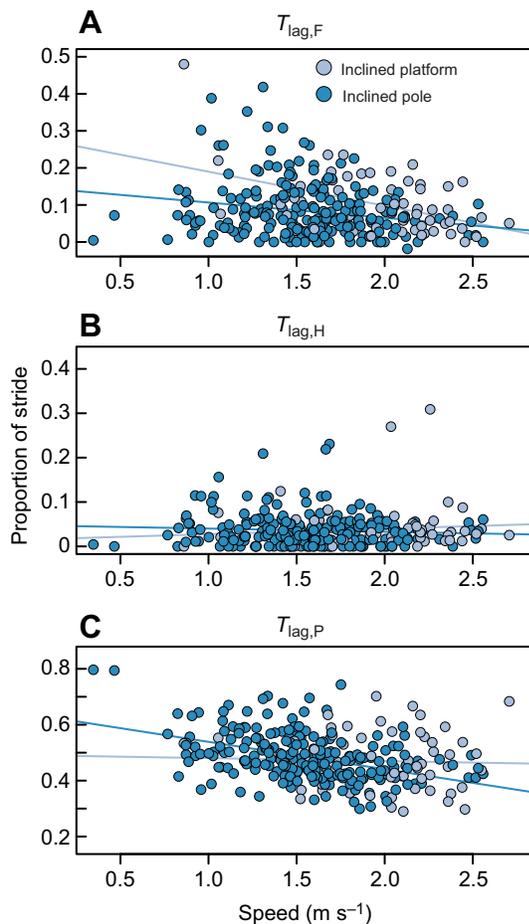

Fig. 4. Timelags for forelimb, hindlimb and fore–hind limbs as a function of speed for quolls running on inclined surfaces. Relationship between speed and (A) forelimb timelag ($T_{lag, F}$), (B) hindlimb timelag ($T_{lag, H}$) and (C) fore–hind timelag ($T_{lag, P}$) for running on the inclined platform and inclined pole. Solid lines indicate linear regression model for each condition. $T_{lag, F}$, $T_{lag, H}$ and $T_{lag, P}$ were calculated as the temporal lag between the mid-stances of the two forefeet, hindfeet and averaged across the ipsilateral feet, respectively, divided by the total stride time.

the total distance, the fore–aft D_H shows a considerable drop, below 2 mm and close to the resolution limit of this method (Fig. 5B).

Total hind-to-fore foot distance was greater on the inclined platform than on the inclined pole ($F_{1,78}=35.73$, $P<0.001$; Fig. 5C), but was unaffected by speed ($F_{1,78}=0.58$, $P=0.446$) and the interaction between speed and surface ($F_{1,78}=2.51$, $P=0.117$). For both the inclined platform and the inclined pole surfaces, no significant relationship exists between speed and total hind-to-fore foot distance. Results for the fore-aft displacement only (fore–aft D_P) largely reflect those of D_P, as might be expected, given that much of the displacement between the fore and hindfeet is expected to occur along this fore–aft axis.

Ground reaction forces

To determine the relative contribution of each of the feet towards propulsion, we recorded the output of the forces transferred to the substrate (platform or pole) by each limb individually wherever possible, or by pairs of feet in instances where they touched the force transducer simultaneously (Fig. 1D).

The integral of the fore–aft force trace with respect to time (impulse) throughout the stance phase was significantly different among the feet ($F_{5,100}=34.3$, $P<0.001$), but did not significantly differ between the surfaces ($F_{1,100}=1.49$, $P=0.224$), nor did it vary with speed ($F_{1,100}=0.15$, $P=0.698$) (Fig. 6A). Higher forces were produced by the paired hindfeet compared with the paired forefeet ($z=-12.3$, $P<0.001$) and between the paired hindfeet with either the left ($z=-8.0$, $P<0.001$) or right ($z=-6.0$, $P<0.001$) forefoot alone, with no other comparison being significant. The hindfeet (0.39 ± 0.026 N s^{-1}) provide over three times the propulsive force of the forelimbs (0.12 ± 0.010 N s^{-1}) during locomotion on the inclined surfaces. The maximum SRF, for quolls against pushing themselves forward, increased significantly with speed ($F_{1,100}=9.43$, $P=0.003$). Like impulse, there was no effect of surface ($F_{1,100}=0.41$, $P=0.521$) on maximum fore–aft force, but there was significant variation among feet ($F_{5,100}=52.2$, $P<0.001$). As for the impulse above, the hindfeet provided the greatest propulsive force.

