

RESEARCH ARTICLE

Running faster causes disaster: trade-offs between speed, manoeuvrability and motor control when running around corners in northern quolls (*Dasyurus hallucatus*)

Melissa L. Wynn, Christofer Clemente, Ami Fadhilah Amir Abdul Nasir and Robbie S. Wilson*

ABSTRACT

Movement speed is fundamental to all animal behaviour, yet no general framework exists for understanding why animals move at the speeds they do. Even during fitness-defining behaviours like running away from predators, an animal should select a speed that balances the benefits of high speed against the increased probability of mistakes. In this study, we explored this idea by quantifying trade-offs between speed, manoeuvrability and motor control in wild northern quolls (*Dasyurus hallucatus*) – a medium-sized carnivorous marsupial native to northern Australia. First, we quantified how running speed affected the probability of crashes when rounding corners of 45, 90 and 135 deg. We found that the faster an individual approached a turn, the higher the probability that they would crash, and these risks were greater when negotiating tighter turns. To avoid crashes, quolls modulated their running speed when they moved through turns of varying angles. Average speed for quolls when sprinting along a straight path was around 4.5 m s^{-1} but this decreased linearly to speeds of around 1.5 m s^{-1} when running through 135 deg turns. Finally, we explored how an individual's morphology affects their manoeuvrability. We found that individuals with larger relative foot sizes were more manoeuvrable than individuals with smaller relative foot sizes. Thus, movement speed, even during extreme situations like escaping predation, should be based on a compromise between high speed, manoeuvrability and motor control. We advocate that optimal – rather than maximal – performance capabilities underlie fitness-defining behaviours such as escaping predators and capturing prey.

KEY WORDS: Performance, Predator–prey, Running speeds

INTRODUCTION

Movement underlies all animal behaviours – governing the use of home ranges, interactions with mates, competitors, predators and prey, and the negotiation of human-modified landscapes (Biewener, 2003; Wilson, 2005; Wilson et al., 2007; Börger et al., 2008; Nathan et al., 2008). Variation in movement speed directly affects an animal's energetic expenditure, time needed to complete a task, and the overall probability of success in an activity. But what determines how fast an animal chooses to move? Despite the importance of movement speeds, we still have no universal framework for understanding – and predicting – how fast or slow animals move under natural conditions.

Studies of optimal flight speed in birds and bats provide the foundations for a predictive framework of animal movement speed.

According to aerodynamic theory, the total mechanical power needed to propel a bird through the air is characterized by a U-shaped curve (Pennycuik, 1975), where energetic costs are greatest at both high and low speeds. Minimising these costs over time (Hedenstrom and Alerstam, 1995; Bruderer and Boldt, 2001) or distance (Pennycuik, 1975; Rayner, 1999) appears to drive the selection of flight speeds for most organisms. Similarly, studies of horses (Hoyt and Taylor, 1981) and mice (Chappell et al., 2004) reveal that over long distances these animals select sub-maximal speeds, allowing them to optimise their locomotor energetics (Pennycuik, 1975; Pagan et al., 2012). Yet, these studies focus on energetic efficiency, and tell us little about how individuals optimise speed in response to environmental variation (i.e. predation risk or food detectability) or physical constraints (i.e. motor control or manoeuvrability). A broader framework for understanding animal movement speeds must consider energetics, safety, motor control and manoeuvrability across the full spectrum of ecological contexts.

Most studies exploring the importance of locomotor performance to survival assume that animals move fastest when escaping predators (Bennett and Huey, 1990; Miles, 2004; Husak, 2006; Irschick and Meyers, 2007; Irschick et al., 2008). After all, there is no sense in optimising the energetics of running speeds if one does not survive long enough to reproduce. Animal movement speed is of course an important determinant of survival during predator–prey interactions (Bennett and Huey, 1990; Miles, 2004; Husak, 2006; Irschick and Meyers, 2007; Irschick et al., 2008), but the idea that animals should move at their maximal capabilities when being chased by a predator is based on an unrealistic assumption – that there is no cost associated with moving at maximal speeds. One simply has to watch any professional motor racing event to observe the substantial costs that occur when maximum speeds are used across all contexts. When the locomotor speeds of animals have been observed under natural conditions, studies reveal that animals rarely, if ever, use maximal performance, even when escaping from predators (Van Damme and Van Dooren, 1999; Irschick, 2003; Husak, 2006; McElroy et al., 2012). These slower, modulated speeds should not be surprising. Biomechanical constraints on movement mean that mistakes are more likely to occur at high speeds – and in certain contexts like running away from predators, these slips or falls may increase the likelihood of death.

Movement speeds, even during extreme situations like escaping predation, should be based on a compromise between speed, manoeuvrability (Howland, 1974) and motor control, or the probability of making mistakes (Trommershäuser et al., 2003; Landy et al., 2012; Wolpert and Landy, 2012). Manoeuvrability allows animals to rapidly change direction and negotiate obstacles (Jindrich and Qiao, 2009); strategies likely to be crucial during predator escape or prey capture. Manoeuvrability of an animal is defined by: its rate of change in direction, or its turning rate (angular velocity),

School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia.

