



SYMPOSIUM

Modeling escape success in terrestrial predator–prey interactions

Robbie S. Wilson,^{1,*} Theodore P. Pavlic,^{†,‡} Rebecca Wheatley,^{*,§} Amanda C. Niehaus* and Ofir Levy[¶]

*School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia; [†]School of Computing, Informatics, and Decision Systems Engineering, Arizona State University, Tempe, AZ, USA; [‡]School of Sustainability, Arizona State University, Tempe, AZ, USA; [§]School of Natural Sciences, University of Tasmania, Hobart, Tasmania 7001, Australia; [¶]School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Israel

First and last authors contributed equally to this work.

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¹E-mail: r.wilson@uq.edu.au

Synopsis Prey species often modify their foraging and reproductive behaviors to avoid encounters with predators; yet once they are detected, survival depends on out-running, out-maneuvering, or fighting off the predator. Though predation attempts involve at least two individuals—namely, a predator and its prey—studies of escape performance typically measure a single trait (e.g., sprint speed) in the prey species only. Here, we develop a theoretical model in which the likelihood of escape is determined by the prey animal’s tactics (i.e., path trajectory) and its acceleration, top speed, agility, and deceleration relative to the performance capabilities of a predator. The model shows that acceleration, top speed, and agility are all important determinants of escape performance, and because speed and agility are biomechanically related to size, smaller prey with higher agility should force larger predators to run along curved paths that do not allow them to use their superior speeds. Our simulations provide clear predictions for the path and speed a prey animal should choose when escaping from predators of different sizes (thus, biomechanical constraints) and could be used to explore the dynamics between predators and prey.

Introduction

Predation is one of the most pervasive biotic factors shaping animal behavior, community structure, and ecosystem dynamics (Lima and Dill 1990). Predators affect prey fitness directly, by reducing survival, and indirectly, by inducing behavioral changes that lower growth or reproductive output (Lima and Dill 1990; Schmitz 1998; Pavey, Eldridge and Heywood 2008; Wesner et al. 2012). A prey species’ first line of defense is to avoid detection, and individuals modify habitat use (Werner et al. 1983; Brown 1999), activity patterns (Daly et al. 1992; Hughes et al. 1994), reproductive behavior (Fontaine and Martin 2006), and foraging strategies (Metcalf et al. 1987; Jones and Rydell 1994) to reduce encounters with predators. If these measures fail and the prey is detected,

its survival depends on successfully evading capture by out-running, out-maneuvering, or fighting off the predator (Howland 1974; Elliott et al. 1977; Arnold 1983; Huey et al. 1990; Jayne and Bennett 1990; Husak 2006). The prey’s probability of escape or capture should depend on the relative performances of the predator and the prey, along with the escape strategy the prey chooses (Howland 1974; Elliott et al. 1977; Wilson et al. 2018). It is surprising, then, that few studies of whole-animal performance have contributed to our understanding of predator–prey interactions (but see Walker et al. 2005; Corcoran and Conner 2016). Consequently, little is known about how relative performances between predator and prey dictate their interactions, nor

how prey compensate for potentially poorer performance through different escape strategies.

Intuitively, we expect faster individuals to be better at avoiding capture. This logic has led to an almost exclusive focus on maximal speeds in studies of animal escape (Miles 2004; Irschick and Meyers 2007; Irschick et al. 2008). However, while in some cases, faster individuals are more likely to survive than slower conspecifics (Miles 2004; Irschick and Meyers 2007), other studies find that sprint speeds are unrelated to survival (Bennett and Huey 1990). Speed is only one element in a prey's predator-evasion arsenal (Humphries and Driver 1970; Howland 1974; Elliott et al. 1977; Brown and Taylor 1995; Wilson et al. 2015a; Clemente and Wilson 2016). Abrupt changes in direction and acceleration are also key in a prey's capacity for successful escape—as can be seen in any predator–prey chase scene shown in many wildlife documentaries. Focusing entirely on maximum sprint speed is overly simplistic for three main reasons. First, predators are often larger and subsequently often faster than their prey (Garland 1983; Hirt et al. 2017) and yet are not always successful at capturing them. Even the world's fastest land mammal, the cheetah, routinely fails to capture prey despite their superior speed (Wilson et al. 2013a; Wilson et al. 2013b; Wilson et al. 2018). Second, prey rarely flee along straight paths but instead curve and turn abruptly to exploit increased agility at lower speeds (Humphries and Driver 1970; Howland 1974; Brown and Taylor 1995; Wilson et al. 2013a; Wilson et al. 2018). Third, studies of animals in nature reveal that prey rarely use maximum speeds when attempting to escape predators, suggesting that high speeds do not always offer the best strategy for successful escape (Irschick et al. 2005; Husak and Fox 2006; Wilson et al. 2013a; Wheatley et al. 2018). Maximum sprint speed alone is therefore unlikely to determine an animal's escape ability (Wilson et al. 2015b).