The integral of the vertical force trace throughout the stance phase was not affected by surface ($F_{1,100}=1.08$, $P=0.302$), foot ($F_{1,100}=0.67$, $P=0.647$) or speed ($F_{1,100}=0.00$, $P=0.996$), suggesting that all feet contribute near equally to body weight support during movement (Fig. 6B). The mean vertical impulse for all feet was 0.055 ± 0.0072 N s^{-1}. The maximum SRF (which represents the peak reaction force against quoll body weight) was not affected by speed ($F_{1,100}=0.11$, $P=0.743$) or surface ($F_{1,100}=0.01$, $P=0.935$), but was weakly affected by foot ($F_{5,100}=2.78$, $P=0.022$), with a *post hoc* test showing only differences between the fore-left foot alone, with the combined forefeet ($z=3.15$, $P=0.024$).
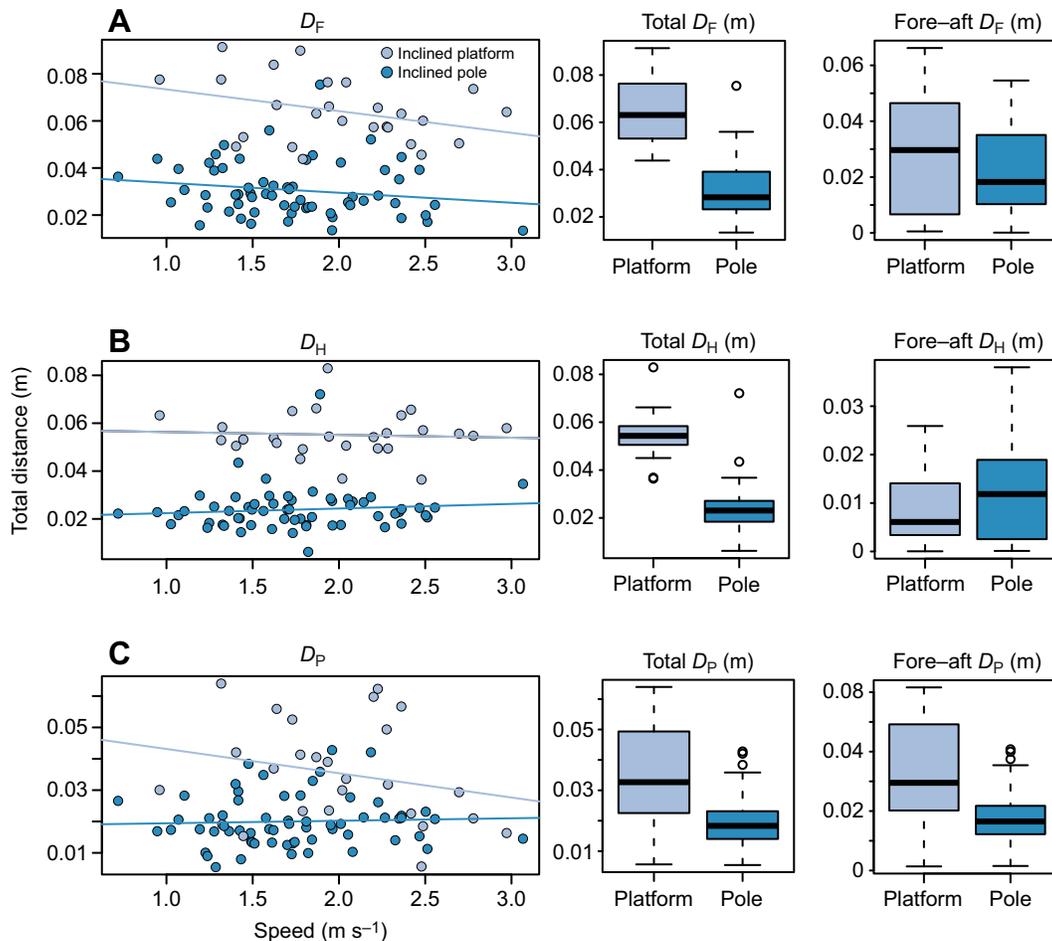
Fig. 5. Distances between foot falls in quolls running on inclined surfaces. Distance between footfalls for (A) the left and right forefeet (D_F), (B) the left and right hindfeet (D_H) and (C) the mean distance between the forefoot pair and the hindfoot pair (D_P) for quolls on the inclined platform and inclined pole. Box plots show median values with other parameters as per Fig. 2. Given that lateral distances are constrained on the narrow inclined pole, we also report the median fore–aft distances between each foot pair (right).

