

1 **Moving in complex environments: a biomechanical analysis of locomotion on inclined**
2 **and narrow substrates.**

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10 **Abstract**

11 Characterisation of an organisms' performance in different habitats provides insight into the
12 conditions that allow it to survive and reproduce. In recent years, Northern quolls (*Dasyurus*
13 *hallucatus*)—a medium-sized semi-arboreal marsupial native to northern Australia—have
14 undergone significant population declines within open forest, woodland and riparian habitats,
15 but less so in rocky areas. To explore this decline, we quantified the biomechanical
16 performance of wild Northern quolls over inclined narrow (13 mm pole) and inclined wide
17 (90 mm platform) substrates. We predicted that quolls may possess biomechanical
18 adaptations to increase stability on narrow surfaces, which are more common in rocky
19 habitats. Our results display that quolls have some biomechanical characteristics consistent
20 with a stability advantage on narrow surfaces. This includes the coupled use of limb pairs and
21 high grip torques (Max = 68.9 N.m, Min = -69.9 N.m), highlighting their ability to generate
22 corrective forces to counteract the toppling moments commonly encountered during gait on
23 narrow surfaces. However, unlike other arboreal specialists such as primates, speed was
24 constrained on narrow surfaces, and quolls did not adopt diagonal sequence gaits. Quolls
25 appear to adopt similar performance characteristics to cats and dogs which may limit their
26 ability to outperform these key predators (invasive or otherwise) in particular habitats. This
27 overlap may contribute to the declining population of Northern quolls on mainland Australia.

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36 **Keywords:** performance, northern quoll, torque, ground reaction force, kinematics, kinetics

37 **Introduction**

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

50 Northern quolls are primarily nocturnal, partially arboreal marsupial carnivores, found in
51 grassy or rocky habitats across northern Australia (Schmitt et al., 1989, Oakwood, 2000). The
52 Northern quoll has declined from a broad distribution across northern Australia to several
53 disjunct populations often centred on rocky plateaus with local extinctions primarily
54 occurring in lowland savanna (Braithwaite and Griffiths, 1994, Morris, 1996, Braithwaite and
55 Muller, 1997). Dingoes and feral cats are the main predators of Northern quolls, and both
56 have been historically present across their range for 4000 and over 100 years, respectively
57 (Burbidge et al., 1988, Corbett, 1995). The reason for the recent rapid decline in population is
58 therefore complex. However, it has been hypothesised that habitat loss or fragmentation (due
59 to land clearing, altered fire regimes, or grazing by invasive herbivores) can leave smaller
60 mammalian species more vulnerable to predation (Newsome, 1975, Burbidge and McKenzie,
61 1989, McKenzie et al., 2007). In a study on quoll survival, Oakwood (2000) reported that all
62 Northern quolls killed by predators were killed within forest, woodland and riparian habitats,
63 and that few kills occurred in rocky outcrops. Also, females whose home ranges included a
64 greater proportion of rocky habitat, were more likely to survive to a second breeding season.
65 This suggests that rocky habitats may increase the survival of Northern quolls.

66 Greater survival in rocky habitats could be due to either a higher density of refugia or a lower
67 abundance of large predators in these habitats. Dingoes, a major predator of quolls, mainly
68 hunt on floodplains during the dry season and in the forest during the wet season, and are

69 most successful in open habitats (Corbett, 1995). Dingoes were never observed on the rocky
70 hills during this study, suggesting that the locomotion of dingoes may be compromised in
71 these habitats relative to open areas. Similar strategies have been shown in feral cats, which
72 occupy open habitats more frequently than complex ones (Hohnen et al., 2016) and display
73 better hunting success in these open habitats when compared to complex ones (McGregor et
74 al., 2015).

75 The differential survival of a species across various habitats will be due to changes in their
76 detection by predators or ease of capture after detection. Studying the performance of a
77 species vulnerable to predation across various types of terrain allows one to make predictions
78 about the relative performances between predator and prey. This can provide the basis for a
79 mechanistic understanding of predation and its conservation significance.

80 Our study examined the kinematics and kinetics of Northern quolls in both simplified
81 terrestrial and arboreal environments, designed to represent aspects of their natural habitat.
82 We categorised their biomechanics across two different substrates: an inclined wide platform,
83 and an inclined narrow pole. We then compared the quolls' biomechanics on each of these
84 substrates with biomechanical strategies used by arboreal specialists (such as primates and
85 possums) and terrestrial specialists (such as rats, cats, and dogs) to compare the relative
86 performances of quolls to these groups of animals. We hypothesized that within complex
87 arboreal-like habitats quolls would modify biomechanical characteristics to be more
88 reflective of arboreal species, and therefore help to explain their increased survival in these
89 habitats.

90 **Materials and Methods**

91 *Morphology*

92 Northern quolls were trapped on Groote Eylandt, Northern Territory, Australia, between July
93 and August 2013 using Tomahawk original series cage traps (20 x 20 x 60 cm; Tomahawk
94 ID-103, Hazelhurst, Winconsin, USA) baited with canned dog food. Traps were set overnight
95 and checked early in the morning (no later than 7:30 am) to avoid quolls being subjected to
96 warmer parts of the day. A total of 24 individual quolls (9 males, 15 females) were captured
97 throughout the study period. Each quoll was taken to the Anindilyakwa Land and Sea Ranger
98 Research Station for subsequent experiments. All individuals received a micro-chip (Trovan
99 nano-transponder ID-100, Keysborough, Australia) that was placed subcutaneously between
100 the shoulder blades to ensure identification during any subsequent recaptures. Research
101 methodologies were approved by the University of Queensland animal ethics committee
102 (SBS/541/12/ANINDILYAKWA/MYBRAINSC) and were conducted under the Northern
103 Territory Parks and Wildlife Commission (permit number: 47603).

104 Body mass was measured for each individual using an electronic balance (± 0.1 g; A & D
105 Company Limited HL200i, Brisbane, Australia) and eleven morphological variables were
106 each measured three times using digital calipers, with an average used as the overall measure
107 (Whitworth, Brisbane, Australia, ± 0.01 mm) (Wynn et al., 2015). These body dimensions
108 were included as covariates in our initial analysis, but none appeared to have a significant
109 effect on our results and thus were not included in further analysis. Mean body mass was
110 384.3 ± 21.5 g, head width (widest point of jaw) 36.07 ± 0.47 mm, head length (from nuchal
111 crest to tip of snout) 67.22 ± 0.73 mm, body length (nuchal crest to base of tail) 179.92 ± 3.32
112 mm, right and left fore-limb length (radius-ulna) 50.91 ± 0.75 mm, right and left hind-limb
113 length (tibia-fibula) 63.75 ± 0.79 mm, right and left hind-foot length (heel to claw base)
114 38.49 ± 0.48 mm, tail width (maximum tail diameter) 14.54 ± 0.43 mm and tail length (base
115 to tip of tail) 228.48 ± 4.49 mm. To minimize long-term stress on the animals, all
116 performance measures and tests were completed within 6 hours of capture, after which the
117 animals were released at the exact point of capture.