To understand what underlies escape ability, studies must incorporate the complexity of an animal's escape tactics (i.e., its path trajectory) and the range of performance parameters that are likely to contribute to success (i.e., evasion of capture) along a given path. These include acceleration, top speed, agility, and deceleration (Webb 1976; Elliott et al. 1977; Huey and Hertz 1984; Carrascal and Polo 1999; Husak 2006; Wilson et al. 2013a; Wilson et al. 2013b; Clemente and Wilson 2016). It is also important to recognize that in nature, escape performance is a relative measure between predator and prey and is likely to vary among species and situations. Predator–prey dynamics are a game, and

characterizing the performance of only one player ultimately says little about the eventual success of either player (Elliott et al. 1977; Carrascal and Polo 1999; Wilson et al. 2013b; Wilson et al. 2015a). By knowing key performance traits of predators and prey, we can predict outcomes in interactions between them and determine how prey might optimize their escape success via their selection of the best escape path and use of their performance attributes.

The objective of our study is to explore how terrestrial escape performance—specifically, successful escape—is shaped by physical performances and path curvature. We develop a theoretical framework that predicts the time taken for an animal to run along a path, and we use sensitivity analyses to show the relative importance of acceleration, top speed, agility, and deceleration when running along paths of varying curvature. We explore only the pursuit phase of the predator–prey interaction in our model and exclude both the initial prey detection and avoidance phase and the moments of final capture. Our model forms the basis for future empirical work on performance in terrestrial animals and demonstrates that maximum running speeds on their own have limited relevance to performance along curved paths. Because performance characteristics are not always available for species of interest, we also model the relationship between limb length and performance and show how differences in limb length between larger predators and smaller prey affect the time taken to run along curved paths. Assuming that prey that complete a path faster than a predator will survive, we can then estimate the minimum path curvature required for the prey to escape a particular predator of known limb length. Our model shows that acceleration, top speed, and agility are all important determinants of escape performance. Because speed and agility are biomechanically related to size (Garland 1983; Wilson et al. 2013a), smaller prey with higher agility should force larger predators to run along curved paths that do not allow them to use their superior speeds. Our simulations provide clear predictions for how prey should best escape from specific predators and define a clear path for further mechanistic work on predator–prey interactions.

Methods

Modeling time to complete a path

We developed a model that calculated the amount of time it takes an animal to run along a path of different lengths and curvatures based on measures of

acceleration, top sprint speed, agility, and deceleration. Agility was defined as the relationship between running speed and an individual’s ability to move around a turn. To do this, we created virtual paths for the theoretical animals to run along, with diversity among paths in length, number of turns, and total curviness. Paths consisted of straight lines interspersed by turns, with each turn represented as a specific turning angle and a given turning radius. We could then calculate how long it would take an animal to run along the path and determine the relative importance of each performance attribute to completion time.

Constructing a feasible path for simulation

We generated random paths based on path length (L , m), number of turns (N_t), and curviness (C , the average density of angular rotations throughout a path in rad m^{-1}). For a path of length L and curviness C , the total amount of rotation along the path is:

$$\text{Total Rotation}(\text{rad}) = L(\text{m}) \cdots C(\text{rad m}^{-1}). \quad (1)$$

We divided Total Rotation randomly among N_t turns such that:

$$\sum_{i=1}^{N_t} a_i = \text{Total Rotation}, \quad (2)$$

using a uniform distribution, where a_i (rad) represents the total rotation of the i th turn along the path. We also chose the radii of each turn so that the animal is turning over two-thirds of the total path length. Formally,

$$\sum_{i=1}^{N_t} a_i r_i = \frac{2}{3} L, \quad (3)$$

where r_i is the radius of the i th turn along the path. The remaining one-third of the total path length was distributed randomly over a set of $(N_t + 1)$ straight lines connected to turn segments using a uniform distribution. That is,

$$\sum_{i=1}^{N_t+1} s_i = L - \sum_{i=1}^{N_t} a_i r_i \quad (4)$$

or, equivalently,

$$L = \sum_{i=1}^{N_t} (s_i + a_i r_i) + s_{N_t+1}, \quad (5)$$

where s_i is the length of the i th straight segment.

Calculating the maximum speed and travel time for a given turn

The biomechanical properties of an animal limit the maximum speed the animal can move through a turn without slipping. Following the approach of Wilson et al. (2015a), we consider an animal of mass m (kg) moving through a circular arc of radius r_{turn} (m) at the maximum speed v_{turn} (m s^{-1}) possible before slipping. In this condition, the centripetal acceleration keeping the animal moving along the arc must be equivalent to the maximum force F_{slip} (N or kg m s^{-2}) that the interface between the animal’s limb and the ground permits before friction gives way to slipping. Consequently,

$$F_{\text{slip}} = \frac{m v_{\text{turn}}^2}{r_{\text{turn}}},$$

or, equivalently,

$$v_{\text{turn}} = \sqrt{r_{\text{turn}}} \cdot \sqrt{\frac{F_{\text{slip}}}{m}}.$$

So, for a given average volumetric density ρ (kg m^{-3}) and limb length ℓ (m) of an animal, we approximate the mass of an arbitrary animal by $\rho \ell^3$ and take v_{turn} to be proportional to:

$$\sqrt{r_{\text{turn}}} \cdot \sqrt{\frac{F_{\text{slip}}}{\rho \ell^3}} = \sqrt{r_{\text{turn}}} \cdot \sqrt{\frac{F_{\text{slip}}/\ell^2}{\rho \ell}},$$

where the term F_{slip}/ℓ^2 ($\text{kg m}^{-1} \text{s}^{-2}$) is a constant representing the contact force of the animal’s limb with the ground. By combining this contact-force constant with the proportionality constant, we approximate:

$$v_{\text{turn}} \approx \sqrt{r_{\text{turn}}} \cdot \sqrt{\frac{k}{\rho \ell}},$$