*Author for correspondence (r.wilson@uq.edu.au)

Received 7 August 2014; Accepted 25 November 2014

its turning path (radius of curvature) and its rate of change in circular motion (centripetal acceleration) (Combes et al., 2012). Making mistakes such as slips, foot misplacements and falls whilst moving at high speeds can also compromise an animal's ability to perform survival-related tasks. Motor control is the complex interaction between sensory and musculoskeletal systems during locomotion (Biewener, 2003) and determines an animal's probability of making mistakes. Several studies indicate that animals may modulate their movement speeds to maintain control through complex habitats. For example, Hyams and colleagues found that white-footed mice (*Peromyscus leucopus*) decreased their speed in high-complexity habitats, as obstacles got in the way of running fast (Hyams et al., 2012). Similarly, arboreal *Anolis* lizards were found to decrease their speeds by up to 50% when manoeuvring around tight corners (Higham et al., 2001). In complex habitats – where obstacles and rough terrain may affect the probability of mistakes – an animal should therefore optimise its movement speed and turning radius whilst maintaining motor control. However, in more open and flat habitats where there are fewer obstacles, the optimal movement speed is more likely to approach the maximal capabilities of the animal.

The first step to developing a framework for predicting animal movement speeds during predator–prey encounters is to determine the interaction between speed, manoeuvrability and motor control. In this study, we explored these trade-offs in wild northern quolls (*Dasyurus hallucatus*, Gould 1842) to discover how they balance these competing constraints on locomotion. Northern quolls offer an excellent model system for exploring trade-offs between speed, manoeuvrability and motor control because their primary method of escape from their main predators of birds, snakes and dingoes is to out-maneuvre and out-run them. Quolls are also voracious predators that rely upon their stealth, speed and agility to capture their prey of insects, mammals, reptiles, amphibians and birds, and their terrestrial and arboreal lifestyle requires them to constantly move through a varied and unpredictable habitat. First, we explored how running speed affected their probability of making a mistake when negotiating corners of differing magnitudes. We expected that higher running speeds would increase the likelihood of slipping or tripping, and that this effect would be greater when negotiating tighter turns. Second, we aimed to examine how animals modulate their speed choice when running around corners of differing degrees – we expected that animals would decrease their running speeds when negotiating tighter turns. Finally, we aimed to explore how an individual's morphology affects their manoeuvrability and ability to run around corners – we expected that larger individuals and those with smaller feet would be poorer at negotiating tighter corners and would need to take these turns at lower speeds.

RESULTS

Sex, speed and morphology

Maximum sprint speed was not significantly correlated with body mass ($F_{1,64}=3.68$, $R^2=0.05$, $P=0.059$) or body shape [principal component (PC)_{shape}; $F_{1,64}=0.473$, $R^2=0.01$, $P=0.494$]. Males exhibited an average body mass of 499.7 ± 161.2 g, which was significantly greater than females (308.8 ± 75.8 g; $F_{1,57}=21.57$, $P<0.001$). Males also possessed greater overall body sizes ($F_{1,57}=33.5$, $P<0.001$). No other metrics of locomotor performance or kinematic variables differed between the sexes (maximum sprint speed V_{max} , $P=0.87$; turning speed V_{turn} , $P=0.194$; angular velocity ω_{turn} , $P=0.803$; turning radius r_{turn} , $P=0.877$) and were thus combined in all analyses.

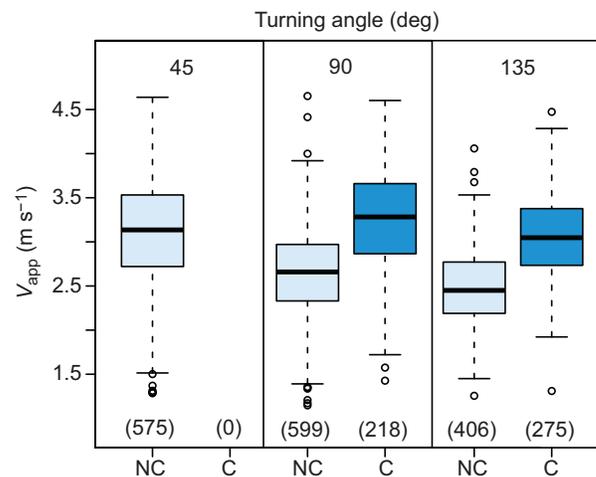


Fig. 1. Effect of approach speed on the probability of crashing (C) or not crashing (NC) through all three turning angles (45, 90 and 135 deg). Faster approach speeds (V_{app}) resulted in more crashes at all angles (except 45 deg, where no crashes were observed). V_{app} significantly decreased the tighter the turn became ($F_{2,2061}=104.73$, $P<0.001$). Boxes represent the median with hinges representing the 1st and 3rd quartiles. Whiskers represent the 95% confidence interval (CI) and circles represent outliers. Sample sizes are shown in parentheses under each plot.

Probability of a crash

The probability of crashing during a turn was significantly affected by both approach speed (V_{app} ; $F_{1,2061}=169.78$, $P<0.001$) and turning angle ($F_{2,2061}=104.73$, $P<0.001$) using a within-subjects one-way ANOVA, with subject included as the error term. Quolls experienced a greater probability of crashing when running through a turn when they approached the corner at high speeds and when running around tighter turning angles (Fig. 1). The effect of approach speed on the probability of crashing was also dependent on the turning angle ($F_{2,2061}=46.18$, $P<0.001$; two-way within-subjects ANOVA, with subject included as the error term), such that the magnitude in approach speed for crashes and non-crashes varied with each turning angle. The probability of crashing was also significantly affected by body size, with larger quolls crashing more frequently ($F_{1,2070}=4.074$, $P=0.0433$).