118 *Kinematics and kinetics*

119 To assess the biomechanics of Northern quolls, we filmed each individual as it moved over
120 two different raised platform trackways. Trackways were suspended within a Perspex box

121 (2600 × 470 × 160 mm) with a release and escape box at the start and end, respectively
122 (Figure 1).

123 Quolls were run along the two trackways (angle, pole) in a random order, to represent
124 different habitat types that a quoll is likely to encounter in its natural environment. The
125 inclined platform was a 90 mm wide plank of wood, covered in fine sandpaper (P120) to
126 provide traction at a 40^o angle, and represented a terrestrial environment. The inclined pole
127 was a 12 mm diameter wooden dowel running the length of the box at a 40^o angle, and
128 represented an arboreal environment. A third flat platform trackway (90 mm wide platform)
129 was also tested, but later excluded (see excluded strides). Both tracks ran the length of the
130 box with a force platform (Nano-17 titanium, ATI instruments) placed level and centrally
131 with the trackway, with either a 90 x 90 mm platform or a 90 mm long doweling attached to
132 its top.

133 Two cameras (Fastec IL-3, Fastec Imaging, 1280 x 700 pixels, @ 250 fps) were positioned
134 approximately perpendicular to each other, to capture a ventral/lateral, and lateral/dorsal view.
135 These camera positions were used to ensure footfalls were visible in both camera views, yet
136 allowed enough variation in viewing angle that 3-dimensional position information was still
137 accurate. Cameras were synchronized using internal triggers. The cameras were calibrated
138 using a wand based camera calibrate, implemented in the Argus software in Python Ver 2.1,
139 (Jackson et al., 2016). The Matlab GUI DLTdv5 (Hedrick, 2008) was then used to track
140 individual feet and a single spot on the back, close to the body centre of mass.

141 *Analysis*

142 (i) Timing parameters and gait

143 Feet were digitised for the duration of contact with the surface of calibrated racetrack. A
144 mark near the body centre of mass was used to calculate speed. Footfall sequence and gait
145 parameters were calculated using antero-posterior sequence methods (Abourachid, 2003,
146 Chadwell and Young, 2015). The first forefeet touchdown defined the start of a sequence and
147 its subsequent touchdown defined the end of the sequence. F-lag, H-lag and P-lag were
148 calculated as the temporal lag between the mid-stances of the two forefeet, hindfeet and
149 averaged across the ipsilateral feet respectively. We used the gait parameters described by
150 Abourachid (2003) and Chadwell and Young (2015). Speed was calculated for the duration of
151 the sequence, and duty factor was calculated as the average duty factor of feet within a

152 sequence. We examined the effects of, and interaction between, speed and surface for the
153 time lag between footfalls of the forefeet (F.lag), hindfeet (H.lag) and the difference between
154 the fore and hindfeet (P.lag) to determine which pairs of limbs may be contributing most to
155 increasing stability on narrow perches.

156 (ii) Spatial parameters

157 We further examined the effects of the absolute distance between the left and right fore-foot
158 (F.dist), the left and right hindfoot (H.dist) and the mean distance between the forefoot pair
159 and the hindfoot pair (P.dist). Since the lateral distance effects are likely to be constrained on
160 narrow supports we further examined the distance in the fore-aft axis for each variable
161 (F.distX, H.distX and P.DistX respectively).

162 (iii) Substrate reaction forces

163 Substrate reaction forces were recorded for each foot individually or for multiple feet
164 simultaneously using an ATI Nano17 6 dof micro force transducer (ATI instruments). The
165 forceplate was calibrated by the company with estimated error of $< 0.75\%$ in the x, y, and z
166 axes. The force plate was aligned with the x-axis representing the fore-aft direction, y
167 representing the lateral direction, and z representing vertical forces. The transducer output
168 forces in these three axes along with torques about each axis. Torques about the axes are
169 likely dependent on the position of the footfall relative to the centre of the force transducer
170 and therefore of limited use, with the exception of the torque about the x-axis on the narrow
171 trackway. In this setup, the narrow pole was less than the width of the foot. Thus, we assume
172 the position of the footfall must more or less align with the x-axis of the force plate, and
173 therefore we included this torque in our analysis.

174 Strides where any foot partially stepped on the plate were excluded from further analysis.
175 Forces were synchronised with the video footage to identify each foot as it struck the
176 platform. For each foot stride we measured the maximum and minimum force, as well as the
177 integral of the force-time profile using the trapezoidal numeration integration function
178 (trapz.m) in matlab, for the fore-aft, medial-lateral and dorsal-ventrally directed forces. We
179 corrected for the inclined slope in the fore-aft forces, by multiplying fore-aft force by the
180 cosine of the slope (40 degrees), and removing the sine of the vertical force. Similarly we
181 corrected vertical forces by multiplying it by the sine of the angle and adding the cosine of
182 the fore-aft forces. This rotated forces such that they were comparable to flat-trackway forces.

183 (iv) Excluded strides

184 To determine the extent to which steady state trials were included in this study we estimated
185 the average acceleration over several strides within the field of view for each run.
186 Acceleration was estimated as the slope of speed over time throughout the run. While runs
187 over the angle and pole surface had a median value around zero, runs over the flat surface
188 show a distinct decelerating trend (Supp Fig. 2). Therefore we excluded all these strides from
189 our main analysis, but we chose to present them in the supplementary material as a means of
190 visual comparison of differences between angled platforms and the pole runs. Caution should
191 be used in the interpretation of the runs along the flat surface, as it will be ambiguous the
192 extent to which changes are the result of surface differences, or result from the inclusion of
193 predominately breaking strides.

194 (v) Statistics

195 For all analyses, a within subject design was used, including subject as random factor using
196 the lme.R function from the nlme package (Pinheiro et al., 2017) in R (ver 3.2.3 -- "Wooden
197 Christmas-Tree"). To examine variation between factors we specified the model with lme.R
198 function, and then used glht.R function from the multcomp package (Hothorn et al., 2008)
199 to perform Tukey post hoc tests, correcting the P values using the Bonferroni adjustment
200 method.

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208 **Results**

209 *Speed*

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

213 Speed also varied significantly with gait. For the inclined surfaces, speeds varied between
214 gaits on the narrow pole ($F_{4,206} = 3.68$, $P = 0.006$), but not on the platform ($F_{4,52} = 1.87$,
215 $P = 0.130$). On the narrow pole, transverse gallops were slower than bounds ($z = 3.49$, $P =$
216 0.004), and half bounds ($z = 3.44$, $P = 0.005$), but speeds during other gaits were not
217 significantly different. Speed differences with gait were most prominent on the flat platform
218 as reported in supplementary materials.