The minimum SRF, which indicates whether the surface is pulled toward the body during the stance phase, increased significantly with speed ($F_{1,100}=4.97$, $P=0.028$), with slower strides requiring a greater pulling force, and with surface ($F_{1,100}=4.15$, $P=0.044$). The minimum SRF was lower on the inclined pole than the inclined platform ($-1.07\pm$
0.155 N versus -0.36 ± 0.112 N), likely as a result of quolls being better able to grip underneath the narrow pole. However, it was not significantly different between feet ($F_{1,100}=0.55$, $P=0.732$).

The lateral force trace integral was not significantly affected by speed ($F_{1,100}=0.24$, $P=0.626$) or surface ($F_{1,100}=0.01$, $P=0.937$), but like the vertical and fore–aft impulse, there was a significant effect among feet ($F_{5,100}=5.91$, $P<0.001$) (Fig. 6C). *Post hoc* tests highlighted that the single forelimbs (fore-left and fore-right) were capable of producing significantly different lateral forces, yet this trend was only evident on the narrow pole (Fig. 6C).

Corrective torques
We explored the magnitude of corrective torques (rolling torque, i.e. around the anterior–posterior axis) applied along the narrow inclined pole (Fig. 7). We do not report these for the inclined platform, as they are unlikely to contribute to stability on a wide substrate, where limbs cannot grasp. Neither counter-clockwise nor clockwise torque was significantly related to speed or foot