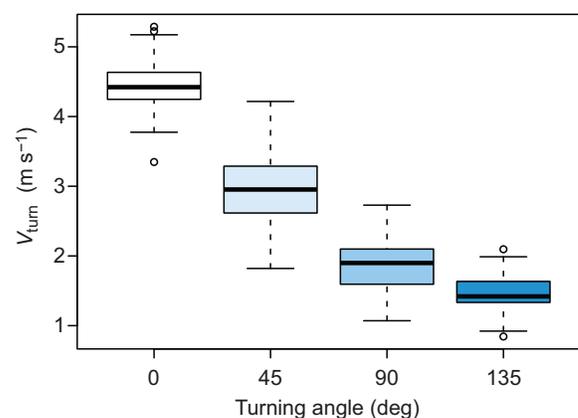


Fig. 2. Relationship between average turning speed and turning angle. Turning speed (V_{turn}) decreased significantly as angle increased. A Tukey HSD *post hoc* test suggested all turning angles were significantly different from each other. Boxes represent the median with hinges representing the 1st and 3rd quartiles. Whiskers represent the 95% CI and circles represent outliers.

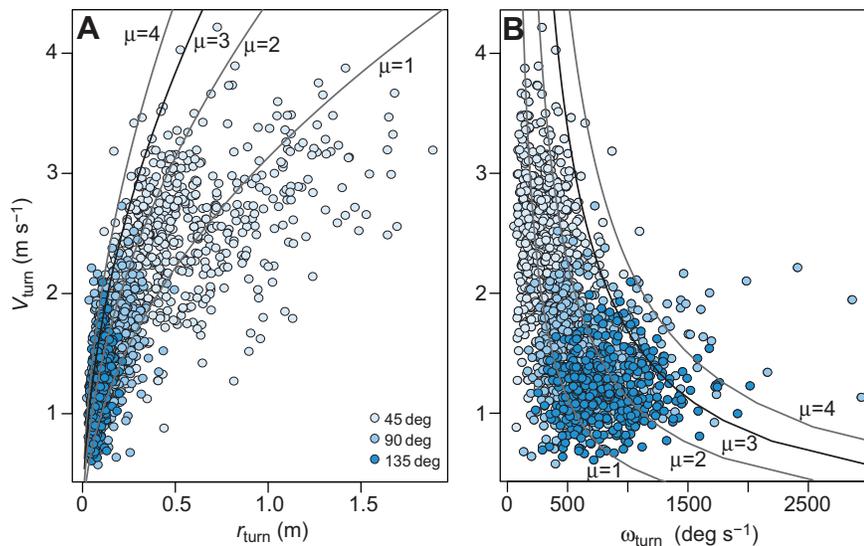


Fig. 3. Velocity data for all quolls running around all turns ($N=1580$). See Fig. 6 for racetrack diagram. (A) The relationship between turning radius (r_{turn}) and forward velocity through the 135, 90 and 45 deg turns (V_{turn}). The solid lines represent the relationship between turning radius and horizontal velocity predicted by the friction limit model, with static coefficients of friction between 1 and 4. (B) The relationship between turning rate, represented as angular velocity (ω_{turn}) of the horizontal speed vector with forward velocity through the turn. The solid lines represent the relationship between turning radius and horizontal velocity predicted by the friction limit model, with static coefficients of friction of between 1 and 4.

Speed through a turn

We defined turning speed as the average forward velocity during the turn. When considering only successful turns (those not resulting in a crash) and selecting the fastest turn speed per individual at each turning angle ($N=177$), average turning speed significantly decreased as the magnitude of the turn angle increased ($F_{3,174}=923$, $P<0.001$; Fig. 2; one-way within-subjects ANOVA with subject included as the error term). Turning speed was significantly different at all turning angles (Tukey *post hoc* test). Larger quolls were faster around the 45 deg ($F_{1,57}=8.183$, $R^2=0.12$, $P=0.006$) and 90 deg turns ($F_{1,57}=10.94$, $R^2=0.16$, $P=0.002$), but there was no effect of size at 135 deg turning angle.

The lower running speed through the tighter turns is probably attributable to limitations in both the turning rate and turning radius. When all successful turns were examined ($N=1580$; Fig. 3), quolls reduced their speed more during turns with a smaller radius than during turns with a larger radius. Four different models for the coefficient of friction were used to compare these results in order to determine how grip limits turning speed. Here, the coefficient of friction with the ground is estimated by $\mu=V^2/rg$ (Alexander, 1982), where V is the turning speed, r is the turning radius and g is gravitational acceleration. The data show a coefficient of friction for the quoll between 3 and 4, though this agreement is strongest for smaller turning radii. Similarly, turning rate was limited by speed, whereby the maximum angular velocity achieved decreased at higher turning speeds (Fig. 3B). These data also agree closely with a coefficient of 3–4, given a relationship between angular velocity, turn radius and speed of $\omega_{\text{turn}}=r_{\text{turn}} \cdot V_{\text{turn}}$. Thus, in order to avoid crashes, quolls reduce their speed when running through turns to allow for an increased turning rate and decreased turning radius.

We found the interaction between turning radius, turning rate and turning speed is complex. Again, considering only successful turns, and selecting the fastest turn speed per individual at each turning angle ($N=177$), turning radius was significantly negatively associated with turning rate ($F_{1,175}=1597$, $R^2=0.90$, $P<0.001$; Fig. 4), which means quolls turned at a faster rate through tighter turns but at a slower rate through wider turns. Faster turning speeds (Fig. 4, red circles) occurred at larger radii compared with slow turning speeds (Fig. 4, blue circles), but this was associated with reduced turning rates. Conversely, quolls with a slower turning speed could turn through a smaller radius, and could do so at a higher turning rate. Therefore, it is the turning rate, the turning radius and the

interaction between the two parameters ($\omega_{\text{turn}} \cdot r_{\text{turn}}$, $F_{1,115}=1498$, $P<0.001$) that determines the speed at which quolls turn.