where k ($\text{kg m}^{-1} \text{s}^{-2}$) is a family-specific contact-force constant. So, for the i th turn with a radius r_i , we set the target speed $v_{\text{end}, i}$ coming out of the preceding straight segment s_i to be:

$$v_{\text{end}, i} = \sqrt{r_i} \cdot c, \quad (6)$$

where c is an animal-specific agility constant with:

$$c = \sqrt{\frac{k}{\rho \ell}}. \quad (7)$$

By the approximation of v_{turn} above, the magnitude of this agility constant c is equivalent to the

maximum speed the animal can travel in a circle with 1 m radius. Moreover, as an animal's leg length ℓ decreases, its agility c increases and experiences less limitations in speed around tight turns. Intermediate-sized animals (~ 119 kg) have the fastest top speeds (Garland 1983; Hirt et al. 2017), but beneath this size, larger animals with longer limbs have faster top speeds. Our agility parameter thereby captures a speed–agility trade-off in animals of less than intermediate size (approximate mass of the largest terrestrial predators). Because the animal travels the constant speed $v_{\text{end},i}$ over the entire turn, the time spent in this turn is:

$$t_{\text{turn}} = \frac{a \cdot i \cdot r_i}{v_{\text{end},i}} = \frac{a \cdot i \sqrt{r_i}}{c}.$$

Calculating time to run along a straight line

Because we assume that each animal may travel a different constant speed on each of its turns, the animal must properly accelerate and decelerate along the straight paths between turns to match the speed leaving one turn with the speed entering the next. We calculate how to distribute acceleration, constant velocity, and deceleration time on each straight according to the flowchart shown in Fig. 1.

We first consider the case where the straight segment s_i is long enough for the animal to start from a speed v_{start} (e.g., the speed at the start of the simulation or the end of the previous turn), accelerate to maximal speed v_{max} , assume that maximal speed for some period of time, and then decelerate to the speed $v_{\text{end},i}$ of the upcoming turn. Thus, the time t_{s_i} on this segment is the sum:

$$t_{s_i} = t_{\text{acc}} + t_{\text{max}} + t_{\text{dec}}, \quad (8)$$

where t_{acc} , t_{dec} , and t_{max} are durations of acceleration, deceleration, and constant maximum velocity, respectively. Assuming the animal accelerates at constant, maximal acceleration a , the acceleration duration:

$$t_{\text{acc}} = \frac{(v_{\text{max}} - v_{\text{start}})}{a}. \quad (9)$$

Similarly, at the end of s_i , the duration decelerating at a constant, maximal deceleration d is:

$$t_{\text{dec}} = \frac{(v_{\text{max}} - v_{\text{end},i})}{d}, \quad (10)$$

where $v_{\text{end},i}$ is the speed required to make the next turn without sliding. To determine the duration of time the animal spends at constant maximal velocity v_{max} , one must subtract the distance traveled during

both the acceleration and deceleration phase from the total length s_i . The acceleration distance is:

$$\begin{aligned} x_{\text{acc}} &= v_{\text{start}} t_{\text{acc}} + 0.5 a t_{\text{acc}}^2 \\ &= v_{\text{start}} \left(\frac{v_{\text{max}} - v_{\text{start}}}{a} \right) + 0.5 \left(\frac{(v_{\text{max}} - v_{\text{start}})^2}{a} \right), \end{aligned}$$

which can be rearranged into the simpler expression:

$$x_{\text{acc}} = 0.5 t_{\text{acc}} (v_{\text{max}} + v_{\text{start}}). \quad (11)$$

Similarly, the distance traveled while decelerating is:

$$x_{\text{dec}} = 0.5 t_{\text{dec}} (v_{\text{max}} + v_{\text{end},i}). \quad (12)$$

Consequently, the distance traveled at constant velocity is:

$$x_{\text{max}} = s_i - x_{\text{acc}} - x_{\text{dec}}, \quad (13)$$

and the corresponding duration of constant velocity is:

$$t_{\text{max}} = \frac{x_{\text{max}}}{v_{\text{max}}}. \quad (14)$$

Although we ensured that straight lines are long enough to allow deceleration and acceleration between turns, we must consider the case in which the straight line is too short to achieve maximum speed. In these cases, one or both of t_{max} and t_{dec} may be zero. For this special case, we calculate a special $v_{\text{max},i}$ for this short segment, which represents the maximum speed achieved if the animal accelerates as much as possible before decelerating to reach $v_{\text{end},i}$ at the end of the segment. That is, we apply Equation (14), replacing v_{max} with:

$$v_{\text{max},i} = \sqrt{\frac{2 \cdot a \cdot d \cdot s_i + d \cdot v_{\text{start}}^2 + a \cdot v_{\text{end},i}^2}{a + d}}. \quad (15)$$

So the total time spent along the path is:

$$t_{\text{total}} = \sum_{i=1}^{N_t} (t_{s,i} + t_{\text{turn},i}) + t_{s, N_t+1}, \quad (16)$$

where t_{s, N_t+1} is the duration on the final straight segment when assuming that the animal finishes the path at its maximum speed v_{max} .