219 *Stride characteristics*

220 Duty factor varied with both speed ($F_{1,266} = 238.39$, $P < 0.001$) and surface ($F_{1,266} = 224.71$, P
221 < 0.001), though there was no significant interaction between speed and surface ($F_{1,266} = 1.39$,
222 $P = 0.238$). Duty factor was highest on the inclined pole, reflecting the lower speeds on this
223 surface. After removing the interaction term, surface still had a significant effect on the
224 relationship between speed and duty factor, suggesting a significant difference in the
225 intercept between the surfaces (Figure 3a). Thus, quolls are able to move along the pole at
226 similar speeds to the inclined platform, but do so using a higher duty factor. This increase in
227 duty factor is probably required in order to maintain stability, via increased contact time
228 between the surface and the feet. However, in order to maintain similar speeds at higher duty
229 factors, swing time must be greatly reduced. At any given speed the stride duration tends to
230 be shorter for strides on the inclined pole when compared to the inclined platforms (Surf:
231 $F_{1,267} = 6.72$, $P = 0.010$, Speed: $F_{1,267} = 291.52$, $P < 0.001$; Fig. 3b).

232 *Timing between footfalls.*

233 Differences in footfall timing between the forefeet (F.lag) was associated with speed, surface,
234 and the interaction between the two (Speed, $F_{1,263} = 20.98$, $P < 0.001$; Surface, $F_{1,263} = 10.16$,
235 $P = 0.002$; Speed:Surface, $F_{1,263} = 4.59$, $P = 0.033$). Removing the interaction term affected
236 the model fit, suggesting significant differences in the slope and intercept between the
237 surfaces ($L.ratio = 4.55$, $P = 0.033$). F.lag decreased rapidly with speed on the inclined
238 platform (Fig. 4a) This effect was reduced on the inclined pole, with shorter F.lag being
239 preferred across speeds, indicating the forefeet are acting in unison on narrow poles (Figure
240 4a). Results from flat surfaces, presented only in the supplementary materials, show a

241 significantly steeper slope than both the inclined platform and the inclined pole (Supp. Figure
242 5). Overall this suggests that there is a tendency to increase the temporal distance between the
243 forefeet at higher speeds, but this is greatly constrained on narrower surfaces.

244 Conversely, the time difference between footfalls of the hindfeet (H.lag) was not significantly
245 affected by speed or surface on the inclined surfaces (Square root transformed H.lag: Speed,
246 $F_{1,266} = 0.05$, $P = 0.825$; Surface, $F_{1,266} = 0.22$, $P = 0.636$; Figure 4b). H.lag was negatively
247 and linearly related to speed for the flat surface ($F_{1,160} = 82.2$, $P < 0.001$; See Supplementary
248 Material). On flat surfaces, H.lag tended to be highest for the low speeds, but was greatly
249 restrained with values close to zero (indicating simultaneous footfall of both hindfeet) at
250 higher speeds. Overall hindfeet tend to be used simultaneously (indicated by short time lags)
251 on all speeds and surfaces.

252 Time lag between the mean forefeet and hindfeet strike (P.lag) was significantly correlated
253 with speed ($F_{1,266} = 18.75$, $P < 0.001$; Fig. 4c), but not with surface ($F_{2,266} = 1.89$, $P = 0.169$),
254 while the interaction between surface and speed was close to statistical significance ($F_{1,266} =$
255 3.63 , $P = 0.057$). When analysing each surface separately, there was no significant effect of
256 speed on P.lag for the inclined platform ($F_{1,59} = 0.09$, $P = 0.758$), but a significant effect of
257 speed was found on the inclined pole ($F_{1,220} = 34.5$, $P < 0.001$). On this latter surface, higher
258 speeds were associated with a reduction in the phase lag between the fore and hindfeet (Fig.
259 4c).

260 *Distance between footfalls*

261 The hindfeet were generally kept much closer together (0.033 ± 0.002 m; mean \pm se for all
262 trials) than the forefeet (0.040 ± 0.002 m). The absolute total distance between the forefeet
263 was significantly larger on the inclined platform than the inclined pole ($F_{1,78} = 151.17$, $P <$
264 0.001 ; Figure 5a), but was not affected by speed ($F_{1,78} = 0.98$, $P = 0.323$), nor by the
265 interaction between speed and surface ($F_{1,78} = 0.74$, $P = 0.394$). When examining footfall
266 distance in only the fore-aft axis, forelimb distance (F.distX) decreased with speed ($F_{1,78} =$
267 6.36 , $P = 0.014$), and was greater on the inclined platform than the inclined pole ($F_{1,78} = 8.51$,
268 $P = 0.005$; Figure 5a). Similarly, the interaction between speed and surface did not affect
269 F.distX.

270 The absolute distance between the hindfeet was significantly smaller on the inclined pole
271 than the inclined platform ($F_{1,76} = 2.05.97$, $P < 0.001$; Fig. 5b). However, unlike the forefeet,

272 the absolute distance between the hindfeet increased significantly with speed ($F_{1,76} = 16.12$, P
273 < 0.001 ; Fig. 5a), with no significant interaction between surface and speed ($F_{1,76} = 0.49$, $P =$
274 0.483). Compared with the absolute distance, the fore-aft distance between the hindfeet
275 shows a considerable drop, below 2 mm and close to the resolution limit of this method
276 (Figure 5b).

277 Absolute hind-to-fore foot distance was greater on the inclined platform than on the inclined
278 pole ($F_{1,78} = 35.73$, $P < 0.001$; Fig. 5c), but was unaffected by speed ($F_{1,78} = 0.58$, $P = 0.446$)
279 and the interaction between speed and surface ($F_{1,78} = 2.51$, $P = 0.117$). On the flat surface,
280 absolute hind-to-fore foot distance was greater at faster speeds ($F_{1,54} = 14.9$, $P < 0.001$),
281 suggesting faster strides could be achieved by reaching further forwards with the forelimb
282 pair (Supplementary material). Yet for both the inclined platform and the inclined pole
283 surfaces, no significant relationship exists between speed and absolute hind-to-fore foot
284 distance. Results for the fore-aft displacement only (P.distX) largely reflect those of P.dist,
285 as might be expected, given that much of the displacement between the fore and hindlimbs is
286 expected to occur along this fore-aft axis.

287 *Ground reaction forces*

288 To determine the relative contribution of each of the feet towards propulsion, we recorded the
289 output of the forces transferred to the substrate (platform or pole) by each limb individually
290 wherever possible, or by pairs of feet in instances where they touched the force plate
291 simultaneously (Figure 1d).

292 The integral of the fore-aft force trace with respect to time (impulse) throughout the stance
293 phase was significantly different among the feet ($F_{5,100} = 34.3$, $P < 0.001$), but did not
294 significantly differ between the surfaces ($F_{1,100} = 1.49$, $P = 0.224$), nor did it vary with speed
295 ($F_{1,100} = 0.15$, $P = 0.698$) (Figure 6a). Higher forces were produced by the paired hindfeet
296 compared with the paired forefeet ($z = -12.3$, $P < 0.001$), and between the paired hindfeet
297 with either the left ($z = -8.0$, $P < 0.001$) or right ($z = -6.0$, $P < 0.001$) forefoot alone, with no
298 other comparison being significant. The hindfeet (-0.39 ± 0.026 N.sec) provide over three
299 times the propulsive force of the forelimbs (-0.12 ± 0.010 N.sec) during locomotion on the
300 inclined surfaces. The minimum of the fore-aft force (which represents the peak reaction
301 force against quolls pushing themselves forward) decreased significantly with speed ($F_{1,100} =$
302 9.43 , $P = 0.003$), indicating an increase in fore-aft force with increasing locomotor speed.