Morphology and manoeuvrability

Residual turning rate was weakly, but significantly positively correlated with body mass ($F_{1,57}=7.817$, $R^2=0.10$, $P=0.007$) and body size ($F_{1,57}=6.797$, $R^2=0.09$, $P=0.011$), suggesting – contrary to our hypothesis – that larger quolls may be marginally more manoeuvrable. This did not appear to be related to sex, as there were no significant differences in manoeuvrability between males and females ($F_{1,57}=2.619$, $P=0.111$). Similarly, overall body shape, which was the second dimension from a principal component

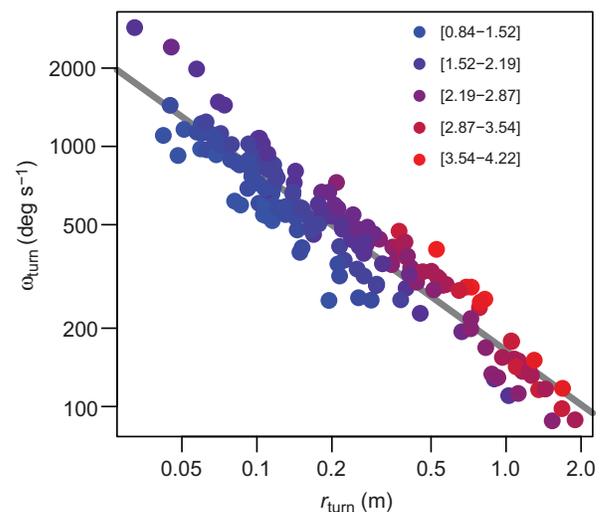


Fig. 4. The negative log-log correlation between turning rate (angular velocity, ω_{turn}) and turning radius (r_{turn}) and the interaction of turning speed (V_{turn}). V_{turn} is represented in colour, ranging continuously from blue (slowest speeds) to red (fastest speeds). Quolls turned at a faster rate through tighter turns, but at a slower rate through wider turns. Additionally, quolls running at faster turning speeds turned at larger radii than those running at slow turning speeds, but this is associated with reduced turning rates. Turning speed is slightly more limited by turning rate (ω_{turn} , $F_{1,115}=2078$, $P<0.001$) than it is by turning radius (r_{turn} , $F_{1,115}=1746$, $P<0.001$); however, both significantly influenced speed. Therefore, it is the turning rate, the turning radius and the interaction between the two ($\omega_{\text{turn}} \cdot r_{\text{turn}}$, $F_{1,115}=1498$, $P<0.001$) that determines the speed at which quolls turn.

Table 1. Percentage of independent effects for each size-corrected morphological variable with manoeuvrability

	% Independent effects
Body length	1.51
Tail length	9.95
Tail diameter	8.35
Foot length	54.13
Tibia–fibula length	1.35
Radius–ulna length	1.23
Head width	22.19
Head length	1.25

Manoeuvrability was calculated from residuals of the log-linear relationship between turning rate and turning radius.

analysis performed on all morphological parameters, was not significantly related to manoeuvrability ($F_{1,57}=1.813$, $R^2=0.01$, $P=0.183$).

We were interested in the effect of body shape on manoeuvrability, but as morphological variables were possibly collinear, we examined these variables using two different methods. First, multiple linear regression indicated that foot length was the strongest predictor of manoeuvrability ($P=0.023$), suggesting quolls with relatively large feet were able to turn faster at any given radius. Second, we used the function `hier.part.R` from the ‘`hier.part`’ package in R to calculate a list of relative importance for these size-corrected segment lengths with manoeuvrability (Table 1). This method also supported foot size as the most important metric describing manoeuvrability, explaining 54% of the total variance. Head width appeared to be the second most important variable, with relatively wide heads explaining 22% of the variance in manoeuvrability.

DISCUSSION

We investigated the consequences and limitations of speed and manoeuvrability when negotiating corners of varying angles using wild northern quolls (*D. hallucatus*). First, we explored how running speed affected the probability of mistakes, and we expected higher running speeds to increase the likelihood of errors. Supporting this idea, we found that the speed at which a quoll approached a turn affected the probability of a resultant crash; the faster an individual approached a turn, the higher the probability that it would crash, and these risks were greater when negotiating tighter turns. The average approach speed into a corner decreased from around 3.0 m s^{-1} for 45 deg turns to around 2.5 m s^{-1} for 135 deg turns; in fact, the average approach speed for successfully negotiated 45 deg turns was similar to the average speed that led to crashes for 135 deg turns. Thus, our data clearly indicate that northern quolls must modulate their speeds when approaching corners of varying tightness if they are to avoid potentially costly crashes. To avoid such crashes, we found quolls modulated their running speed when they moved through turns of varying angles. Average speed for quolls when sprinting along a straight path was around 4.5 m s^{-1} but this decreased to speeds that were 33% of straight-line trials when running through 135 deg turns. Similarly, three different species of *Anolis* lizards also modulated their speeds when running around corners of varying magnitude, and decreased their running speeds to around 48–79% of their straight-line speeds when negotiating turns of 90 deg (Higham et al., 2001).