We tested how both animal and path characteristics affect the time to complete a curved path. For animals' characteristics, we computed times to complete a path for animals that differ in top speed, agility, acceleration, and deceleration. We used the measured characteristics of northern quolls, *Dasyurus*

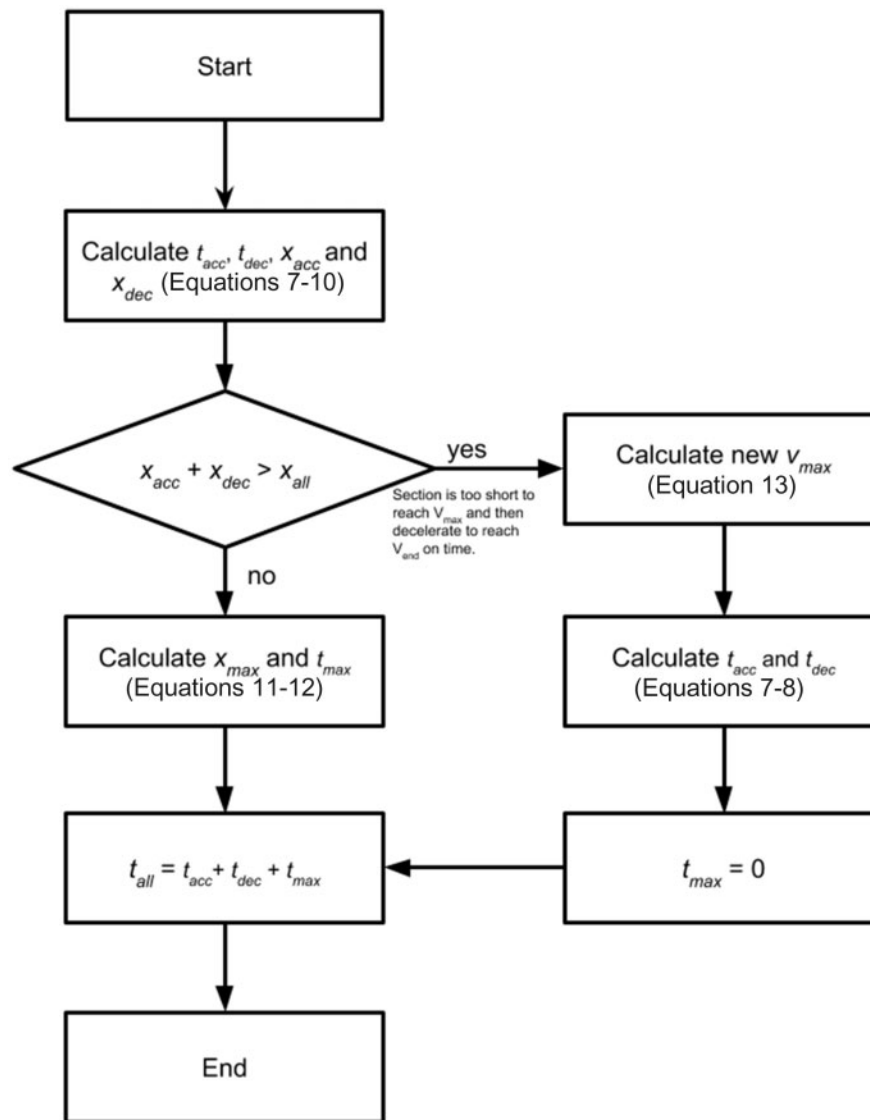


Fig. 1 Calculation of animal speed profiles on straight lines between curves in simulation. See “Methods” section for notations.

Table 1 The baseline parameters for our simulation analysis of time to complete a path

Parameter	Base measures		
Speed (m s ⁻¹)	4.5		
Acceleration (m s ⁻²)	9.0		
Deceleration (m s ⁻²)	9.0		
Agility (m s ⁻¹)	4.0		
Path length (m)	30 m		
Number of turns	6		
Curviness (rad m ⁻¹)	0.5	1.0	1.5

We used three different baseline values for curviness (0.5, 1.0, and 1.5 rad m⁻¹) and we varied each parameter by ±66%. We run each sensitivity analysis for 1000 randomly simulated curves.

hallucatus (Wynn et al. 2015), as the baseline for our analysis because it is one of the few species where we could estimate all performance parameters (Table 1).

We estimated the acceleration of northern quolls based on their average acceleration over the time taken to run from standstill to top speed rather than an animal’s maximum instantaneous acceleration. An animal’s time to reach top speed is more relevant to estimating the time to run along a path, rather than instantaneous acceleration. In particular, we calculated the time to complete a curved path (30 m length, 15 turns, and a curviness of 1.5 rad m⁻¹) for a northern quoll with ±66% values of top speed, agility, acceleration, and deceleration. To analyze how path characteristics affect the time to complete a path, we simulated the time it takes a northern quoll to complete the path with ±66% of path length, number of turns, and curviness. We ran each analysis for 1000 randomly simulated curves.

Modeling relative performances of prey and predators

To explore the relative performance of predators and prey, we estimated how limb length affected the time needed to complete paths of varying curvature. In particular, we calculated the travel time for animals with limb lengths of 12–30 cm along a path of 30 m and curviness of 0.01–2.5 rad m⁻¹. We ran our simulation 1000 times at each combination of limb length and path curvature. We then calculated relative performances of specific pairs of predators and prey, with survival occurring when prey finished a path of 30 m faster than the predator.

First, for each limb length, we calculated the maximum speed, acceleration, deceleration, and agility. Agility was calculated using Equation (7).

