

## RESEARCH ARTICLE

# Greater agility increases probability of survival in the endangered northern quoll

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### ABSTRACT

Introduced predators combined with habitat loss and modification are threatening biodiversity worldwide, particularly the ‘critical weight range’ (CWR) mammals of Australia. In order to mitigate the impacts of invasive predators on native species in different landscapes, we must understand how the prey’s morphology and performance determine their survival. Here, we evaluated how phenotypic traits related to escape performance predict the probability of survival for an endangered CWR mammal, the northern quoll (*Dasyurus hallucatus*). We measured mass, body size, body shape, body condition and age, as well as maximum sprint speed, acceleration and agility of female quolls over two consecutive years. Those with higher body condition and agility around a 135 deg corner were more likely to survive their first 21 months of life but were not more likely to survive after this period. No other morphological or performance traits affected survival. Heavier second-year individuals were more agile than first years but second years experienced higher mortality rates throughout the year. Females with higher body condition and agility around a 135 deg corner tended to have shorter limbs and feet but longer heads. Our findings suggest that higher body condition and agility are advantageous for survival in female northern quolls. These results can be used to develop predictive models of predator–prey interactions based on performance capacity and how performance is affected by habitat, aiding conservation efforts to predict and manage the impact of introduced predators on native species.

**KEY WORDS:** Escape, Morphology, Performance, Predation, Predator–prey interaction

### INTRODUCTION

Predation is one of the most important factors shaping animal behaviour, community structure and ecosystem dynamics (Lima and Dill, 1990). Successful management of the effect of predators on ecosystem function has received increased attention because of the catastrophic impact that introduced predators have on many of the world’s terrestrial fauna (Johnson, 2006; Johnson and Isaac, 2009). One avenue to better predict the long-term impact of specific predators on community structure is by identifying the factors that lead to predators capturing prey. An animal’s first line of defence is avoiding detection by predators, but if an individual is detected, its survival is determined by its ability to successfully escape, typically

through its physical performance (Arnold, 1983; Bennett and Huey, 1990; Huey et al., 1990; Jayne and Bennett, 1990; Husak, 2006).

Most studies that have investigated an animal’s ability to avoid predation and survive over extended periods have focused on maximal locomotor speed (Miles, 2004; Husak, 2006; Irschick and Meyers, 2007). Although one may expect faster individuals to be better at avoiding capture, a singular focus on measuring an individual’s maximal speed oversimplifies the dynamics between predators and prey. Escaping an encounter with a predator will often require more than just speed or strength (Clemente and Wilson, 2015). Predators that are larger than their prey are usually faster because of the scaling of mass and speed (up to approximately 100 kg body mass) (Hirt et al., 2017). Therefore, we would expect smaller prey animals to use a variety of performance traits to avoid capture. However, few studies have explored the importance of multiple physical performance traits for survival, which is surprising given that we would expect speed, acceleration and the ability to rapidly change direction (agility) all to be associated with escape ability (Clemente and Wilson, 2015; Walker et al., 2005; Hedenström and Rosén, 2001).

A mechanistic understanding of predator–prey gambits would be valuable, given that introduced predators pose one of the greatest threats to biodiversity worldwide (Medina et al., 2011; Szabo et al., 2012; Bellard et al., 2016; Doherty et al., 2016). Studies of whole-animal performance have contributed little to our understanding of population declines due to introduced or native predators, probably because most have focused on top speed alone (Miles, 2004; Husak, 2005, 2006). Declines in native species are particularly prominent in Australia, where more than 30 Australian mammals have become extinct since European colonisation (Woinarski et al., 2015). Species of Australian non-flying mammals within a critical weight range (CWR) of 35–5500 g (Fisher et al., 2014) have been particularly devastated by predation by invasive species and are currently declining at alarming rates (Murphy et al., 2019). The introduction of predators such as red foxes (*Vulpes vulpes*), cats (*Felis catus*) and dogs (*Canis lupus familiaris*) is implicated as a driver of such declines (Frank et al., 2014, 2003; Johnson, 2006; Leahy et al., 2016; McGregor et al., 2015; Burbidge and McKenzie, 1989; Dickman, 1996; Woinarski et al., 2011a). The impact of invasive predators is thought to be exacerbated by habitat clearance and the introduction of large feral herbivores, as well as the higher incidence of large-scale, intense fires, all of which reduce habitat complexity by limiting cover and refuges, and reducing system productivity (Kutt and Woinarski, 2007; Legge et al., 2011; Russell-Smith and Edwards, 2006; Russell-Smith et al., 2003).

In this study, we examined how an individual’s body condition, speed, acceleration and agility are associated with long-term survival in a population of endangered northern quolls (*Dasyurus hallucatus*). These CWR (220–1100 g) marsupials were once common across the northern third of Australia (Fisher et al., 2014; Hill and Ward, 2010) but their numbers have declined by up to 90% since the 1970s

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(Fitzsimons et al., 2010; Woinarski et al., 2011a), and they are now listed as Endangered under the EPBC Act 1999 (Braithwaite and Griffiths, 1994; www.environment.gov.au/node/16356). Population declines and range contractions on mainland Australia occur partly because of the spread of the introduced cane toad (*Rhinella marina*), which secretes poison when attacked or eaten (Woinarski et al., 2005, 2011b). However, declines have also occurred in areas without cane toads (Braithwaite and Griffiths, 1994; Braithwaite and Muller, 1997) and are thought to be driven by feral cats, and exacerbated by increased hot fires across the north, which simplify landscapes and eliminate refuges (Russell-Smith and Edwards, 2006; Fisher et al., 2014; Frank et al., 2014; Doherty et al., 2015; McGregor et al., 2015). Our study site on Groote Eylandt, an Indigenous Protected Area (IPA) of international conservation significance, has introduced feral cats (Department of Environment and Natural Resources and Anindilyakwa Land Council, 2019), dingoes and domestic dogs (Taylor and Anindilyakwa Land Council, 2016). Most importantly, Groote Eylandt has the highest density of naturally occurring northern quolls of any site in Australia (Heiniger et al., 2020). Because there are no cane toads on Groote Eylandt, the primary selective pressure on survival after the weaning period is predation from both natural and introduced predators.