Animals may employ turning or twisting manoeuvres to avoid obstacles or dangers, yet at faster speeds we have shown that this type of motion can result in collisions. Depending on context, a loss of footing may cause injury or death. Turning when running requires an animal to change the main vector of motion and rotate its body

to the new orientation (Jindrich and Full, 1999). This means that a turning animal must overcome its inertia and undergo angular motion (Zollikofer, 1994), and it must therefore produce greater stabilising forces when turning than are required when running in a straight line. Thus, the constraints placed on an animal's musculoskeletal system whilst manoeuvring can clearly limit locomotion at fast speeds (Jindrich and Qiao, 2009). Because such slips, trips and falls are likely to be the final causal agents of a failed attempt to escape a predatory attack, it seems surprising that biologists rarely, if ever, analyse the determinants of mistakes or quantify their direct ecological consequences. This seems an important oversight in studies of animal locomotor function. Even though we did not specifically quantify the survival costs of crashing when negotiating a turn in our study, it is likely that animals must select their speeds when running away from predators based on the competing demands of rapidly putting distance between themselves and the threat (running at high speed) and increasing the potential probability of crashing when moving too fast (maintaining control).

An animal running around a curve at a given velocity will only be able to deflect the direction of the velocity vector of its centre of mass and realign it with the new heading axis at the end of the turn if its feet maintain a minimum coefficient of friction with the ground and if its limbs are able to withstand the increased requirement to generate centripetal acceleration (Greene, 1985; Tan and Wilson, 2010). We have shown that for quolls the coefficient of friction is high relative to that of ponies (0.6–0.7), and even cheetahs (1.3) running over compliant grassed surfaces (Tan and Wilson, 2010; Wilson et al., 2013). This may be due in part to the thin rubber matting used on the racetrack in our study, but is also likely to be due to the soft pads and long claws found on the hindfeet and forefeet of northern quolls. However, this frictional limitation is only supported at smaller radii. At larger radii, few quolls operate near the frictional limit and, instead, limitations may shift toward the ability of the limbs to produce force, as has been shown for ponies (Tan and Wilson, 2010).

We extracted an individual metric of overall manoeuvrability using residuals from the negative relationship between turning radii and angular velocity. We used this metric to explore the morphological determinants of manoeuvrability by assuming that highly manoeuvrable animals were those individuals that could attain higher angular velocities for any given turning radii. We expected that larger individuals would be poorer at negotiating tighter corners at higher speeds, as larger body size may impart a greater angular momentum on to the body, requiring a larger absolute force to deflect and realign the body's velocity vector. However, we found little evidence to support this, with the suggestion that the opposite may perhaps be the case among quolls (although limited variation in manoeuvrability was explained by this relationship), proposing larger body size may actually benefit manoeuvrability. The underlying mechanism for this is unclear but may lie in an increase in footpad contact area with the ground, as greater applied loads generally accompany larger body masses. Supporting this, we found that individuals with larger relative foot sizes were more manoeuvrable than individuals with smaller relative foot sizes. An increased relative area of the foot would relax the frictional limitation of turning rate for these quolls.

Studies of animal performance and its ecological consequences still overly rely on the assumption that animals use their maximum locomotor capabilities during key survival, reproductive and foraging behaviours (Irschick and Garland, 2001). But field observations show that animals rarely, if ever, move at these maximum speeds in nature (Irschick, 2003; Husak, 2006). Animals

have been shown to perform at near-maximal ability in situations critical to fitness, such as evading a predator (85–90% of maximal) (Van Damme and Van Dooren, 1999), while speeds are lower when chasing prey (70%) (McElroy et al., 2012) and defending territories (50%), with animals moving slowest during undisturbed locomotion throughout their habitat (15%) (Irschick and Garland, 2001; Husak and Fox, 2006; Pagan et al., 2012). In our study, we have shown that biomechanical constraints on movement mean that mistakes are more likely to occur at high speeds – and it is likely that in certain contexts, these slips or falls could lead to death. Movement speeds, even during extreme situations like escaping predation, should be based on a compromise between high speed, manoeuvrability and motor control. We advocate that optimal – rather than maximal – performance capabilities underlie fitness-defining behaviours such as escaping predators and capturing prey; and we encourage those biologists interested in the ecological basis of animal function, a field that has cultivated more than 2000 studies of maximum performance over the last 10 years alone, to explore the evolutionary and ecological basis of optimal performance.

MATERIALS AND METHODS

Northern quolls (*D. hallucatus*) were trapped on Groote Eylandt, Northern Territory, Australia, throughout July and August 2013. Animals were captured using Tomahawk original series cage traps (20×20×60 cm; Tomahawk ID-103, Hazelhurst, WI, USA) that were baited using commercially available dog food. Baited traps were set at sunset, and checked before sunrise to minimise the stress of capture. During the study period, a total of 66 individual quolls (35 males, 31 females) were captured and immediately transferred to the Anindilyakwa Land and Sea Rangers research station for testing. All quolls were individually identified using a permanent, unique Trovan microchip (Trovan nano-transponder ID-100, Keysborough, Australia) implanted subcutaneously between the shoulder blades. Research methodology was approved by the University of Queensland animal ethics committee (SBS/404/12/APA) and was conducted under permit from the Northern Territory Parks and Wildlife Commission (permit number: 47603).