Maximum speed was calculated using the relationship defined by Garland (1983), as in Wilson et al. (2015a):

$$v_{\max} = 10^{1.478+0.2589 \cdot \log_{10}(\rho \cdot \ell^3) - 0.0623 \cdot \log_{10}(\rho \cdot \ell)^2}. \quad (17)$$

Then, to calculate acceleration and deceleration capacities, we first estimated body mass as described by Alexander et al. (1979) for fissipeds (separate-toed carnivorous mammals):

$$m = 162\ell^{0.34}. \quad (18)$$

We were then able to calculate the animal's minimum duty factor or the smallest possible fraction of the stride where the foot is on the ground (Alexander et al. 1981):

$$\beta = 0.1 m^{0.1}. \quad (19)$$

Using these values, we estimated the animal's maximum ground reaction force:

$$F_g = 4 \frac{m}{\beta}. \quad (20)$$

Finally, since force is equal to mass multiplied by acceleration, we used the maximum ground reaction force to estimate maximum acceleration capacity (a) by rearranging this equation as follows:

$$a = \frac{F_g - (9.8m)}{m}. \quad (21)$$

Based on unpublished data for northern quolls (R. S. Wilson, submitted for publication), we have taken maximum deceleration capacity to be equal but opposite to maximum acceleration capacity.

Results

Our model shows that path curviness can significantly increase the time it takes for animals to complete them. When the curviness of a path increased from 0.17 to 1.64 rad m⁻¹, the time to complete the path increased by >70%, from 7 s to ~12 s (Fig. 2). Animals also use a greater range of speeds when running along curvier paths. For example, when running along a path of 0.17 rad m⁻¹, almost all of the animal's time is spent at maximum speed, apart from the initial acceleration (Fig. 2A and B); in contrast, when it runs along a path with a curviness of 1.64 rad m⁻¹, then its speeds range between 30% and 80% of maximum (Fig. 2I and J).

Based on a sensitivity analysis with a base path curvature of 0.5 rad m⁻¹, the time to complete a path was most influenced by an animal's top speed, and subsequently by its agility, acceleration, and then deceleration. The time to complete a path took approximately two times longer when top speed was decreased by 66% from the baseline value for a northern quoll, while the time to complete a path was 10% shorter when top speed was 66% faster (Fig. 3A). However, as the base curviness of the path increased, so did the importance of agility, acceleration, and deceleration for determining the time to complete a path relative to top speed (Fig. 3). When the base curviness of the path was 1.50 rad m⁻¹, the animal's time to complete the path was highly sensitive to agility. The time to complete a path took ~1.6 times longer when an animal's agility was decreased by 66% from the baseline level, and there was a 25% decrease in time to complete a path when there was a 66% increase in agility (Fig. 3C). In contrast, the time to complete a path still took approximately twice as long when top speed was decreased by 66% from the baseline value for a northern quoll, but the time to complete a path was around only 5% when top speed was 66% faster (Fig. 3C).

When we linked the four performance attributes to limb length, we found that the time needed to complete a path was highly dependent on both path curviness and limb length (Fig. 4), with increased curvature dramatically slowing long-limbed animals. For example, an animal with 25 cm limbs (long-limbed) completes a 30 cm straight-line path 2.2 times more quickly than an animal with 14 cm limbs (short-limbed). Yet on a highly curved path, the short-limbed animal is faster. The longer the curvy path, the greater the slowing of long-limbed animals relative to short-limbed ones, both in terms of time