303 Like impulse, there was no effect of surface ($F_{1,100} = 0.41$, $P = 0.521$) on minimum fore-aft
304 force, but there was significant variation among feet ($F_{5,100} = 52.2$, $P < 0.001$). As for the
305 impulse above, the hindfeet provided the greatest propulsive force.

306 The integral of the vertical force trace throughout the stance phase was not affected by
307 surface ($F_{1,100} = 1.08$, $P = 0.302$), foot ($F_{1,100} = 0.67$, $P = 0.647$), nor speed ($F_{1,100} = 0.00$, $P =$
308 0.996), suggesting that all feet contribute near equally to body weight support during
309 movement (Figure 6b). The mean vertical impulse for all feet was -0.055 ± 0.0072 N.sec. The
310 minimum of the vertical force (which represents the peak reaction force against quoll body
311 weight) was not affected by speed ($F_{1,100} = 0.11$, $P = 0.743$) or surface ($F_{1,100} = 0.01$, $P =$
312 0.935), but was weakly affected by foot ($F_{5,100} = 2.78$, $P = 0.022$), with a post-hoc test
313 showing only differences between the fore-left foot alone, with the combined forefeet ($z =$
314 3.15 , $P = 0.024$)

315 The maximum vertical force, which indicates whether the surface is pulled toward the body
316 during the stance phase, decreased significantly with speed ($F_{1,100} = 4.97$, $P = 0.028$), with
317 slower strides requiring a greater pulling force. Maximum vertical force was greater on the
318 inclined pole than the inclined platform (1.07 ± 0.155 N vs 0.36 ± 0.112 N; $F_{1,100} = 4.15$, $P =$
319 0.044), likely as a result of quolls being better able to grip underneath the narrow pole.
320 However, maximum vertical force was not significantly different between feet ($F_{1,100} = 0.55$,
321 $P = 0.732$).

322 The lateral force trace integral was not significantly affected by speed ($F_{1,100} = 0.24$, $P =$
323 0.626) or surface ($F_{1,100} = 0.01$, $P = 0.937$), but like the vertical and fore-aft impulse, there
324 was a significant effect among feet ($F_{5,100} = 5.91$, $P < 0.001$) (Figure 6c). Post-hoc tests
325 highlighted that the single forelimbs (fore-left and fore-right) were capable of producing
326 significantly different lateral forces, yet this trend was only evident on the narrow pole
327 (Figure 6c).

328 *Corrective Torques*

329 We explored the magnitude of corrective torques applied along the narrow inclined pole (Fig.
330 7). We do not report these for the inclined platform, as they could unlikely contribute to
331 stability on a flat surface, where forelimbs cannot grasp. Neither counter-clockwise nor
332 clockwise torque was significantly related to speed or foot (counter-clockwise, speed: $F_{1,59} =$
333 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:

334 $F_{4,59} = 1.57, P = 0.193$). However, when comparing simultaneous foot falls, the paired
335 forefeet and the paired hindfeet produced substantial corrective torques, likely related with
336 the decreased distance between fore and hind feet pairs on the inclined pole in comparison to
337 the inclined platform. The left forelimb produced larger clockwise corrective torques in
338 comparison to the right forelimb (FL = 72.15 ± 18.96 N.mm, FR = 16.22 ± 5.41 N.mm; n=4). In
339 contrast, the right forelimb produced greater counter-clockwise corrective torques than the
340 left forelimb (FL = -16.98 ± 14.17 N.mm, FR = -51.64 ± 16.83 N.mm; n=4). The direction of
341 these corrective torques is consistent with each single forelimb being used in a gripping while
342 pulling forefoot stride.

343 **Discussion**

344 Understanding the extent to which a species has adapted to a specific environment often can
345 require the combination of relevant performance measures and knowledge of the
346 biomechanical limitations imposed by that environment. Greater declines in populations of
347 Northern quoll from open grasslands compared with semi-arboreal rocky habitats suggest
348 greater predation pressure in open habitats. This presents a unique system to quantify the link
349 between performance and survival in natural habitats. To explore the extent to which habitat
350 can compromise the performance of Northern quolls (*Dasyurus hallucatus*) we analysed their
351 kinematics and kinetics while they moved along terrains designed to represent aspects of their
352 natural environment.

353 *Environment-dependent locomotion in the Northern quoll*

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

360 Quolls were capable of moving at similar speeds along the inclined pole as the inclined
361 platform, but did so using a much higher duty factor. Duty factor is the percentage of the
362 stride cycle when the foot is in contact with the substrate, suggesting relatively longer stance
363 phases may be required to provide stabilizing moments on narrow substrates, such as the
364 inclined pole. In order to maintain similar speeds when using higher duty factors, the quolls
365 swung their legs faster on the inclined pole. This may provide evidence for an alternative
366 neuromuscular strategy for arboreal movement in quolls that may not be available to other
367 species. This increased leg swing speed may be responsible for the increase in the probability
368 of mistakes, which is present when quolls run at higher speeds, or on narrower surface (Nasir
369 et al., 2017).

370 We found a similar pattern in the distance and timing of footfalls, whereby distance and time
371 both decreased at faster speeds and on narrower surfaces. This too suggests a change in the
372 biomechanical strategy employed by quolls on narrow surfaces, reflecting a coupled use of
373 limb pairs at higher speeds. Coupled limb behaviour is likely associated with the corrective

374 forces and torques necessary to maintain stability on narrow surfaces (Cartmill, 1985). We
375 found greater changes in both lateral forces and the ability to produce corrective torques on
376 narrow, as compared to wide surfaces. Surprisingly, quolls were not only able to produce
377 corrective torques with simultaneous limb pairs, as previously shown in primates (Chadwell
378 and Young, 2015), but also with single limb surface contacts. These former corrective torques,
379 between left and right limbs of a girdle, likely explains why we observed a decrease in the
380 timing and distance of footfalls, suggesting that like primates, quolls expand their effective
381 grasp by gripping the substrate between limb pairs. But this latter single limb torque pattern
382 indicates a level of complexity in the forefeet which appear in some cases to grip the narrow
383 surface using a single foot and produce significant corrective ‘pulling’ torques.