Body mass of all individuals was measured (± 1 g) using digital scales (Homemaker electronic kitchen scale). Morphological variables were recorded using digital calipers (Whitworth, Brisbane, Australia; ± 0.01 mm; Fig. 5): head length (from nuchal crest to tip of snout), head width (widest point of jaw), body length (nuchal crest to base of tail), tail length (base to tip of tail), maximum tail width (diameter), left and right hindfoot lengths (heel to claw base), hindlimb lengths (tibia–fibula) and forelimb lengths (radius–ulna). We then conducted a principal components analysis on all measures of morphology using the `princomp.R` function in R. The first component of the PCA explained 83% of the variation observed and, because all vectors loaded in the same direction, this represented an overall measure of body size (Table 2). The second component of the PCA explained 5% of the variation and this was indicative of body shape. All performance measures were tested within 6 h of capture. Maximum sprint speed was always recorded first for each animal. To aid in subsequent frame-

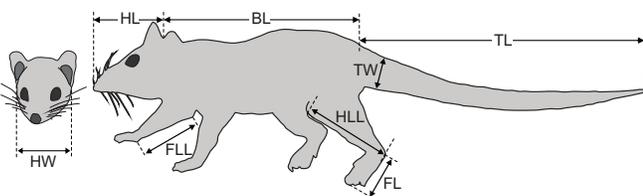


Fig. 5. Diagram of a lateral view of a northern quoll (*Dasyurus hallucatus*). Morphological variables were measured using digital calipers (± 0.01 mm): HL, head length (from nuchal crest to tip of snout); HW, head width; BL, body length (from nuchal crest to base of tail); TL, tail length; TW, tail width; FL, hindfoot length (heel to claw base); HLL, hindlimb length (tibia–fibula); and FLL, forelimb length (radius–ulna).

Table 2. Principal component loadings for the northern quolls ($N=66$) used in the study

Variable	PC1	PC2
Body length	-0.30393	-0.19187
Tail length	-0.26546	0.236761
Tail diameter	-0.27035	-0.54802
Right foot length	-0.30825	-0.21566
Right tibia–fibula length	-0.32213	0.023624
Right radius–ulna length	-0.3186	0.183051
Left foot length	-0.3091	-0.14424
Left tibia–fibula length	-0.32079	0.057841
Left radius–ulna length	-0.32152	0.139826
Head width	-0.31392	-0.14582
Head length	-0.25181	0.679161
Proportion of variance	0.829	0.051

by-frame analyses of video recordings, a marker (4×4 cm) was fixed to the dorsal side of the neck of each quoll.

Maximum sprint speed

Maximum sprint speed was obtained by encouraging an individual to run down a straight wooden racetrack that was 4 m long and 1 m wide, with wooden sides 1.2 m high. The floor of the racetrack was lined with a thin, rubber mat that provided traction. The width of the racetrack allowed the experimenter to chase the quoll along the racetrack to elicit maximal sprint speeds. A high-speed digital camera (Casio EXILIM HS EX-ZR200, Casio, Tokyo, Japan) was positioned 2 m above the racetrack over the central 1 m to record dorsal views at 240 frames s^{-1} . A maximum of five runs were recorded for each individual quoll. Videos were analysed using the Tracker video analysing software (Open Source Physics, Boston, MA, USA), which captured the position of the marker in each frame over the 1 m section. Instantaneous velocities were calculated from the raw positional data for each of the five sprints, and smoothed by a cubic smoothing spline (`spaps.m`, TOL=0.05) using a custom-written script in MATLAB R2013a (MathWorks, Natick, MA, USA). This spline reduces the noise in the instantaneous speed data without shifting or skewing the data, with a mean absolute instantaneous difference between smoothed and raw data of ~ 0.07 m s^{-1} . An average velocity over the entire 1 m central section of the racetrack was calculated for each sprint, and the fastest single value of these was used as a measure of maximum sprint speed, V_{max} (m s^{-1}), for each individual.

Manoeuvrability

The manoeuvrability of each individual quoll was assessed by quantifying its ability to run around corners of 45, 90 and 135 deg. Manoeuvrability was measured in a modified racetrack, consisting of two mobile ‘wings’. Each wing (of length 3.4 m, height 1.23 m and width 0.4 m) was made from wood, and was tapered and hinged at the centre with one of three removable angle structures (45, 90 and 135 deg; Fig. 6). The width at the centre point of the runway, or the radius of the given turning circle, was 0.15 m to allow individuals to manoeuvre around the turn, without providing excess space. The floor of the racetrack was lined with a thin rubber mat to provide traction and was cleaned daily to remove obstructions. As above, each trial was filmed dorsally at 240 frames s^{-1} with a high-speed digital camera (Casio EXILIM HS EX-ZR200) positioned 3 m directly above the midpoint of the racetrack. Individual quolls were released at one end of the racetrack via a trap-door, and were allowed one habituation trial run/walk to familiarise themselves with the turning angle on the racetrack before being encouraged to run around the corner. One experimenter at the start position of the racetrack encouraged the quoll through the turn by following it with a polystyrene block the width of the track, attached to a pole. Once the quoll reached the start position at the other end of the racetrack, this method was then repeated in the opposite direction to ensure both left and right turns were represented. Quolls were run a maximum of 20 times with a minimum of 30 min rest time between successive trials at each angle. To minimize the effects of motor learning and time, the order of testing across the three turning angles was randomised at the start of every day.