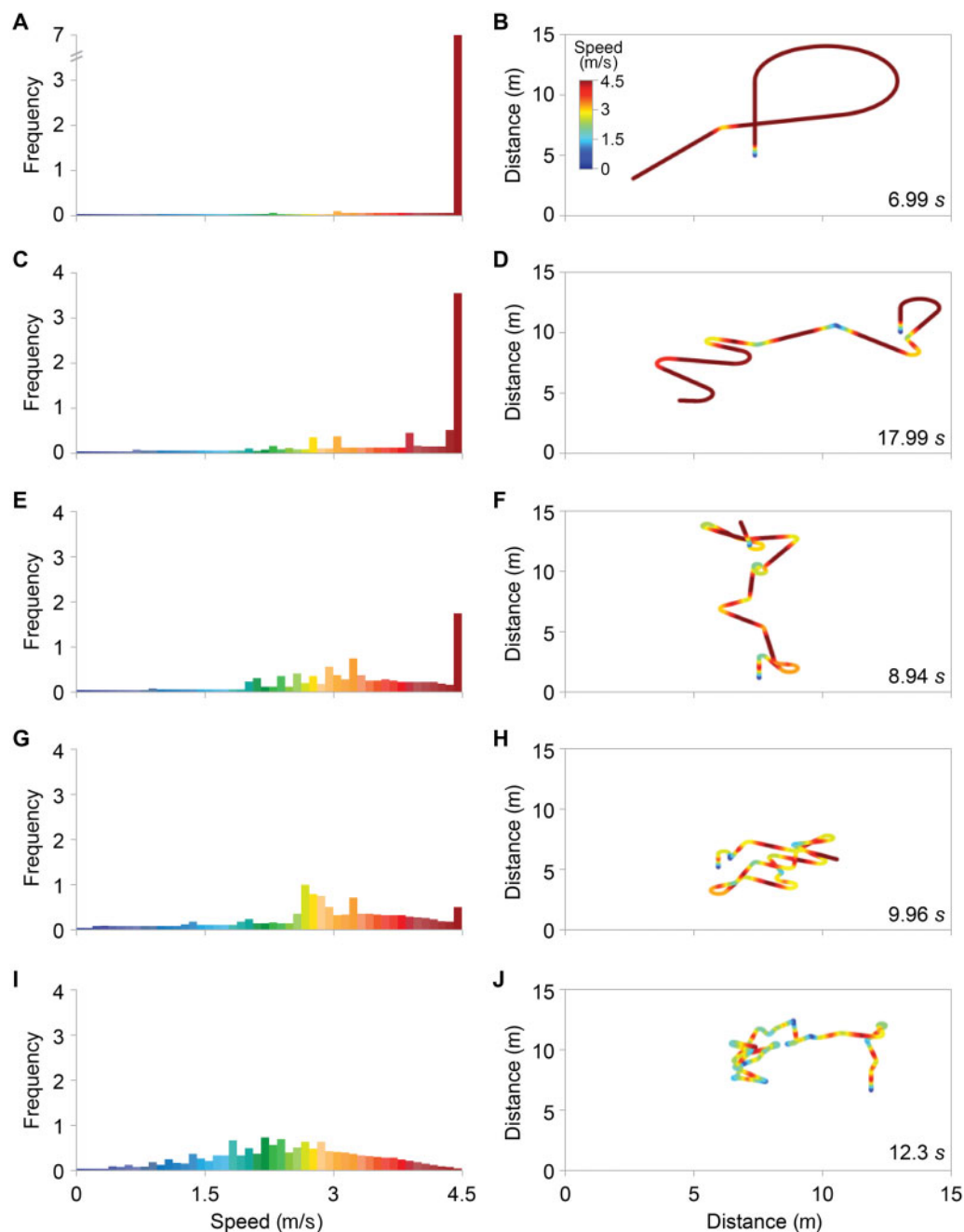


Fig. 2 Based on our model of running performance, we calculated the frequency distribution of speeds when running along paths with curvatures of 0.17 (A), 0.67 (C), 1.03 (E), (G) 1.24, and (I) 1.64 rad m⁻¹. We also show the instantaneous speeds along each section of the paths curvatures of 0.17 (B), 0.67 (D), 1.03 (F), (H) 1.24, and (J) 1.64 rad m⁻¹.

taken to complete the course and the median speed used to do so (Fig. 5A).

When we compared predators (longer-limbed) and prey (shorter-limbed), we found that path curviness dramatically affected the potential survival of prey (Fig. 5B)—assuming that prey would survive if they completed the path in the same time or faster than a predator. Furthermore, we determined the path curviness that theoretical prey would need to

run along to survive predation attempts by specific predators. For example, a prey animal with a limb length of 12 cm could outrun a predator with a limb length of 15 cm if they chose a 30 m path with a curviness of 1.0 rad m⁻¹ or greater (Fig. 5B). As the difference in limb length between predator and prey increased, the path curviness needed to survive also decreased (Fig. 6). Prey with a limb length of 12 cm could complete a 30 m path faster than a

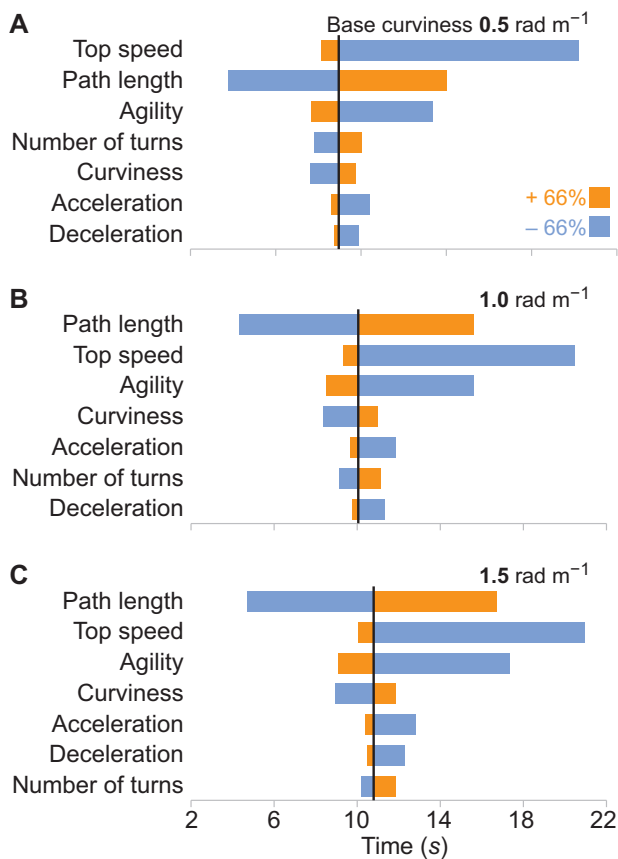


Fig. 3 We tested how the time to complete a path varied with changes in path length, curviness, number of turns, top speed, agility, acceleration, and deceleration. Each parameter was varied by $\pm 66\%$ while all other parameters were maintained constant at their baseline values (see Table 1). Each sensitivity analysis for 1000 randomly simulated paths with baseline path curviness of 0.5 (A), 1.0 (B), and (C) 1.5 rad m^{-1} . The order of traits is based on most (top) to least (bottom) important.

predator with a limb length of 25 cm if they selected a path with a curviness of 0.45 rad m^{-1} or greater (Fig. 6).