(counter-clockwise: speed, $F_{1,59}=0.37$, $P=0.543$; foot, $F_{4,59}=1.14$, $P=0.348$; clockwise: speed, $F_{1,59}=0.02$, $P=0.879$; foot, $F_{4,59}=1.57$, $P=0.193$). However, when comparing simultaneous foot falls, the paired forefeet and the paired hindfeet produced substantial corrective torques, likely related with the decreased distance between fore and hind feet pairs on the inclined pole in comparison to the inclined platform. The left forelimb produced larger clockwise corrective torques in comparison to the right forelimb (left, -72.15 ± 18.96 N mm; right, -16.22 ± 5.41 N mm; $n=4$). In contrast, the right forelimb produced greater counter-clockwise corrective torques than the left forelimb (left, 16.98 ± 14.17 N mm; right, 51.64 ± 16.83 N mm; $n=4$). The direction of these corrective torques suggests the shear components of the linear vertical and medio–lateral force acting about the cross-section of the pole exerts this torque (i.e. the foot is pushing down slightly off the centre of the pole to produce the torque). This has been described as 'SRF torque' (Lammers and Gauntner, 2008; Chadwell and Young, 2015) and appears to be different from the effects of grasping limbs actively 'twisting' the substrate or 'muscular torque', for which we might expect the opposite trend of torques. This suggests that single forelimbs are not capable of generating excessive gripping torques, although a more thorough investigation including the centre of pressure of footfall would be required to investigate this further.
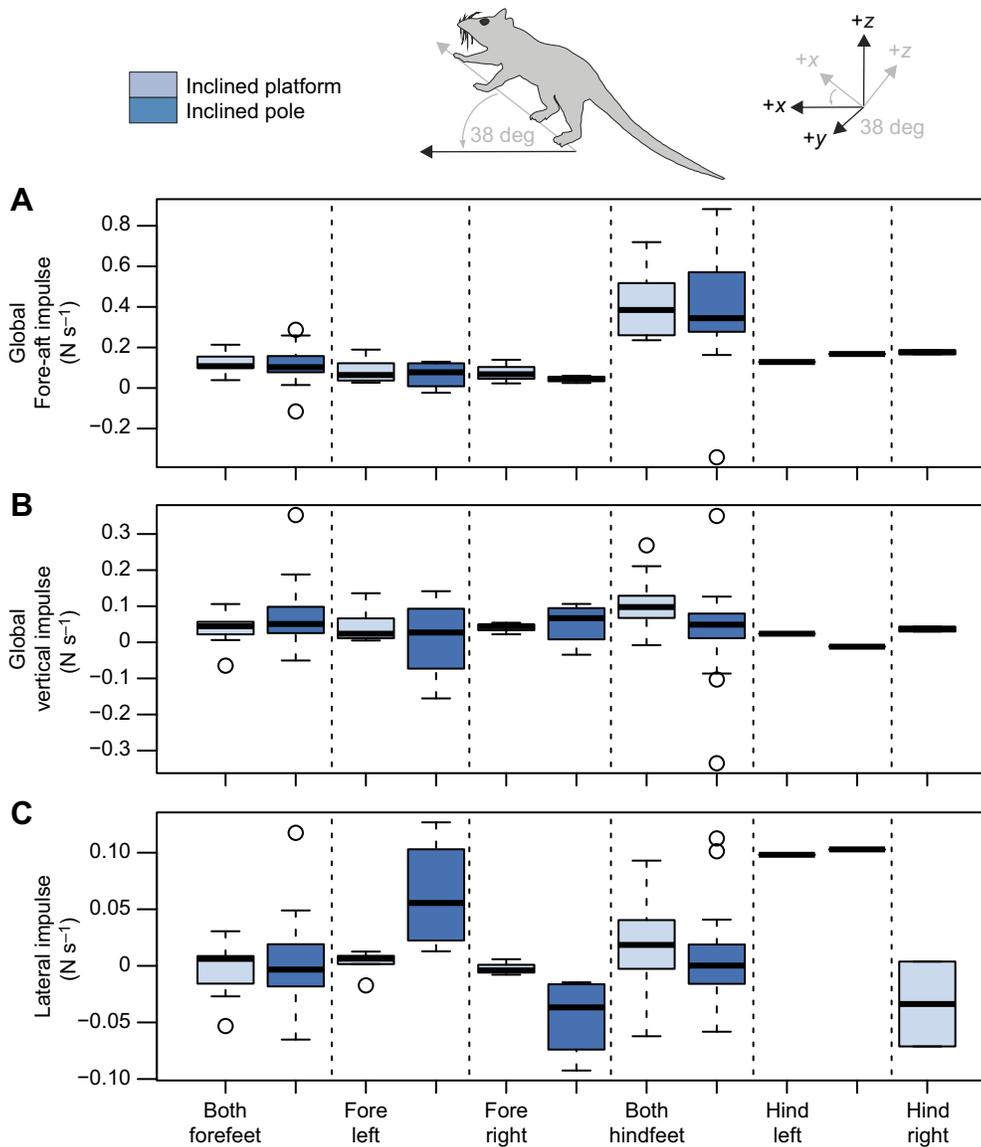
Fig. 6. Impulse determining the relative contribution of each of the feet or for pairs of feet where they touch the force plate simultaneously. Impulse was calculated as the integral of the force trace with respect to time for the global (A) fore–aft, (B) vertical and (C) lateral directions for the inclined platform (light) and inclined pole (dark). Positive lateral impulses indicate force directed towards the left and vice versa. Data have been transformed about the y-axis by 38 deg (see Materials and Methods for details). Untransformed data are available in Fig. S1. Box and whisker plots as per Fig. 2.

DISCUSSION

Understanding the extent to which species fitness is high in a specific environment often requires knowledge of the relevant performance requirements and the biomechanical limitations imposed by that environment. Greater declines in northern quoll populations in open grasslands compared with semi-arboreal rocky habitats suggest greater predation pressure in open habitats. This presents a unique system to quantify the link between performance and survival in natural habitats. To explore the extent to which habitat can compromise the performance of northern quolls, we analysed their kinematics and kinetics while they moved up inclined narrow and wide substrates.

Environment-dependent locomotion in the northern quoll

We found that quolls used slower speeds when moving on a narrower surface, but used similar gaits on both wide and narrow inclined structures. This suggests that a quoll's gait choice is independent of both speed and the structure of the terrain. This highlights the limitations of examining only variation in classical gait characterizations when comparing the movement of small, agile animals within habitats of differing complexity. Therefore, we also measured variation in the kinematic and kinetic patterns of quoll movement.