384 *Cats and dogs: changes in gait parameters*

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

405 In contrast to quolls and cats, which both decrease their speeds on narrower surfaces, dogs
406 adopt higher speeds. These higher speeds are achieved via an increase in both stride
407 frequency and stride length, and a decrease in stance phase duration, leading to lower duty
408 factors on narrower substrates (Gálvez-López et al., 2011). Combined, the biomechanical
409 traits evident in dogs on narrow substrates suggest a reduced degree of static stability and an
410 increased reliance on dynamic stability. Static stability is the process by which an animal
411 remains stable because the forces and torques produced by gravity are near equal and
412 opposite to the ground reaction forces and moments (Lammers and Zurcher, 2011a).
413 However, at higher speeds it becomes increasingly difficult to maintain static stability.
414 Dynamic stability is the process whereby an animal remains stable due to the presence of an
415 angular momentum created by the cyclical motion of the limbs. This cyclical motion
416 produces a ‘gyroscopic effect’ where if a small disturbance changes the lean of a body, the
417 gravitational force produces a restoring torque about the fore-aft axis to maintain stability.
418 Truly arboreal species appear to avoid highly dynamically stable gaits (Lammers and
419 Zurcher, 2011a), which is likely related to the discontinuous, multi-dimensional, and
420 frequently unstable characteristics of arboreal habitats. This suggests larger terrestrial animals,
421 like dogs, may be at risk of increasing the probability of mistakes on narrow substrates,
422 though this remains to be shown. However, this may not be true in small arboreal specialists,
423 like chipmunks who exploit dynamic stability during locomotion (Lammers and Zurcher,
424 2011b).

425 *How do Northern quolls compare with other arboreal species?*

426 Kinematic comparisons of semi-arboreal Northern quolls with other arboreal species may help
427 to determine the extent to which quolls are selected for an arboreal versus terrestrial
428 environment. Like quolls, among 7 species of marsupials (opossums), relative velocities
429 increased with support diameter (Delciellos and Vieira, 2009), indicating a transition to
430 slower and more stable gaits on narrower structures. Similar control strategies to quolls were
431 evident among mouse lemurs, where limb contact time increased on narrow structures, likely
432 to aid stability through an increase in the time available to apply corrective torques (Shapiro
433 et al., 2016). Though this latter species did differ by showing an increase (rather than a
434 decrease in quolls) in the time between the trailing and leading limbs (P.lag) on narrow
435 surfaces.

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

442 A kinematic pattern common among arboreal specialists, particularly among primates, is the
443 use of a diagonal-sequence footfall pattern during walking, where the fore-left and hind-right
444 limbs (or vice-versa) are used in conjunction during stance (Muybridge, 1887, Prost, 1965,
445 Prost, 1969, Hildebrand, 1966, Hildebrand, 1977, Hildebrand, 1980, Hildebrand, 1985,
446 Vilensky and Larson, 1989, Lemelin and Grafton, 1998, Cartmill et al., 2002). This footfall
447 pattern is often thought to be beneficial when used in association with grasping extremities
448 when moving and foraging on thin flexible branches. This theory was tested among the grey
449 short-tailed opossum (*Monodelphis domestica*) and the woolly opossum (*Caluromys*
450 *philander*) – and showed that the latter species, which possessed more developed grasping
451 extremities, showed a greater use of diagonal-sequence walking gaits (Lemelin et al., 2003).
452 In the current study, this walking sequence was not observed among quolls, with P.lag values
453 approximating 0.5, indicating forefeet or hindfeet pairs are used (rather than diagonals)
454 during bounds and half-bounds. Thus despite at least some ability to grasp, quolls display gait
455 characteristics which suggest an important role of terrestrial locomotion and an increased
456 reliance on dynamic stability while on narrow structures.

457 Kinetic comparisons also showed differences between classically arboreal species and quolls.
458 Like quolls, the grey short-tailed opossum (*Monodelphis domestica*) showed both fore- and
459 hind limbs had equal roles in body weight support (vertical force) on inclined surfaces
460 (Lammers and Biknevicius, 2004). However, differences arose in propulsive forces (fore-aft):
461 in quolls, the hindlimbs produced the majority of the propulsive impulse whereas in
462 opossums, it was the forelimbs which exerted the greater propulsive impulse (Lammers et al.,
463 2006).

464 It has further been hypothesised that much of the kinematic changes to gait on narrow
465 supports are linked to a functional reduction in the vertical impulse, which would reduce
466 oscillations of the centre of mass and increase stability on narrow structures (Gálvez-López et
467 al., 2011, Schmitt and Lemelin, 2002, Schmitt et al., 2006, Young, 2009, Lemelin and

468 Cartmill, 2010). However, in the current study we found little or no evidence for a decrease
469 in vertical impulse on narrow supports which may function to reduce these oscillations. In
470 other species, vertical impulses were lower on arboreal supports for the common marmoset
471 (*Callithrix jacchus*) (Chadwell and Young, 2015) and the grey short-tailed opossum
472 (Lammers and Biknevicius, 2004), although the authors caution that in this latter species, this
473 may be attributed to differences in speed between the treatments.

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

488 *A biomechanical framework to predict the survival of key species*

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

495 Historically Northern quolls occupied both floodplains (terrestrial) and rocky (semi-arboreal)
496 habitats. Our biomechanical analyses suggest that cats and dogs are likely superior in
497 terrestrial environments, owing to their larger body size and greater speeds (Gálvez-López et
498 al., 2011). This may partially explain the declines and/or reduced populations of Northern

499 quolls in these terrestrial environments (Oakwood, 2000). Conversely, quolls appear to have
500 biomechanical characteristics consistent with a stability advantage at higher speeds on narrow
501 supports when compared to cats and dogs (Gálvez-López et al., 2011), likely explaining why
502 the decrease in quoll populations in semi-arboreal habitats (such as rocky outcrops) has not
503 been as severe (Oakwood, 2000). However, quolls did not show many of the characteristics
504 common in truly arboreal specialists (e.g. diagonal sequence gaits) such as opossums, which
505 may explain why populations of quolls are showing more obvious signs of decline than other
506 native species such as possums (Woinarski et al., 2001). Quolls appear to share a larger
507 percentage of their performance space with cats and dogs, and this overlap, combined with
508 reductions in habitat complexity, may be directly related to their declining population on
509 mainland Australia.

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

517 **Acknowledgements**

518 We thank members and volunteers of the Wilson Performance Lab for assistance with
519 running the experiments in the field. We also thank the Anindilyakwa Land and Sea Rangers
520 of Groote Eylandt for their generous assistance, logistical support and use of laboratory
521 facilities. We also thank the traditional owners of Groote Eylandt for their generous support
522 and access to their land.