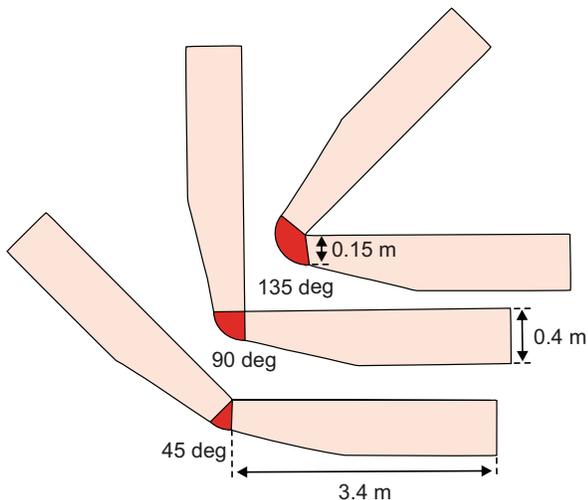


Fig. 6. Experimental racetrack setup for testing the manoeuvrability of northern quolls. The racetrack consisted of two mobile 'wings' made from pine (length 3.4 m, height 1.23 m, width 0.4 m), hinged at the centre with one of three removable angle structures, at 45, 90 and 135 deg, to allow for three turning angles. The width of the wings was tapered at the centre point of the runway (the radius of the given turning circle) to a distance of 0.15 m.

The position of the marker on each quoll was tracked using Tracker video analysing software (Open Source Physics) for a distance of 40 cm either side of the given turning angle (chosen as the minimum distance from where animals changed their trajectory) and smoothed by a mean squared error algorithm (TOL=0.05) using custom-written script in MATLAB R2013a (MathWorks). The start and end of a turn were manually defined by a change in heading of the quoll's trajectory (θ_v ; typically <5 deg).

Each trial was characterized by five variables: (i) approach speed, V_{app} ($m\ s^{-1}$), the average of all instantaneous velocities from 40 cm before the turn until the start of the turn; (ii) turning speed, V_{turn} ($m\ s^{-1}$), the average of all instantaneous velocities throughout the turn; (iii) the radius of the turn, r_{turn} , for each run, determined by circle fitting positional data of the path taken by the quoll throughout the turn; (iv) the angular velocity, ω_{turn} ($deg\ s^{-1}$), calculated as the rate of change in heading ('turning rate') through the turn; and (v) the probability of a crash, defined as a presence or absence value when the quoll contacted a wall, and when the minimum instantaneous velocity, V_{min} , dropped below $0.4\ m\ s^{-1}$. An example of a successful and unsuccessful (crash) turn through a corner is provided in supplementary material Movies 1 and 2.

We used the residuals from the log-linear relationship between turning rate and turning radius to produce an individual metric of manoeuvrability, working on the assumption that quolls that were able to turn faster at any given radius were more manoeuvrable. The mean residual for all three angles was determined per individual and compared with body size and shape. To further explore the influence of body segment lengths on manoeuvrability, we used size (PC1)-corrected segment lengths, averaging both the right and left lengths together, to reduce parameter size to eight segment lengths. We then compared models with all subsets of size-corrected segment lengths against manoeuvrability, using the package 'leaps' in R, which supported using a model including all eight variables.

Statistical analyses

All statistical analyses were implemented using the base package functions in R Studio (R Studio Inc., v. 0.97.551, 2013). ANOVA was performed using the `aov.R` function in the base package of R. Morphology (PC_{size}) was included in each model as an interaction term, and individual ($N=66$) was used as a random factor in each analysis.

Acknowledgements

We thank members and volunteers of the Wilson Lab for assistance with running the experiments. We also thank the Anindilyakwa Land and Sea Rangers of

Groote Eylandt for their generous assistance, logistical support and use of laboratory facilities. We also thank the traditional owners of Groote Eylandt for their generous support and access to their land.

Competing interests

The authors declare no competing or financial interests.

Author contributions

M.L.W., A.F.A.A.N., C.C. and R.S.W. conceived and designed the study; M.L.W. and A.F.A.A.N. collected the data; M.L.W. and C.C. analysed the data; M.L.W., A.F.A.A.N., C.C. and R.S.W. wrote the paper.

Funding

This project was supported by the Anindilyakwa Land Council, a University of Queensland Collaboration and Industry Engagement Fund (UQ-CIEF) grant awarded to R.S.W., an Australian Research Council (ARC) Discovery Grant awarded to R.S.W., and an ARC Discovery Early Career Researcher Award (DECRA) grant awarded to C.C.

Supplementary material

Supplementary material available online at <http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.111682/-DC1>