We studied long-term survival in female northern quolls, as males die after a 2–3 week synchronised reproductive bout each year (Oakwood, 2000; Heiniger et al., 2020). Females can survive and reproduce successfully for up to 3 years. Therefore, survival of female northern quolls from across a 2 year period could be used as a proxy for an individual's ability to successfully avoid predation. On Groote Eylandt, northern quolls reach sexual maturity at 10 months of age (June), just prior to the yearly synchronised breeding period (July) (Heiniger et al., 2020). During this time, males significantly expand their home range to increase mate acquisition (~128–1616 ha; Heiniger et al., 2020). Females, however, maintain consistent home ranges throughout their life (~18 ha) (Heiniger et al., 2020). Females give birth to pouch young in August, denning young once they get too large for the pouch (October). Denning young are weaned just prior to juvenile dispersal (January) which coincides with the wet season (November–February) (see Table 1 for more details) (Oakwood, 2000; Heiniger et al., 2020). The largest decline in population density of females within this population occurs between years when lactation demand is highest (Heiniger et al., 2020). During the drier season, from the end of February to October, resource availability remains the same; therefore, individual mortality during this period is more likely to be due to predation events. We expected that survival of female northern quolls would be associated with higher speed, acceleration and/or agility, which would enable them to survive predation attempts. Based on previous studies (Charters et al., 2018),

we also expected to find significant relationships between morphological and performance traits.

## MATERIALS AND METHODS

Female northern quolls (*Dasyurus hallucatus* Gould 1842) were captured over a 2 year period (2017–2018) using baited cage traps (20×20×60 cm; Tomahawk ID-103, Hazelhurst, WI, USA). Our 128 ha study site on Groote Eylandt, NT, Australia (13°50'8.91"S, 136°25'3.10"E) is part of an 8 year long-term monitoring programme for this species and contains five permanent 540×300 m trapping grids placed 200 m apart. Each grid contained 40 cage traps at 60 m intervals along four transect lines that were spaced 100 m apart (see Heiniger et al., 2020). The trapping grids were designed to encompass the entire home range of individual female quolls based on previous home range size estimates by Heiniger et al. (2020) (18.16±8.27 ha using the same location and grid system as in the current study). Each quoll was microchipped between the shoulder blades (Trovan nano-transponder ID-100, Keysborough, VIC, Australia) and marked with an ear tag (1005-1 MONEL, National Band and Tag Co.) for individual identification. Quolls were captured across four important life stages within each year of the study: post-weaning period (February–March), pre-breeding period (May–June), breeding period (July–August) and pouch young period (September–October) (see Table 1 for further details). For the purposes of this study, the term 'post-weaning' was chosen because it could be used to describe all individuals at this time: recently weaned juveniles are seeking to establish a home territory, while second-year females have finished weaning a litter of young (if they were able to do so).

Morphological and performance measurements were taken for each quoll during the post-weaning period. Captured quolls were taken to the Anindilyakwa Land and Sea Ranger Station for the collection of morphological and performance measures before being released back at the capture location at the end of each day.

All research methodologies were approved by the University of Queensland's Animal Ethics Committee (permit number SBS/009/16/ARC) and the Northern Territory Parks and Wildlife Commission (permit number 585566). This research was conducted with permission from the Traditional Owners of Groote Eylandt, specifically the Bara Clan, who allowed access to their land. An Anindilyakwa Indigenous Protected Area Research Approval permit from the Anindilyakwa Land Council of Groote Eylandt was obtained for this research.

## Morphology

We recorded the age (based on molar condition and reproductive stage as per Heiniger et al. (2020), mass and morphologies for each female quoll captured. Mass was measured using an electronic

**Table 1. The life stages of female (first-, second- and third-year) and male (first-year) northern quolls (*Dasyurus hallucatus*) across a typical 1 year period on Groote Eylandt, NT, Australia**

Sex	Age	Wet season				Dry season						Wet season	
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Females	1st year	Juvenile	Recently weaned		Sub-adult		Sexually mature	Breeding	Birthing	Pouch young	Denning		Weaning
Females	2nd year	Weaning	Post-weaning		Pre-breeding			Breeding	Birthing	Pouch young	Denning		Weaning
Females	3rd year	Weaning	Post-weaning		Pre-breeding			Breeding	Birthing	Pouch young	Denning		Weaning
Males	1st year	Juvenile	Recently weaned		Sub-adult		Sexually mature	Breeding	Birthing	Semelparous die-off			

The sex and age of northern quolls is broken down by month of the year to reflect the primary life stages undertaken at each time. As males typically live for just over 1 year, all males were classed as first years.

balance scale ( $\pm 0.1$  g; A & D Company Limited HL200i, Brisbane, QLD, Australia). All morphological variables were measured 3 times and the mean taken to reduce measurement error. Six morphological variables were recorded using digital callipers (Whitworth, Brisbane, QLD, Australia;  $\pm 0.01$  mm): head length (from nuchal crest to tip of snout), head width (widest point of jaw), maximum tail width (diameter), mean hindfoot length (heel to claw base), mean hindlimb length (tibia–fibula) and mean forelimb length (radius–ulna) (see Wynn et al., 2015). Two morphological variables were recorded using tailor's tape ( $\pm 1$  mm): body length (nuchal crest to base of tail) and tail length (base to tip of tail) (see Wynn et al., 2015).