523 **Competing Interests**

524 The authors declare no competing interests.

525 **Funding**

526 This project was supported by the Anindilyakwa Land Council, a University of Queensland
527 collaboration and Industry Engagement Fund (UQ-CIEF) grant awarded to RSW, an

528 Australian Research Council (ARC) DECRA awarded to CJC (DEXX), an ARC Discovery
529 Grant awarded to RSW and CJC (DEXX), and an ARC Future Fellowship awarded to RSW
530 (FT150100492)

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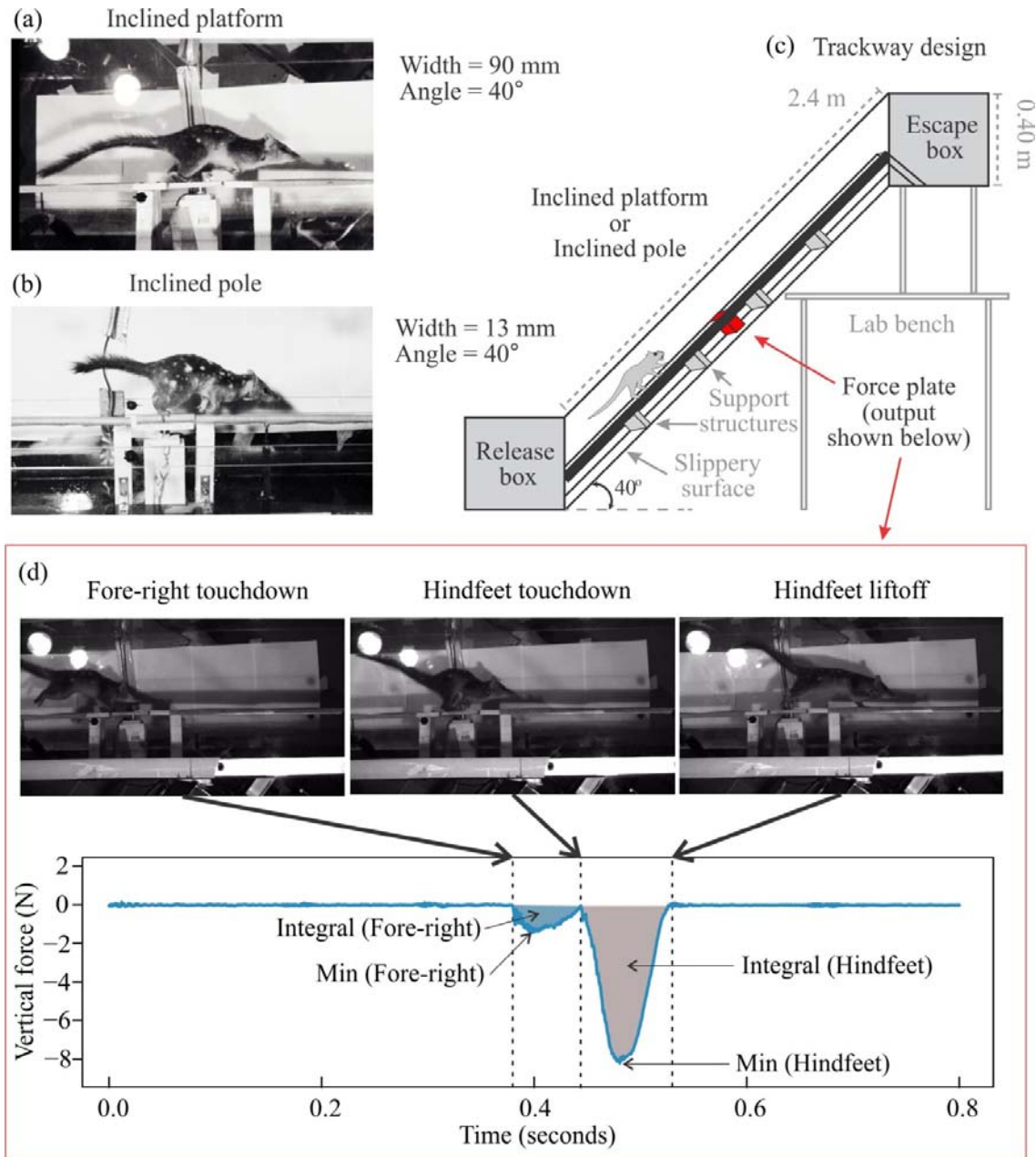
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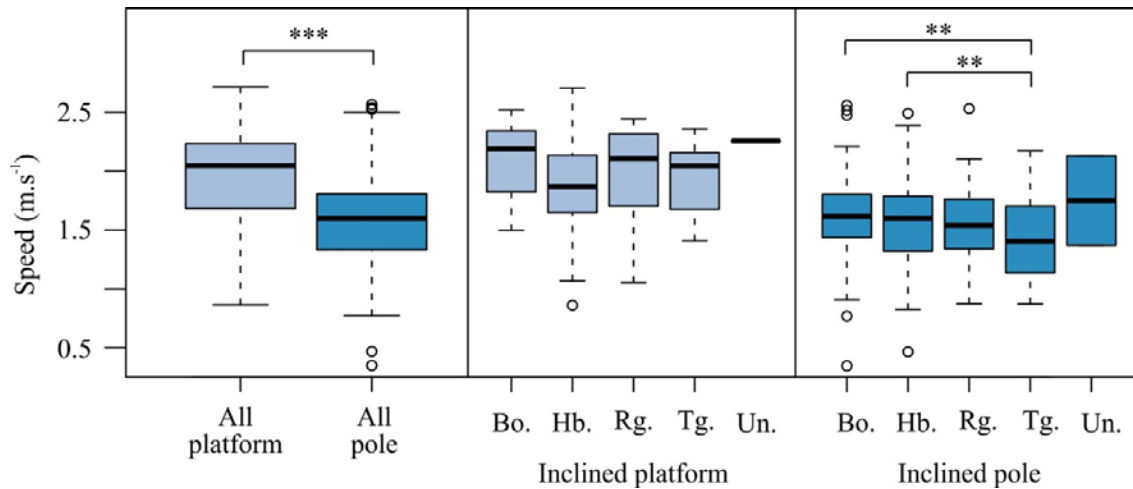
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654 **Figure 1. Schematic of experiment setup: a) Northern quoll (*Dasyurus hallucatus*)**
655 **running on inclined platform, b) quoll running on inclined narrow pole, c) schematic of**
656 **custom made experimental setup showing location of force plate, and d) vertical**
657 **substrate reaction force trace over time for a single forelimb followed by both hindlimbs**
658 **with representative images shown above. Shaded regions represent integral with respect**
659 **to time (impulse) for the fore-right (blue) and hind-left and hind-right combined (grey).**