Quolls were capable of moving at similar speeds along the inclined pole as the inclined platform, but did so using a much higher duty factor. Duty factor is the percentage of the stride cycle when the foot is in contact with the substrate, suggesting relatively longer stance phases. Yet, in order to maintain similar speeds when using higher duty factors, the quolls swung their legs faster on the inclined pole. These longer stance phases may be required to provide stabilizing moments on narrow substrates, such as the inclined pole. Alternatively, swinging limbs faster may contribute to increased dynamic stability. In either case, this suggests that an alternative neuromuscular strategy for arboreal movement is used in quolls. This increased leg swing speed may also be responsible for the increase in the probability of mistakes, which is present when quolls run at higher speeds, or on narrower surfaces (Nasir et al., 2017).

We found a similar pattern in the distance and timing of footfalls, whereby distance and time both decreased at faster speeds and on narrower surfaces. This too suggests a change in the biomechanical strategy employed by quolls on narrower surfaces, reflecting a
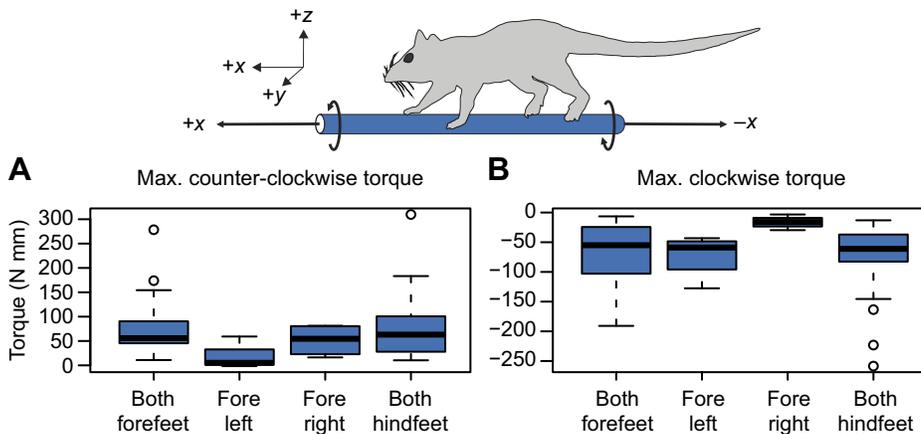
Fig. 7. Maximum corrective torques on the inclined pole for foot limb pairs in the northern quoll. Maximum corrective torques in the (A) counter-clockwise and (B) clockwise directions on the inclined pole for the different combinations of foot limb pairs. The direction of torques is consistent with the right-hand rule. Sufficient data were not available for single hindlimbs. Box and whisker plots as per Fig. 2.

coupled use of limb pairs at higher speeds. Coupled limb behaviour is likely to be associated with the corrective forces and torques necessary to maintain stability on narrow surfaces (Cartmill, 1985). We found quolls that were able to produce corrective torques with simultaneous limb pairs, as previously shown in primates (Chadwell and Young, 2015), but not with single limb surface contacts. These former corrective torques, between left and right limbs of a girdle, probably explains why we observed a decrease in the timing and distance of footfalls, suggesting that like primates, quolls expand their effective grasp by gripping the substrate between limb pairs.

Cats and dogs: changes in gait parameters

The decreased population density of northern quolls in open grassland habitats is often attributed to introduced predators such as cats and dogs, and a decrease in habitat complexity due to land clearing, altered fire regimes or grazing by invasive herbivores (Newsome, 1975; Burbidge and McKenzie, 1989; Oakwood, 2000; McKenzie et al., 2007). A comparison of the biomechanical capacities between quolls, cats and dogs may therefore provide insight into the relative performance of these predators and quolls in different habitats. Gálvez-López et al. (2011) compared the kinematics of cats and dogs on a raised narrow wooden beam to that of unconstrained overground locomotion, mirroring the experimental protocol used in this study. Similarly to quolls, cats adopted lower speeds on narrow supports as compared to overground surfaces, but unlike quolls, swing phase duration was independent of speed during narrow support locomotion (Gálvez-López et al., 2011). During overground locomotion, the swing phase duration of cats decreased with increasing speed, but did not change on narrow surfaces, suggesting that cats are unable to take faster steps on narrow structures but instead appear to take longer strides. In contrast, quolls use an absolutely lower swing phase duration at any speed on narrow structures, implying different control strategies between cats and quolls. Furthermore, unlike quolls, where we found a significant decrease in the timing between forefeet contact on the narrow compared with wide substrates, cats deviate from this pattern and increase the timing between forefeet contacts on these narrow structures. The extent to which this limits their ability to produce corrective torques, as found in quolls, remains to be shown.