To create an overall measure of body size and shape, we conducted a principal component analysis (PCA) on all eight morphological traits. However, we found that tail length and body length together accounted for the majority of variation in the first principal component (tail length 86.2%, body length 48.2%), indicating that the first principal component was essentially a measure of overall length rather than size. We therefore excluded body length, tail length and tail width (which was included for measuring body condition) from the PCA, which was conducted on the remaining five morphological variables: hindfoot length, hindlimb length, forelimb length, head width and head length. The first principal component,  $PC_{\text{bodysize}}$ , explained 80.01% of the variation and all vectors loaded in a positive direction (Table 2). The second principal component,  $PC_{\text{bodyshape}}$ , indicated that longer heads were associated with smaller limbs and feet, and accounted for 9.9% of the variation. All other principal components accounted for <6% variation in the data and were therefore excluded from further analyses.

To estimate body condition for individual quolls, we divided tail diameter by body length. Quolls store fat in the base of their tails and so tail diameter has been used as a marker of condition for quoll species (Serena and Soderquist, 1988).

### Whole-animal performance traits

We quantified individual performance capacity of quolls during the first post-weaning period they were captured by measuring their maximum sprint speed, maximum acceleration and agility (mean angular and forward velocities around a 90 and 135 deg corner). The order of performance measures was randomised each day to account for performance in one activity influencing that in another. Prior to each performance measure, a reference point consisting of a piece of masking tape (2×2 cm) with a black dot in the centre was placed between the shoulder blades of each quoll to enable accurate analysis of their movement. All trials were filmed using a high-speed digital camera (Casio ELIXM EX-100F, Casio Computer CP, Ltd) filming at 240 frames  $s^{-1}$ .

**Table 2. Principal component analysis matrix of the five morphological variables of female northern quolls**

Morphological trait	$PC_{\text{bodysize}}$	$PC_{\text{bodyshape}}$
Percentage variance	80.1	9.9
Hindfoot length	0.091	0.3
Hindlimb length	0.511	0.534
Forelimb length	0.519	0.25
Head width	0.336	0.034
Head length	0.588	−0.75

Factor loadings of each measured variable and the direction in which they contribute towards the principal components (PC) are shown. Measurements were hindfoot length (heel to claw base), hindlimb length (tibia–fibula and femur), forelimb length (radius–ulna and humerus), head width (widest point of jaw) and head length (nuchal crest to tip of snout).  $n=76$  quolls.

### Maximum acceleration and sprint speed

All running tests were measured on a linear racetrack (4×0.6 m) with 1.5 m high sides and a rubber floor. A 1 m long tape measure was fixed to the rubber floor across the central area to calibrate the movement speed of quolls. The camera was placed 2 m above the centre of the racetrack and positioned to capture the central 2.0 m. Quolls were held at 1.25 m from the end of the racetrack, to ensure a standing start acceleration was captured. They were released and immediately chased towards the opposite end (3.25 m from start line), ensuring a minimum of 4 linear acceleration strides was achieved within the 2 m field of view of the camera. Charters et al. (2018) noted a maximum of 4 strides of a quoll was required to reach top acceleration, which is achieved within 2 m from a standing start. Quolls were then chased back and forward down the full extent of the runway a minimum of 3 times. Maximum sprint speed was recorded from the central 2 m of the racetrack to allow quolls to reach maximum speed after making a turn at the end of the racetrack, and prior to slowing down before reaching the opposite end (Charters et al., 2018). This was repeated a minimum of 2 times per individual to gain 2×measures of acceleration and 6×measures of maximum sprint speed. The frame-specific velocities over the central 1 m were averaged to get the measure of sprint speed for each run. Videos were analysed using TRACKER software (Open Source Physics, Boston, MA, USA) that extracted the position and instantaneous velocity of the reference point on each quoll. The fastest measures for acceleration and sprint speed were used as an individual's maximum performance.

### Agility

We assessed the agility of each quoll by measuring the velocity at which individuals could sprint around a 90 or 135 deg corner, modifying methods of Wynn et al. (2015). Agility was measured in a 5 m long×1.5 m high racetrack consisting of two mobile wings; (each wing 2.5 m long×0.3 m wide at the widest point) with a rubber floor and an interchangeable, hinged angle (either 90 or 135 deg). The camera was suspended 2 m above the angle in the racetrack, encompassing 0.5 m of each wing in its field of view. A white-tape marker was fixed at the tip of the hinged angle of the racetrack with additional tape markers at 10 cm intervals along the first 30 cm of each wing of the racetrack to calibrate movement around the corner. Individual quolls were released into one end of a wing and encouraged to sprint around the corner 3 times in each direction (i.e. left turn and right turn). Quolls were chased for all runs in order to evoke the fastest speed that they were able to navigate the corner without crashing.