Discussion

We developed a model based on biomechanical principles to predict the optimal movements of prey during chases by predators. Though most studies of animal escape performance focus on top speeds, we show that top speed is only singularly important for straight-line paths and using top speeds is almost never the best option for an animal being chased by a larger, faster predator. Because large animals are likely to have greater sprint speeds but reduced agilities, our model suggests prey should use curvier paths when escaping pursuit predators. In addition, prey should choose paths that best suit their performances relative to the specific predator in pursuit. Running in straight lines away from a larger predator will play to the strengths of the predator because they are more likely to be faster than their prey. But running along curved paths will better suit the performance attributes of the smaller, more agile prey. The advantages of specific curved running paths are directly associated with the relative performances of the predator versus the prey. The closer the predator is in size (and therefore performance) to the prey, the curvier the path the prey must use to maintain any advantage. However, the greater the differences in size (and therefore straight-line running performance) between predators and prey, the wider the range of strategies (i.e., path curviness) that are feasible for the prey to use when escaping.

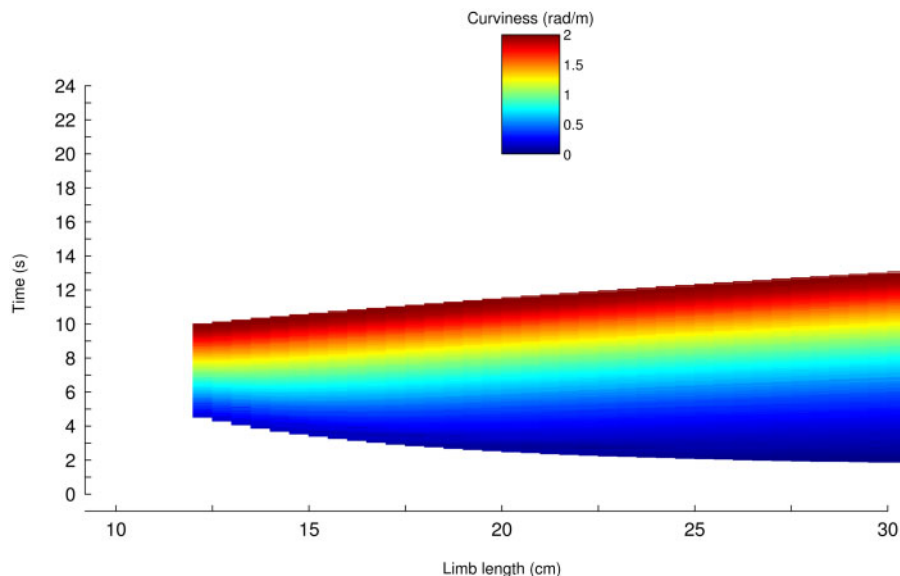


Fig. 4 The relationship between an animal's limb length and the time it takes to run along a 30 m path of different curviness.

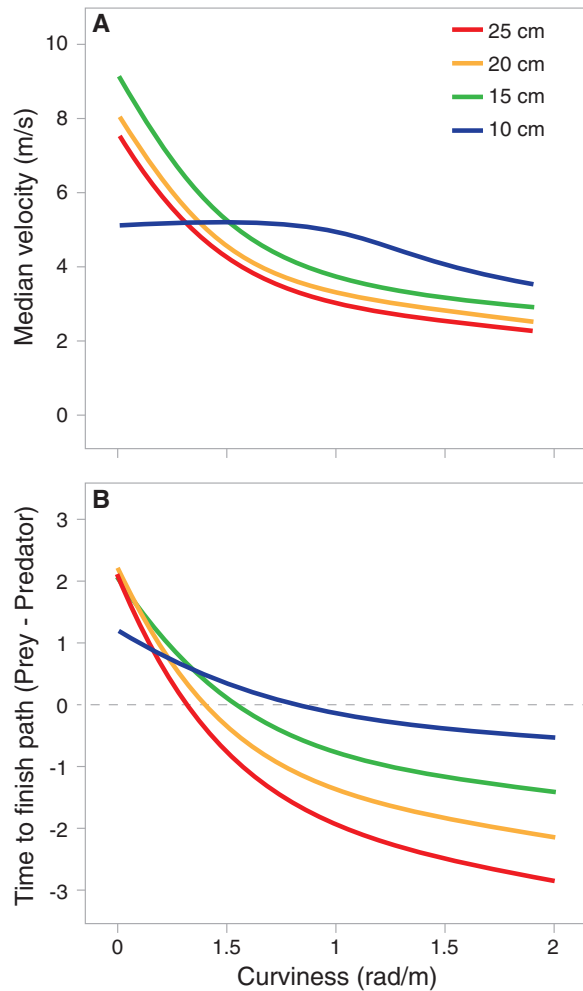


Fig. 5 (A) The relationship between curviness of a 30 m path and the median speed used by an animal with a limb length of 10, 15, 20, and 25 cm. (B) The relationship between the curviness of a 30 m path and the difference in time to complete the path between a prey of 12 cm limb length and predators of limb length of 15 (blue), 20 (green), 25 (yellow), and 30 cm (red).

Based on our model, we expect that prey should modify their escape behavior when running away from predators of different sizes. For aquatic animals, we know that salmon use more tortuous paths when attempting to escape from the larger, less agile orca (Wright et al. 2017), and tadpoles turn more when swimming away from predators during the developmental stages when they are most vulnerable to predation (Brown and Taylor 1995).