In contrast to quolls and cats, which both decrease their speeds on narrower surfaces, dogs adopt higher speeds. These higher speeds are achieved via an increase in both stride frequency and stride length, and a decrease in stance phase duration, leading to lower duty factors on narrower substrates (Gálvez-López et al., 2011). Combined, the biomechanical traits evident in dogs on narrow substrates suggest a reduced degree of static stability and an increased reliance on dynamic stability. Static stability is the process by which an animal remains stable because the forces and torques produced by gravity are near equal and opposite to the ground reaction forces and moments (Lammers and Zurcher, 2011a,b). However, at higher speeds it becomes increasingly difficult to maintain static stability. Dynamic stability is the process whereby an animal remains stable due to the presence of an angular momentum created by the cyclical motion of the limbs. This cyclical motion produces a 'gyroscopic effect' where if a small disturbance changes the lean of a body, the gravitational force produces a restoring torque about the fore–aft axis to maintain stability. Some truly arboreal species appear to avoid highly dynamically stable gaits (Lammers and Zurcher, 2011a,b), which is likely related to the discontinuous, multi-dimensional and frequently unstable characteristics of arboreal habitats. This suggests that larger terrestrial animals, like dogs, may be at risk of increasing the probability of mistakes on narrow substrates, although this remains to be confirmed. However, this may not be the case in other small semi-arboreal species, such as chipmunks, that exploit dynamic stability during locomotion (Lammers and Zurcher, 2011a,b).

How do northern quolls compare with other arboreal species?

Kinematic comparisons of semi-arboreal northern quolls with other arboreal species may help to determine the extent to which quolls are selected for an arboreal versus terrestrial environment. Like quolls, among 7 species of marsupials (opossums), relative speeds increased with support diameter (Delciellos and Vieira, 2009), indicating a transition to slower and more stable gaits on narrower structures. Similar control strategies to quolls were evident among mouse lemurs, where limb contact time increased on narrow structures, likely to aid stability through an increase in the time available to apply corrective torques (Shapiro et al., 2016). Though this latter species did differ by showing both relative fore- and hindlimb lead intervals consistently increasing as substrates decreased in diameter.

Greater differences were observed between quolls and rats (Camargo et al., 2015). Arboreal rat species tend to increase stride frequency and decrease stride length on narrow structures, compared with terrestrial species that decrease both stride length and frequency. Thus, arboreal species show an increase in speed on narrow structures, whereas terrestrial species slow down (Camargo et al., 2015). The biomechanical control strategies used by quolls is therefore more akin to terrestrial than arboreal rats.

A kinematic pattern common among arboreal specialists, particularly among primates, is the use of a diagonal-sequence footfall pattern during walking, where the fore-left and hind-right limbs (or vice versa) are used in conjunction during stance (Muybridge, 1887; Prost, 1965, 1969; Hildebrand, 1966, 1977, 1980, 1985; Vilensky and Larson, 1989; Lemelin and Grafton, 1998; Cartmill et al., 2002; Schmitt and Lemelin, 2002). This footfall pattern is often thought to be beneficial when used in association with grasping extremities when moving and foraging on thin flexible branches. This theory was tested among the grey short-tailed opossum (*Monodelphis domestica*) and the woolly opossum (*Caluromys philander*) and showed that the latter species, which possesses more developed grasping extremities, displayed a greater use of diagonal-sequence walking gaits (Lemelin et al., 2003). In the current study, this walking sequence was not observed among quolls, with $T_{\text{lag, P}}$ values approximating 0.5, indicating forefeet or hindfeet pairs are used (rather than diagonals) during bounds and half-bounds. Thus, northern quolls are using relatively fast asymmetrical gaits, whereas many arboreal specialists (like primates and woolly opossums) use slow diagonal sequence walking gaits on narrow supports. This suggests an important role of terrestrial locomotion for northern quolls and an increased reliance on dynamic stability while on narrow structures.