TRACKER video analysing software (Open Source Physics) was used to extract the position and instantaneous velocity of the reference point between frames throughout the turn. Positional data and instantaneous velocity were recorded from 0.4 m before the turn until 0.4 m after the turn. As per Wynn et al. (2015), a crash or mistake occurred when a quoll made contact with the wall when running around the corner and/or when the minimum instantaneous velocity dropped below 0.4 m  $s^{-1}$ . Examples of crashes and successful runs can be viewed in the supplementary information of Wynn et al. (2015). Positional data for successful turns were smoothed using a mean squared error algorithm (tolerance=0.05 error in pixels per frame) using the custom MATLAB script from Wheatley et al. (2018a) and the following variables extracted: (1) forward velocity (m  $s^{-1}$ ), calculated as the mean of all instantaneous velocities throughout the turn; (2) angular velocity (deg  $s^{-1}$ ), calculated as the rate of change in heading throughout the turn; and (3) exact turning radius (cm), calculated by fitting a circle



to the quoll's positional data around the turn using the least squares modelling approach outlined in Pratt (1987). The fastest forward velocity and angular velocity were taken to represent an individual's maximum forward velocity ( $\text{m s}^{-1}$ ) and angular velocity ( $\text{deg s}^{-1}$ ) around each corner.

Both measures of agility (maximum forward velocity and maximum angular velocity) were used in subsequent analyses. Previous studies have used maximum forward velocity ( $\text{m s}^{-1}$ ) as a measure of agility (Wynn et al., 2015; Charters et al., 2018; Wheatley et al., 2018a). However, to be comparable between individual animals, this measure assumes all individuals use the same turning radius and therefore turning angle. Despite the narrow width of the racetrack within the angle (10 cm), we found that quolls used highly variable turning radii: 2.89–57.19 cm for the 90 deg corner ( $n=705$  runs) and 1.98–44.98 cm for the 135 deg corner ( $n=643$  runs). As angular velocity ( $\text{deg s}^{-1}$ ) incorporates both the velocity at which the individual is running and the real angle it is turning through, it is a more suitable measure of agility if not also accounting for the exact turning radius. Therefore, both maximum angular velocity and maximum forward velocity were used as measurements of agility in order to determine any difference this had on the results.

### Statistical analysis

A mark–recapture programme of 85% was used for this study to obtain an accurate measure of female survivability. Females that lived on the edge of the trapping site were excluded from our study, as we could not be confident their absence was due to death. All analyses were conducted in the R statistical software environment v3.5.2 (<http://www.R-project.org/>).

To determine whether a quoll's maximum performance could predict survival, we fitted a Cox proportional hazards regression model to the survival data (months from birth until the first period the individual was not trapped), with body condition, maximum sprint speed, maximum acceleration and maximum agility (both angular and forward velocity) around the 90 and 135 deg corners as predictor variables using the *survminer* v0.4.6 package. Body condition was included because of the direct link it may have had with survival. Body condition and maximum angular velocity around the 135 deg corner both violated the proportional hazards assumption and coefficient estimates for these variables were subsequently generated for two time blocks: 0–21 months and 21–45 months. Females that survive to 21 months have hypothetically been able to wean one litter of young, and this cut-off point ensured proportional hazards for both variables. Kaplan–Meier curves were fitted to the survival data for each influencing performance variable to examine how differences in maximum performance values affected survival.

We assessed the effect that morphology had on performance by fitting linear regression models to each performance trait. Mass, body shape ( $\text{PC}_{\text{bodyshape}}$ ), body condition and age first tested along with their two-way interactions were included as predictor variables in the models. Mass and body size ( $\text{PC}_{\text{bodysize}}$ ) were significantly positively correlated ( $t=6.63$ ,  $\text{d.f.}=74$ ,  $P<0.01$ ). We therefore chose to include mass but not body size in our linear regression models. Statistically significant correlations were assessed using ANOVA.

## RESULTS

### Survival

Overall, a total of 76 females were caught and tested for performance during the post-weaning period of 2017 and 2018. Of the 76 females in this study, we found that 84.2% ( $n=64$ ) survived to their first pouch young period, 36.8% ( $n=28$ ) survived to a second pouch young period and 1.3% ( $n=1$ ) survived to a third

pouch young period (Fig. 1). The highest mortality rate occurred from the pouch young to post-weaning period (September to February) for females of all ages. While 84.2% of first-year females survived from breeding to pouch young period, only 64.5% survived from pouch young to post-weaning period (a drop of 19.5%). For second-year females, 36.8% survived from breeding to pouch young period, but only 17.1% survived from pouch young to post-weaning period (a drop of 19.7%).

Both body condition and maximum angular velocity around the 135 deg corner were found to affect survival, but only within the first 21 months of a quoll's life (Table 3). Females that were in better body condition and females that had greater maximum angular velocity around the 135 deg corner were more likely to survive to 21 months of age (Figs 2 and 3). Subsequently, differences in body condition and maximum angular velocity around the 135 deg corner had little impact on a quoll's chance of survival. No other performance traits were associated with survival.