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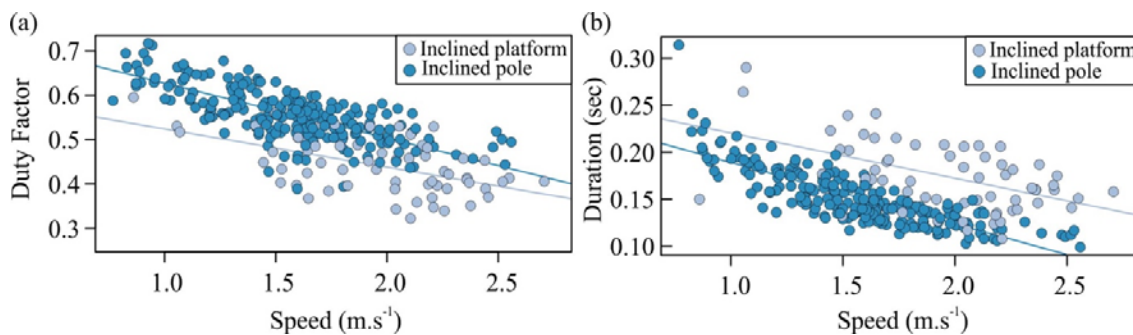
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662 **Figure 2. Variation in speed with surface and gait in Northern quolls (*Dasyurus***
663 ***hallucatus*). Speed varies significantly between the surfaces and with gait choice. Bo –**
664 **Bound, HB – Half bound, Rg – Rotary gallop, Tg – Transverse gallop, Un – Unknown.**
665 ***** indicates $P < 0.001$, ** indicates $P < 0.01$. Boxes represent the median, with hinges**
666 **representing the first and third quartiles; whiskers represent the 95% CIs, and dots**
667 **represent outliers.**

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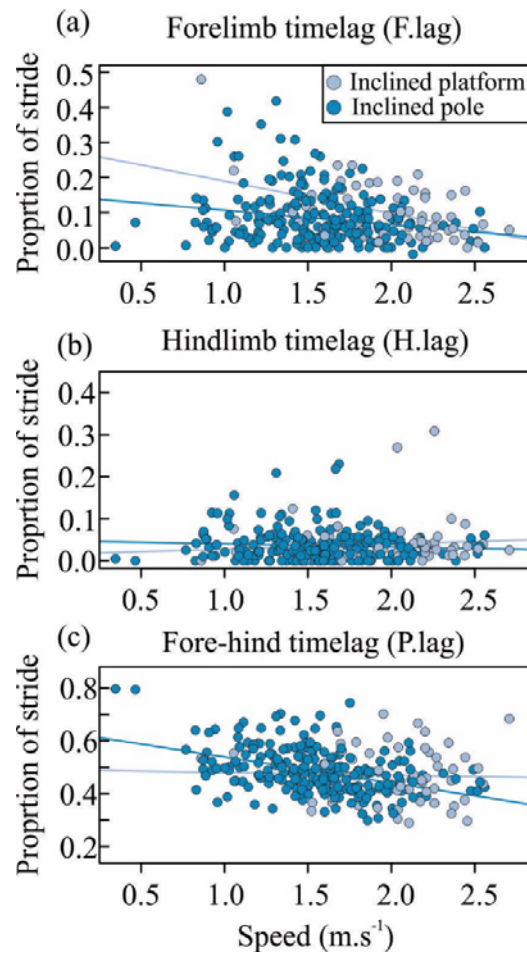
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672 **Figure 3. Relationship between speed and duty factor a) and speed and swing time and**
673 **b) for the inclined platform (light) and inclined pole (dark) conditions. Solid lines**
674 **indicate linear regression model for each condition.**

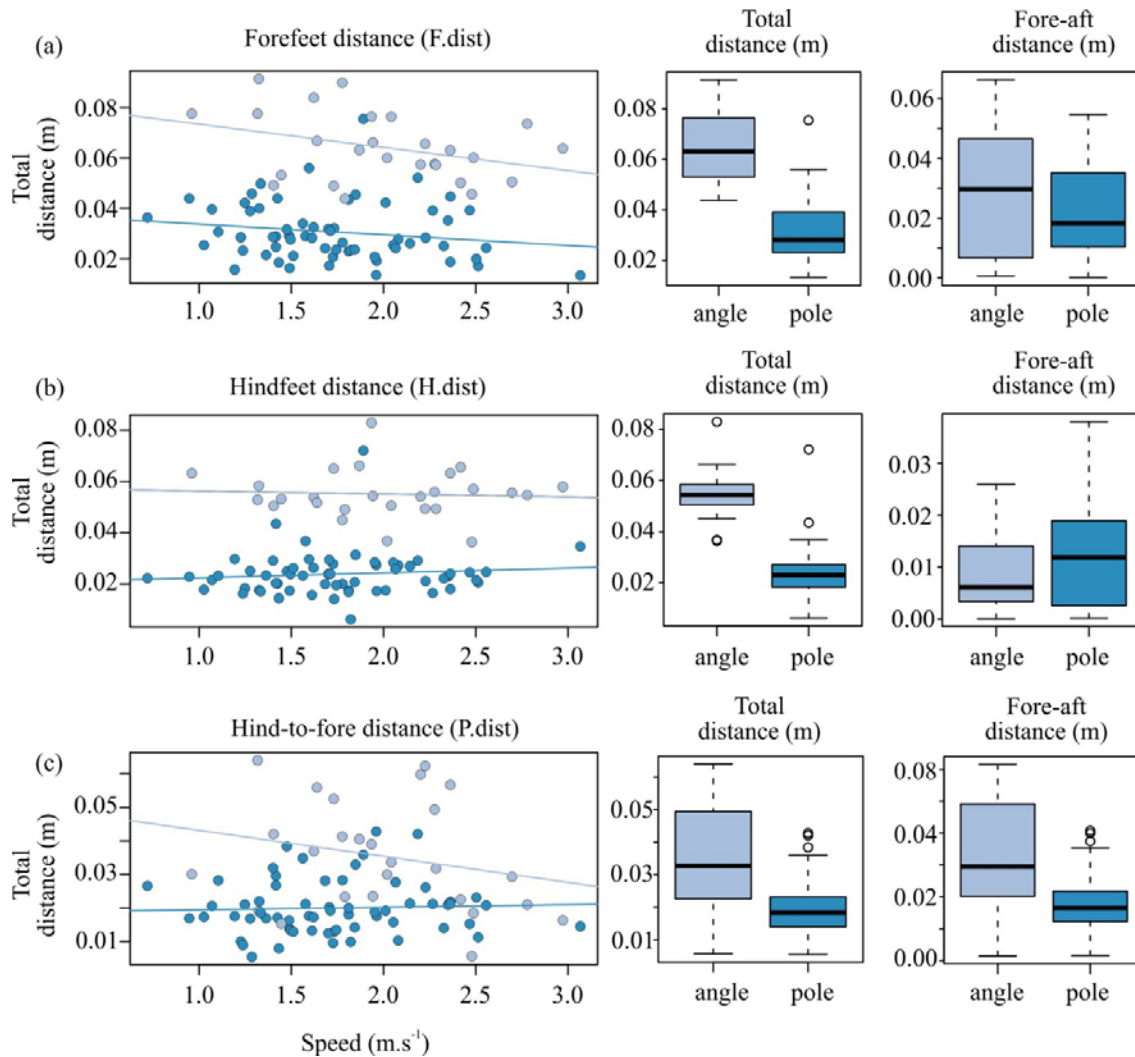
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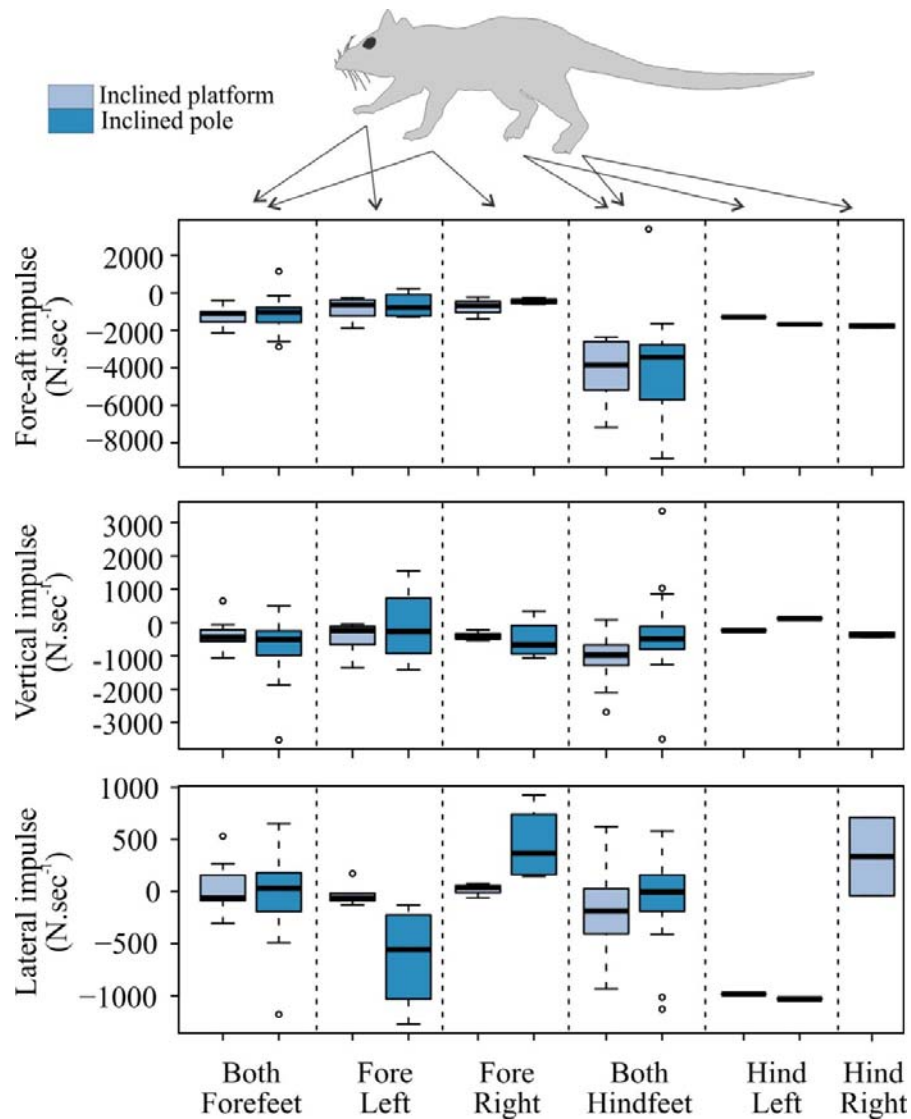
677 **Figure 4. Relationship between a) speed and forelimb timelag (F.lag), b) hindlimb**
678 **timelag (H.lag) and c) fore-hind timelag (P.lag) for the inclined platform (light) and**
679 **inclined pole (dark) conditions. Solid lines indicate linear regression model for each**
680 **condition. F.lag, H.lag, and P.lag were calculated as the temporal lag between the mid-**
681 **stances of the two forefeet, hindfeet, and averaged across the ipsilateral feet,**
682 **respectively divided by the total stride time.**