References

- Alexander, R. M. (1982). *Locomotion of Animals*. Glasgow: Blackie.
- Bennett, A. F. and Huey, R. B. (1990). Studying the evolution of physical performance. *Oxford Surveys in Evolutionary Biology* **7**, 251-284.
- Biewener, A. (2003). *Animal Locomotion*. Oxford: Oxford University Press.
- Börger, L., Dalziel, B. D. and Fryxell, J. M. (2008). Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol. Lett.* **11**, 637-650.
- Bruderer, B. and Boldt, A. (2001). Flight characteristics of birds: I. Radar measurements of speeds. *Ibis* **143**, 178-204.
- Chappell, M. A., Garland, T., Jr, Rezende, E. L. and Gomes, F. R. (2004). Voluntary running in deer mice: speed, distance, energy costs and temperature effects. *J. Exp. Biol.* **207**, 3839-3854.
- Combes, S. A., Rundle, D. E., Iwasaki, J. M. and Crall, J. D. (2012). Linking biomechanics and ecology through predator-prey interactions: flight performance of dragonflies and their prey. *J. Exp. Biol.* **215**, 903-913.
- Greene, P. R. (1985). Running on flat turns: experiments, theory, and applications. *J. Biomech. Eng.* **107**, 96-103.
- Hedenstrom, A. and Ålerstam, T. (1995). Optimal flight speed of birds. *Philos. Trans. R. Soc. B* **348**, 471-487.
- Higham, T. E., Davenport, M. S. and Jayne, B. C. (2001). Maneuvering in an arboreal habitat: the effects of turning angle on the locomotion of three sympatric ecomorphs of Anolis lizards. *J. Exp. Biol.* **204**, 4141-4155.
- Howland, H. C. (1974). Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. *J. Theor. Biol.* **47**, 333-350.
- Hoyt, D. F. and Taylor, C. R. (1981). Gait and the energetics of locomotion in horses. *Nature* **292**, 239-240.
- Husak, J. F. (2006). Does survival depend on how fast you can run or how fast you do run? *Funct. Ecol.* **20**, 1080-1086.
- Husak, J. F. and Fox, S. F. (2006). Field use of maximal sprint speed by collared lizards (*Crotaphytus collaris*): compensation and sexual selection. *Evolution* **60**, 1888-1895.
- Hyams, S. E., Jayne, B. C. and Cameron, G. N. (2012). Arboreal habitat structure affects locomotor speed and perch choice of white-footed mice (*Peromyscus leucopus*). *J. Exp. Zool. A* **317**, 540-551.
- Irschick, D. J. (2003). Measuring performance in nature: implications for studies of fitness within populations. *Integr. Comp. Biol.* **43**, 396-407.
- Irschick, D. J. and Garland, T. (2001). Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Annu. Rev. Ecol. Syst.* **32**, 367-396.
- Irschick, D. J. and Meyers, J. J. (2007). An analysis of the relative roles of plasticity and natural selection in the morphology and performance of a lizard (*Urosaurus ornatus*). *Oecologia* **153**, 489-499.
- Irschick, D. J., Meyers, J. J., Husak, J. F. and Le Galliard, J. F. (2008). How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evol. Ecol. Res.* **10**, 177-196.
- Jindrich, D. L. and Full, R. J. (1999). Many-legged maneuverability: dynamics of turning in hexapods. *J. Exp. Biol.* **202**, 1603-1623.
- Jindrich, D. L. and Qiao, M. (2009). Maneuvers during legged locomotion. *Chaos* **19**, 026105.
- Landy, M. S., Trommershäuser, J. and Daw, N. D. (2012). Dynamic estimation of task-relevant variance in movement under risk. *J. Neurosci.* **32**, 12702-12711.
- McElroy, E. J., McBrayer, L. D., Williams, S. C., Anderson, R. A. and Reilly, S. M. (2012). Sequential analyses of foraging behavior and attack speed in ambush and widely foraging lizards. *Adapt. Behav.* **20**, 16-31.
- Miles, D. B. (2004). The race goes to the swift: fitness consequences of variation in sprint performance in juvenile lizards. *Evol. Ecol. Res.* **6**, 63-75.

- Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. and Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proc. Natl. Acad. Sci. USA* **105**, 19052-19059.
- Pagan, D. N. M., Gifford, M. E., Parmerlee, J. S. and Powell, R. (2012). Ecological performance in the actively foraging lizard *Ameiva ameiva* (Teiidae). *J. Herpetol.* **46**, 253-256.
- Pennycuik, C. J. (1975). Mechanics of flight. In *Avian Biology*, pp. 1-75. New York, NY: Academic Press.
- Rayner, J. M. V. (1999). Estimating power curves of flying vertebrates. *J. Exp. Biol.* **202**, 3449-3461.
- Tan, H. and Wilson, A. M. (2010). Grip and limb force limits to turning performance in competition horses. *Proc. R. Soc. B* **278**, 2105-2111.
- Trommershäuser, J., Maloney, L. T. and Landy, M. S. (2003). Statistical decision theory and trade-offs in the control of motor response. *Spat. Vis.* **16**, 255-275.
- Van Damme, R. and Van Dooren, T. J. M. (1999). Absolute versus per unit body length speed of prey as an estimator of vulnerability to predation. *Anim. Behav.* **57**, 347-352.
- Wilson, R. S. (2005). Temperature influences swimming and sneaky-mating performance of male mosquitofish *Gambusia holbrooki*. *Anim. Behav.* **70**, 1387-1394.
- Wilson, R. S. and James, R. S. (2004). Constraints on muscular performance: trade-offs between power output and fatigue resistance. *Proc. Biol. Sci.* **271** Suppl. 4, S222-S225.
- Wilson, R. S., Hammill, E. and Johnston, I. A. (2007). Competition moderates the benefits of thermal acclimation to reproductive performance in male eastern mosquitofish. *Proc. Biol. Sci.* **274**, 1199-1204.
- Wilson, A. M., Lowe, J. C., Roskilly, K., Hudson, P. E., Golabek, K. A. and McNutt, J. W. (2013). Locomotion dynamics of hunting in wild cheetahs. *Nature* **498**, 185-189.
- Wolpert, D. M. and Landy, M. S. (2012). Motor control is decision-making. *Curr. Opin. Neurobiol.* **22**, 996-1003.
- Zollikofer, C. (1994). Stepping patterns in ants. 1. Influence of speed and curvature. *J. Exp. Biol.* **192**, 95-106.