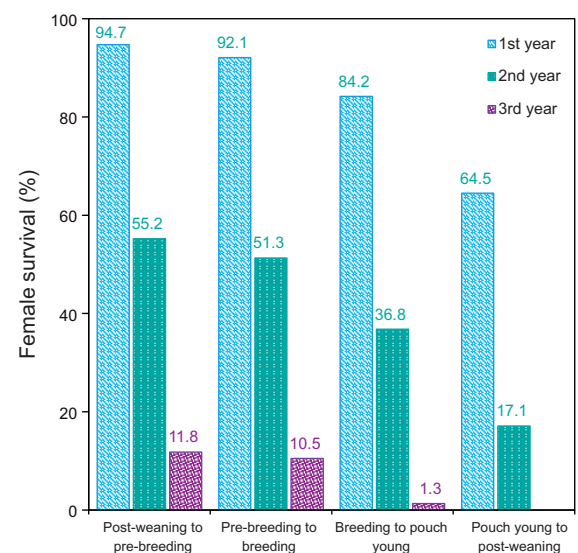
### Performance

#### Correlation between performance traits

Females with faster sprint speed also had faster forward velocity around both corners, and faster angular velocity around the 135 deg corner. Females with faster forward velocity around the 90 deg corner also had faster forward velocity around the 135 deg corner and faster angular velocity around the 90 deg corner. No other performance traits were correlated (Table 4).

#### Morphological traits associated with performance

Body condition was significantly associated with body shape, such that individuals that had longer limbs and feet but shorter heads tended to have lower body condition (Table 5). The interactive effect of mass and age was also correlated with body condition such that lighter first years tended to have better body condition than heavier first years, but for second- and third-year females, body condition was higher for heavier individuals. When this was broken



**Fig. 1. Quoll survival across life stages.** The percentage of female northern quolls ( $n=76$ ) (*Dasyurus hallucatus*) surviving between the periods of: post-weaning to pre-breeding, pre-breeding to breeding, breeding to pouch young and pouch young to post-weaning. A Cox proportional hazards regression model was used to estimate the time of death for individuals that outlived the duration of the 2 year study. Columns show survival of quolls during their first, second and third year.

**Table 3. Cox proportional hazards regression model assessing survival of female northern quolls in response to performance and morphology measures**

	Coefficient	exp(coef)	s.e.	z-value	P-value
Sprint speed	0.38	1.46	0.3	1.27	0.2
Acceleration	0.05	1.06	0.08	0.66	0.51
90 deg forward velocity	-0.06	0.94	0.45	-0.14	0.89
90 deg angular velocity	6.13E-04	1	8.43E-04	0.73	0.47
135 deg forward velocity	0.49	1.62	0.45	1.07	0.28
Body condition before 21 months old	-81.92	2.65E-36	29.05	-2.82	<0.01*
Body condition after 21 months old	34.7	1.18E+15	28.32	1.23	0.22
135 deg angular velocity before 21 months old	-7.63E-03	0.99	2.33E-03	-3.28	<0.01*
135 deg angular velocity after 21 months old	-4.98E-04	0.99	1.90E-03	-0.26	0.79

Survival (months from birth until the first period the individual was not trapped) was categorised into two blocks (before 21 months old and after 21 months old) for the predictor variables body condition and 135 deg angular velocity so that these variables did not violate the proportional hazards test. Maximum sprint speed, maximum acceleration, and maximum agility (both angular and forward velocity) around the 90 and 135 deg turns were also used as predictor variables for survival. Asterisks indicate significance.  $n=76$  quolls.

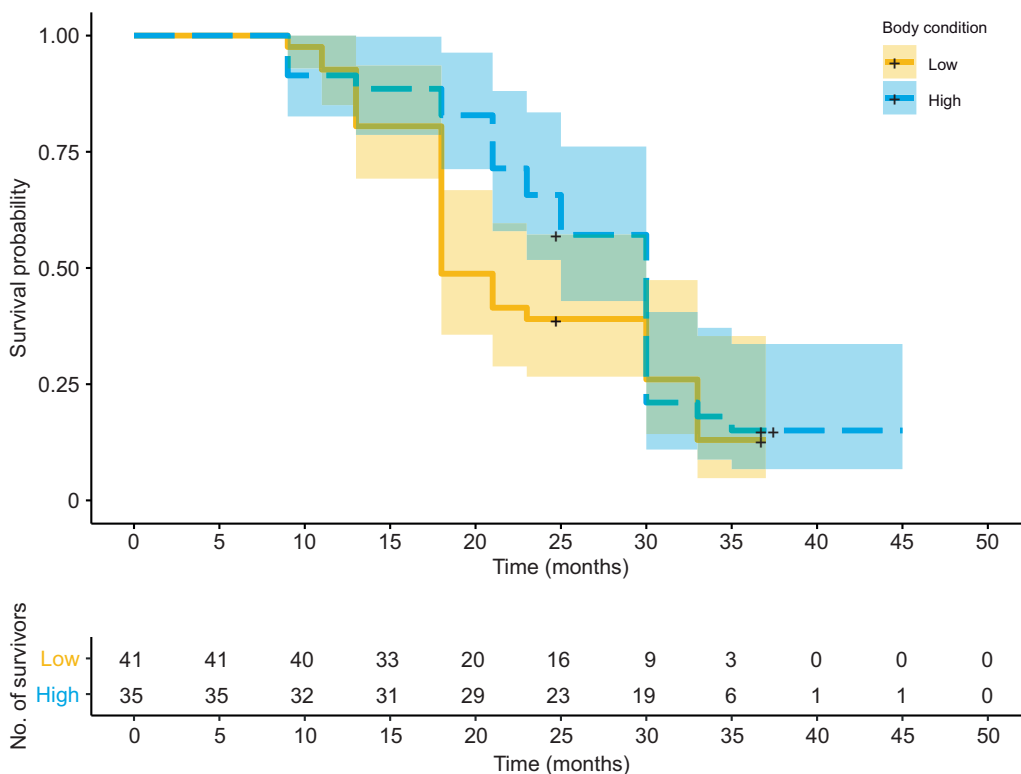
down further, second-year females tended to have the highest body condition ( $0.072\pm0.001$ ), followed by first years ( $0.069\pm0.001$ ) and third years ( $0.068\pm0.006$ ).