Kinetic comparisons also showed differences between classically arboreal species and quolls. Like quolls, the grey short-tailed opossum showed both fore and hindlimbs had equal roles in body weight support (vertical force) on inclined surfaces (Lammers and Biknevicius, 2004). However, differences arose in propulsive forces (fore–aft): in quolls, with the hindlimbs producing the majority of the propulsive impulse whereas in opossums, it was the forelimbs which exerted the greater propulsive impulse (Lammers et al., 2006).

It has further been hypothesised that much of the kinematic changes to gait on narrow supports are linked to a functional reduction in the vertical force, which would reduce oscillations of the centre of mass and increase stability on narrow structures (Schmitt and Lemelin, 2002; Schmitt et al., 2006; Young, 2009; Lemelin and Cartmill, 2010; Gálvez-López et al., 2011). However, in the current study we found little or no evidence for a decrease in the maximum SRF (which represents the peak reaction force against quoll body weight) on narrow supports which may function to reduce these oscillations. In other species, vertical forces were lower on arboreal supports for the common marmoset (*Callithrix jacchus*) (Chadwell and Young, 2015) and the grey short-tailed opossum (Lammers and Biknevicius, 2004), although the authors caution that in this latter species, this may be attributed to differences in speed between the treatments.

The torques generated by the limbs about the long axis of a branch may also be important for stable locomotion on arboreal substrates. Although several characteristics of quoll locomotion resemble those of terrestrial species, quolls are similar to arboreal species in their ability to produce stabilizing torques on narrow supports. For example, the grey short-tailed opossum uses long-axis torque to avoid toppling on a branch, though in this species the forelimbs generated significantly greater torque than the hindlimbs, which is probably explained by the greater weight-bearing role of the former (Lammers and Gauntner, 2008). Similarly, the Siberian chipmunk (*Tamias sibiricus*) produced considerable torque to counteract rolling moments which were equal between the fore and hindlimbs (Lammers and Zurcher, 2011a,b). Furthermore, like quolls, the total impulse of the rolling torques in these chipmunks was usually greater than or less than zero (i.e. not balanced within a stride). This indicates that like chipmunks, quolls may balance out the torques acting on the centre of mass over the course of two or more strides to maintain stability.

A biomechanical framework to predict the survival of key species

These comparisons suggest that there are multiple biomechanical strategies available to achieve support on narrow substrates, and the degree to which different species exploit these strategies varies along a spectrum from fully terrestrial, to semi-arboreal, to fully arboreal. Northern quolls are often described as semi-arboreal specialists (Schmitt et al., 1989). Consistent with this, we show that many of the gait characteristics associated with quolls appear similar to those in terrestrial species, with some characteristics useful in arboreal habitats.

Historically, northern quolls occupied both floodplains (terrestrial) and rocky (semi-arboreal) habitats. Our biomechanical analyses suggest that cats and dogs are likely to be superior in terrestrial environments owing to their larger body size and greater speeds (Gálvez-López et al., 2011). This may partially explain the declines and/or reduced populations of northern quolls in these terrestrial environments (Oakwood, 2000). Conversely, quolls appear to have biomechanical characteristics consistent with a stability advantage at higher speeds on narrow supports when compared with cats and dogs (Gálvez-López et al., 2011), likely explaining why the decrease in quoll populations in semi-arboreal habitats (such as rocky outcrops) has not been as severe (Oakwood, 2000). However, quolls did not show many of the characteristics common in truly arboreal specialists (e.g. diagonal sequence gaits) such as opossums, which may explain why populations of quolls are showing more obvious signs of decline than other native species such as possums (Woinarski et al., 2001). Quolls appear to share a larger percentage of their performance space with cats and dogs, and this overlap, combined with reductions in habitat complexity, may be directly related to their declining population on mainland Australia.

Here, we show the value in using biomechanical analyses to predict the survival and fitness of key species within a habitat (Wilson et al., 2018). The relative performance of a species, results from its ability to employ biomechanical strategies necessary to maintain stability and outperform key predators (invasive or otherwise) within that habitat. This concept may become even more important as we move to a period of increased human impact within the Anthropocene, and may allow us to predict the influence of climate change, urbanisation and deforestation on species of conservation importance.

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