683



685 **Figure 5. Distances between foot falls; a) for the left and right forefeet (F.dist), b) the**
686 **left and right hindfeet (H.dist) and c) the mean distance between the forefoot pair and**
687 **the hindfoot pair (P.dist) for the inclined platform (light) and inclined pole (dark).**
688 **Given that lateral distances are constrained on the narrow inclined pole, we also report**
689 **the fore-aft distances between each foot pair.**

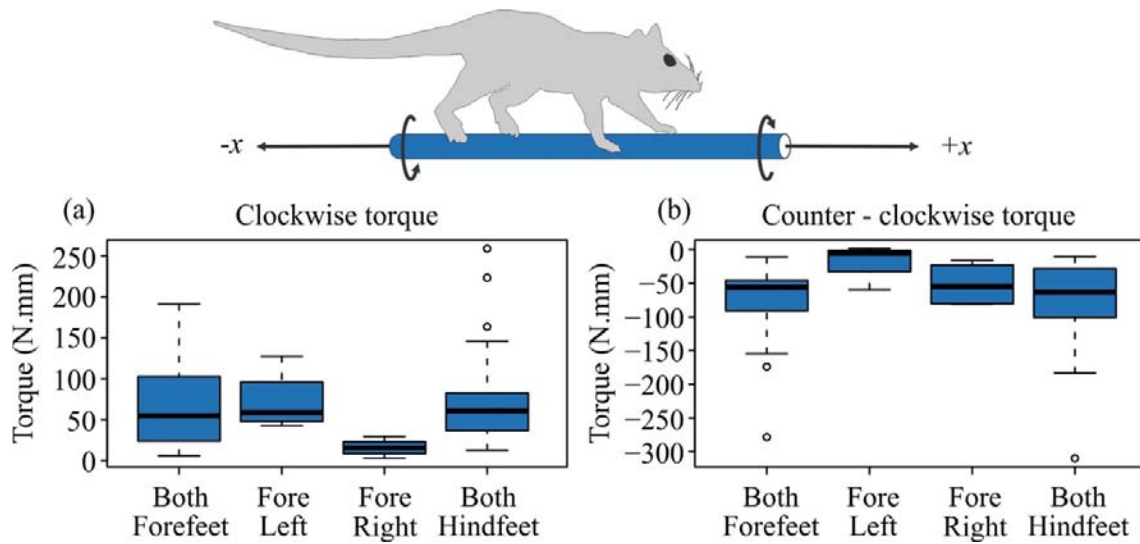
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692 **Figure 6. Impulse determining the relative contribution of each of the feet where**
693 **possible, or for pairs of feet where they touch the force plate simultaneously for the**
694 **Northern quoll (*Dasyurus hallucatus*). Impulse was calculated as the integral of the**
695 **force trace with respect to time for a) the fore-aft, b) vertical, and c) lateral directions**
696 **for inclined platform (light) and inclined pole (dark). Positive lateral impulses indicate**
697 **force directed towards the left and vice versa. Box and whisker plots as per Figure 2.**

698



699

700 **Figure 7. Maximum corrective torques in the a) clockwise and b) counter clockwise**
701 **directions on the inclined pole for the different combinations of foot limb pairs for the**
702 **Northern quoll (*Dasyurus hallucatus*). The direction of torques is consistent with the**
703 **right-hand rule. Sufficient data was not available for single hindlimbs. Box and whisker**
704 **plots as per Figure 2.**