Sprint speed was not associated with any morphological traits (Table S1). Heavier individuals tended to have slower acceleration ( $n=76$ ,  $F=2.87$ ,  $P=0.09$ ), but acceleration was not associated with any other morphological variable (Table S2).

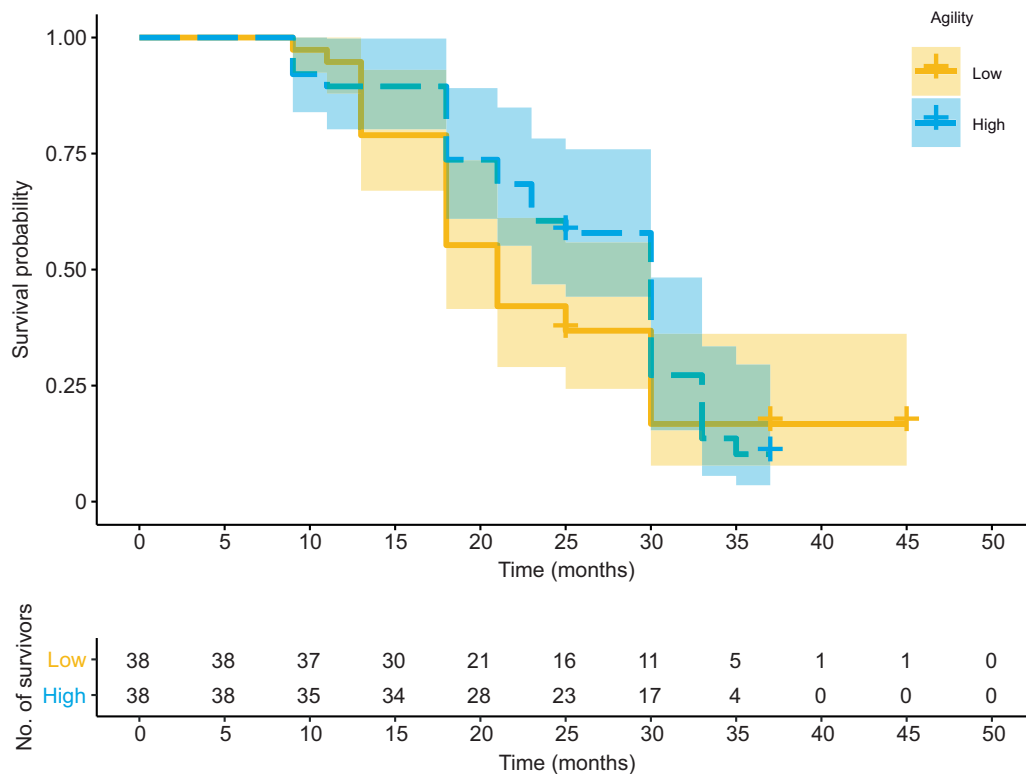
Maximum angular velocity around a 90 deg corner was not associated with any morphological variables (Table S3). However, maximum angular velocity around a 135 deg corner was weakly associated with the interaction between body shape and body condition such that individuals with shorter limbs and longer heads that were in better body condition tended to have greater agility (Table 6). The interaction between mass and age was weakly correlated with maximum angular velocity around the 135 deg corner such that first years that were heavier tended to have greater agility, second years that were lighter tended to have highest agility,

while for third years, lighter females had greatest agility. When this was further broken down, we found that second-year females generally had the greatest agility ( $536.07\pm26.9$  deg s<sup>-1</sup>), followed by first-year females ( $518.69\pm12.54$  deg s<sup>-1</sup>) and then third-year females ( $479.12\pm83.02$  deg s<sup>-1</sup>) but this was not significant ( $n=76$ ,  $F=0.9$ ,  $P=0.41$ ). Maximum angular velocity around a 135 deg corner was not associated with any other variables.

Forward velocity around a 90 deg corner was significantly associated with age, with first years being fastest ( $2.14\pm0.05$  m s<sup>-1</sup>), followed by second years ( $1.96\pm0.1$  m s<sup>-1</sup>) and third years ( $1.78\pm0.05$  m s<sup>-1</sup>), but was not associated with mass, body shape or body condition (Table S4). Forward velocity around a 135 deg corner was also significantly associated with age, with first years being fastest ( $1.79\pm0.04$  m s<sup>-1</sup>), followed by second years ( $1.59\pm0.11$  m s<sup>-1</sup>) and third years ( $1.4\pm0.04$  m s<sup>-1</sup>). Forward velocity around a 135 deg corner was also weakly associated with the interaction between mass and age tested, so that heavier and older individuals



**Fig. 2. Kaplan–Meier survivorship curves for female northern quolls based on an individual's body condition.** Individuals classified as having high body condition were in the top 50% (blue dashed line), while individuals classified as having low body condition were in the bottom 50% (yellow solid line). Shading represents 95% confidence intervals.  $n=76$  quolls. The risk table gives the number of survivors of high/low body condition at 5 month intervals.