Our model assumes that predators and prey run along the same paths during pursuits, but this is unlikely in most predation events. In reality, predators will attempt straight-line shortcuts to intercept turning prey (Kane and Zamani 2014). It is obvious that when prey use too many turns then predators would not take the most direct and easy path toward the prey. Thus, our model may indeed overestimate

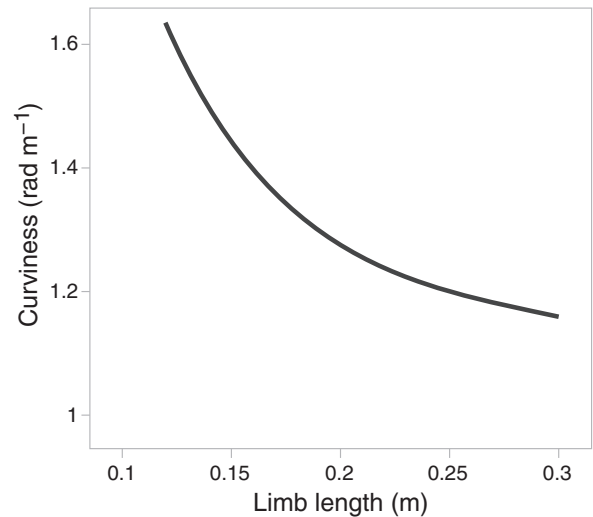


Fig. 6 The minimum path curviness that a 12 cm long prey can run along (30 m path) and survive against a predator of various limb lengths.

the benefits of highly-curved paths. Straight-line shortcuts cannot happen when obstacles prevent a direct path to the prey's new heading (Kruuk and Turner 1967; Wilson et al. 2015a)—in these cases, prey may use obstacles to their advantage, forcing predators to run along the curvier path. Also, the increased agility of small prey means that when predators are close behind them, any rapid change in direction is likely to cause the predator to overshoot in a straight line before they are able to follow the prey's turn (Howland 1974). Future studies should incorporate more realistic predator–prey pursuit models where predators can use shortcuts to head off prey and should incorporate factors that are likely to affect the advantages of using shortcuts like the degree of openness of an environment and the distance between the predator–prey during the pursuit. Empirical studies should also explore how habitat complexity affects the escape paths of prey running away from predators and their choice of escape speed. Our model also suggests prey should routinely use curvy paths when attempting to escape predators. However, the curviness of the escape path should be of limited consideration under some circumstances. For example, if a predator is detected when the prey is close to safety (brush, hole, log) then a straight-line trajectory to the point of safety should be taken, and their selected escape speed should be one that allows the prey to reach safety without risk of catastrophic mistakes. Future studies that model prey escape behavior could incorporate the predator and prey's relative performances, the distance between the two interacting organisms, and the prey's distance to safety.

Though our model assumes the scaling relationships devised by Garland (1983), which show maximum speeds increasing up to a certain “large-intermediate” body size before decreasing, there is a great deal of variation in maximum speeds, even between animals of the same size (Garland 1983; Hirt et al. 2017). The relationship between body size and acceleration is even more variable (Vanhooydonck et al. 2006). While scaling relationships suggest that acceleration should decrease with body size (Hill 1950), empirical studies have found that acceleration can increase with body size (Huey and Hertz 1984; Irschick and Jayne 1999), or have no relationship at all (Little and Williams 2005). The interaction between body size and posture is likely to be just as (if not more) important when it comes to many performance traits (Biewener 2003). Larger animals typically have more upright postures than smaller animals, which usually have more crouched postures and a lower center of mass (Biewener 2003). Though a more upright posture reduces the stresses acting on the limbs, it is also likely to reduce both agility and acceleration in larger animals (Biewener 2003). The speed-agility trade-off we model using limb length is also only likely to apply to smaller animals. For larger animals, such as cheetah and impala or lion and zebra, this trade-off in performance capacity seems not to be apparent (Wilson et al. 2018). It is clear that we need more empirical studies describing how body sizes and limb lengths affect performance parameters—or indeed how other morphological factors affect locomotor performance—across a variety of taxa to provide better predictive models of escape success, and these should be tailored to the specific species of predator and prey that are of interest.

Understanding how predators and prey interact via their relative performances could help us predict the impact of invasive predators on native ecosystems, and assist with developing useful management strategies for invasive species (Medina et al. 2011; Szabo et al. 2012; Bellard, Genovesi and Jeschke 2016). These issues form some of the greatest ecological challenges today (Ritchie and Johnson 2009). Studies of animal performance should be at the forefront of invasive species research. Yet an overreliance on maximum sprint speed as the single metric of escape performance has limited the contributions of performance research to ecological theory. Our model paves the way for a paradigm shift, showing that small prey should take advantage of their inherently better agility and run along curved paths when escaping larger, faster predators. But because few performance studies simultaneously

measure maximum speed, agility, and acceleration, we know little about how these chases manifest in nature. Predators and prey do not move in isolation but relative to each other and to environmental structures present within their habitat, and so it is time to consider escape performance as a relative measure that considers predators, prey, and their environment. In this way, studies of animal performance can provide powerful new insights and strategies for mediating the problem of invasive predators and understanding the mechanistic bases of predator–prey interactions. We hope that the theoretical framework we have built for understanding the dynamics of predator–prey chases will be taken up, tested, and expanded by empirical researchers. There is vast scope for work in this area.

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