**Fig. 3. Kaplan–Meier survivorship curves for female northern quolls based on an individual’s fastest mean angular velocity around a 135 deg corner.** Individuals classified as having high agility were in the top 50% (blue dashed line), while individuals classified as having low agility were in the bottom 50% (yellow solid line). Shading represents 95% confidence intervals.  $n=76$  quolls. The risk table gives the number of survivors of high/low agility at 5 month intervals.

tended to be slower. None of the other variables were associated with forward velocity around a 135 deg corner (Table S5).

## DISCUSSION

In this study, we examined how metrics of speed, acceleration and agility of female northern quolls were associated with survival. We expected that survival would be associated with higher speed, acceleration and/or agility, which would enable them to survive predation attempts. We found that females that were in better body condition and females that were able to turn faster and more sharply around a 135 deg corner (angular velocity,  $\text{deg s}^{-1}$ ) were more likely to survive their first 21 months. However, those with greater sprint speed, acceleration, ability to turn fast and sharply around a 90 deg corner (angular velocity,  $\text{deg s}^{-1}$ ), and faster forward velocity around a 90 or 135 deg corner were not more likely to survive their first 21 months. This result suggests that the more extreme measure of agility (angular velocity around a 135 deg corner) could be an important trait for quoll survival and may be used during predator

escape. Given that quolls experience predation from a range of animals that are larger and likely to be faster than them (dingoes, cats and birds of prey) or that use quick reflexes in ambush attacks (such as snakes), it is reasonable to conclude that agility would be the most significant performance trait for survival. High agility allows a quoll the chance to outmanoeuvre a faster attacker, especially in more complex environments where refuges can be sought. Quolls that can perform short, sharp manoeuvres would also have a better chance at dodging a fast strike from a snake, as has been demonstrated in kangaroo rats (Higham et al., 2017). Our study site on Groote Eylandt is primarily rocky habitat with features typical of existing mainland areas known to be strongholds for northern quoll populations (Hernandez-Santin et al., 2016; Hill and Ward, 2010). This habitat probably favours animals that can perform short, sharp turns around the plethora of rocky obstacles present and into the many shelters available. Northern quolls also inhabit more open forested areas and it is unclear whether individuals with high agility would have similar survival

**Table 4. Correlation between performance traits of female northern quolls using Pearson’s product-moment correlations**

	Sprint speed	Acceleration	Angular velocity		Forward velocity	
			90 deg	135 deg	90 deg	135 deg
Sprint speed	1	0.19	0.14	0.29*	0.34*	0.3*
Acceleration		1	0.05	0.03	0.06	0.11
90 deg angular velocity			1	0.02	0.27*	0.11
135 deg angular velocity				1	0.22	0.21
90 deg forward velocity					1	0.57*
135 deg forward velocity						1

The results from Pearson’s product-moment correlation of female northern quolls ( $n=76$ ) between six performance traits: sprint speed, acceleration, 90 deg angular velocity, 135 deg angular velocity, 90 deg forward velocity and 135 deg forward velocity. Asterisks indicate significant relationships between traits.

**Table 5. ANOVA results for body condition of female northern quolls**

	d.f.	Sum of squares	Mean squares	F-value	P-value
Mass	1	1.04E-04	1.04E-04	2.49	0.12
Body shape	1	3.60E-04	3.60E-04	8.59	<0.01*
Age tested	2	7.89E-05	3.94E-05	0.94	0.40
Mass×age tested	2	2.86E-04	1.43E-04	3.41	0.04*
Residuals	69	2.89E-03	4.19E-05		

The ANOVA results of female northern quolls ( $n=76$ ) contained body condition as the response variable and mass, body shape and age tested as predictor variables. Asterisks indicate significance.

advantages in these habitats (Oakwood, 2000). On mainland Australia, where threatening processes are more prevalent, the greatest declines have occurred in these open habitats (Oakwood, 2000; Hill and Ward, 2010). Future studies should determine whether the performance traits associated with survival change depending on the habitat type occupied.

We found that the survival of females after 21 months of age was not correlated with any performance trait. Considering that the second-year cohort consists of the first years that survived from the previous year, and given we know that first years with higher agility are more likely to survive, intuitively second-year females should be the most agile quolls. While second years tended to be the most agile around 135 deg corner (though this was not significant), they experienced higher mortality rates than first years. While predation may be a key factor in mortality for younger, less experienced quolls, it may not play such a big role in mortality of older, more experienced quolls. Other long-term factors such as disease and parasite load, and defending a home range (Oakwood, 2000) may cause an increase in mortality for older females. We found that the highest mortality for all females occurred between pouch young and post-weaning period (September–February), as expected based on other studies (Heiniger et al., 2020; Oakwood, 2000). The stress of rearing young could be severe enough to cause depletion in body condition and increase mortality directly, or indirectly by making individuals more vulnerable to predation.

We found individuals in better body condition that had shorter limbs and longer heads were better at turning fast and sharply around a 135 deg corner. Similarly, individuals with shorter limbs and longer heads were in better body condition. Agility, or the ability to turn sharply, is constrained by the musculoskeletal system (Jindrich and Qiao, 2009) and basic physical principles (Alexander, 1982). To turn while running, an animal must overcome inertia, change the main vector of motion, and rotate its body to the new

orientation (Jindrich and Full, 1999), undergoing angular motion (Zollikofer, 1994). Individuals with a lower centre of gravity (shorter limbs) are more likely to be able to change the vector of motion without slipping or falling over, thus supporting the morphological correlates of higher agility we saw in our results.

We also examined two different parameters of agility around a 90 deg corner and 135 deg corner, forward velocity ( $\text{m s}^{-1}$ ) and angular velocity ( $\text{deg s}^{-1}$ ), to determine what difference this had on our results. Angular velocity, which measures how fast and sharply an individual can turn around a corner, is a more suitable measurement of agility than forward velocity, which only measures how fast an individual can turn around a corner. We found that angular velocity around a 135 deg corner was the only agility measure associated with survival. Because quolls do not have to turn so sharply around a 90 deg corner compared with a 135 deg corner, it may have been harder to differentiate agility capabilities between quolls using the 90 deg corner. This could be why angular velocity around the 135 deg corner was significantly associated with survival, but angular velocity around the 90 deg corner was not.

It is important to acknowledge that predators and prey do not live in isolation and being able to understand the predictors of survival for prey must be done within the context of specific predators (Hedenström and Rosén, 2001; Bro-Jørgensen, 2013). For animals like the CWR species of Australia, the introduction of cats, foxes and domesticated dogs has primarily been responsible for their catastrophic decline (Dickman, 1996; Frank et al., 2014). Although in our study we have identified that the agility of northern quolls is a key predictor of survival, being able to use this information for conservation management requires one to identify the specific predators involved, assess the specific locomotor capabilities of the predators and determine how the locomotor capabilities of both are mediated by habitat. Future studies should compare locomotor performance traits of introduced predators and the native animals they threaten, to determine which traits are favoured by predators versus prey. This would help us to better understand which prey species and individuals within these species are most vulnerable to predation, and the changes in community structure that result from this. It would also be useful to look at the performance of these same animals in the wild to ascertain how often certain performance traits are used and in what context. This would increase our knowledge on how natural behaviour influences the outcome of predator–prey interactions.

Conservation scientists and managers are interested in understanding which traits are associated with survival for CWR mammals, yet to our knowledge, our study is the first to examine how locomotor performance can affect this capacity in Australia's CWR mammals. Predicting the negative impacts of introduced predators on small native animals relies on our ability to identify when, where and how predators attempt to capture their prey, and how and whether prey can escape from them. The success of capture versus escape during a hunt is defined by the physical and performance attributes of both animals, including traits such as body size and speed or agility. Most studies of performance have focused on the physiology and biomechanics of movement rather than exploring its consequences for activities such as escape from predators, which has a direct relevance to studies of conservation. Of those that have explored the consequences for survival, there has been an almost exclusive focus on maximum speed (Miles, 2004; Husak, 2005, 2006; Irschick and Meyers, 2007), with the expectation that faster should be associated with higher survival. This bias towards linear performances is one reason why performance biology has made little impact to date in the disciplines of ecology or applied conservation. Larger animals are

**Table 6. ANOVA results for maximum angular velocity around a 135 deg corner for female northern quolls**

	d.f.	Sum of squares	Mean squares	F-value	P-value
Mass	1	635	635	0.07	0.79
Body shape	1	14,583	14,583	1.57	0.22
Body condition	1	56	56	0.01	0.94
Age tested	2	16,808	8404	0.90	0.41
Mass×age tested	2	47,892	23,946	2.57	0.08*
Body shape×body condition	1	35,224	35,224	3.78	0.06*
Residuals	67	624,131	9315		

The ANOVA results of female northern quolls ( $n=76$ ) contained maximum angular velocity around a 135 deg corner as the response variable and mass, body shape, body condition and age tested as predictor variables. Asterisks indicate a weak significance.



typically faster but less agile than smaller ones (Hirt et al., 2017), meaning that if a predator is larger than its prey, it is also likely to be faster, but not always successful. Small prey species might be able to more rapidly change speed and direction, allowing them to evade a larger, faster predator (Howland, 1974; Wilson et al., 2015). This highlights an important limitation of many studies of escape (or capture) success which measure only speed: an individual's optimum escape performance will be constrained by trade-offs between performance traits as well as the habitat in which it is escaping (Wheatley et al., 2018b). To move the field forward and link studies of locomotor function with conservation, we need to develop predictive models of predator–prey interactions that incorporate both predator and prey locomotor capabilities and how these performances are affected by habitat. We will then be able to better understand the role of predators on the vulnerability of endangered species and how environmental managers can rehabilitate the landscape to improve the retention of vulnerable prey.

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### Competing interests

The authors declare no competing or financial interests.

### Author contributions

Conceptualization: M.R.-D., S.F.C., N.F., R.S.W.; Methodology: M.R.-D., S.F.C., N.F.; Software: M.R.-D.; Validation: M.R.-D., S.F.C.; Formal analysis: M.R.-D., R.W., J.M.L.; Investigation: M.R.-D.; Resources: R.S.W.; Data curation: M.R.-D., S.F.C., N.F., J.M.L.; Writing - original draft: M.R.-D., S.F.C., R.S.W.; Writing - review & editing: M.R.-D., S.F.C., N.F., R.W., R.S.W.; Supervision: S.F.C., N.F., R.S.W.; Project administration: S.F.C., N.F., R.S.W.; Funding acquisition: N.F., R.S.W.

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### Data availability

Data are available from the Dryad digital repository (Rew-Duffy et al., 2020): dryad.cvdncj11x.

### Supplementary information

Supplementary information available online at <https://jeb.biologists.org/lookup/doi/10.1242/jeb.218503.supplemental>

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