



SYMPOSIUM

How Fast Should an Animal Run When Escaping? An Optimality Model Based on the Trade-Off Between Speed and Accuracy

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From the symposium “Towards a General Framework for Predicting Animal Movement Speeds in Nature” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2015 at West Palm Beach, Florida.

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Synopsis How fast should animals move when trying to survive? Although many studies have examined how fast animals can move, the fastest speed is not always best. For example, an individual escaping from a predator must run fast enough to escape, but not so fast that it slips and falls. To explore this idea, we developed a simple mathematical model that predicts the optimal speed for an individual running from a predator along a straight beam. A beam was used as a proxy for straight-line running with severe consequences for missteps. We assumed that success, defined as reaching the end of the beam, had two broad requirements: (1) running fast enough to escape a predator, and (2) minimizing the probability of making a mistake that would compromise speed. Our model can be tailored to different systems by revising the predator’s maximal speed, the prey’s stride length and motor coordination, and the dimensions of the beam. Our model predicts that animals should run slower when the beam is narrower or when coordination is worse.

Introduction

Animals perform a variety of motor tasks to survive, grow, and reproduce (Irschick et al. 2008). To quantify how well an animal can perform such tasks, ecologists routinely measure maximal performance across a range of environmental conditions (Garland 1984; Grant 1990; Robson and Miles 2000; Adolph and Pickering 2008). An individual’s maximal performance during standardized motor tasks is likely to reflect its performance during ecologically relevant activities. For example, the fastest prey should escape predators most often (Lopez and Martin 2002; Husak 2006), and the fastest predator should catch the most prey (Greenwald 1974; Domenici 2002). Similarly, the male with the hardest bite should best defend its territory from other males (Huyghe et al. 2005; Husak et al. 2006; Hall et al. 2010; Cameron et al. 2013). Thus, animals with higher capacities to perform should enjoy greater fitness (Adolph and Pickering 2008; Irschick et al. 2008).

Assuming an animal should always perform at its maximum implies that there is little or no cost associated with maximal performance. However, all levels of performance involve costs that may offset the benefits. For example, high speed comes at the cost of manoeuvrability (Vanhooydonck et al. 2001; Full et al. 2002; Van Damme et al. 2002). Consequently, cheetahs, which run faster than any other land mammal (Sharp 1997; Wilson et al. 2013), rarely hit their maximum during successful predation attempts (Wilson et al. 2013). Most studies of locomotion have been more concerned with the physiological causes and ecological consequences of maximal performance than with understanding how an animal chooses to use its performance capacity. Yet, ecologists should also focus on the level of performance that yields the greatest chance of successfully executing a task. Here, we develop a model based on biomechanical trade-offs associated with speed to predict how fast an animal should move when escaping a predator.

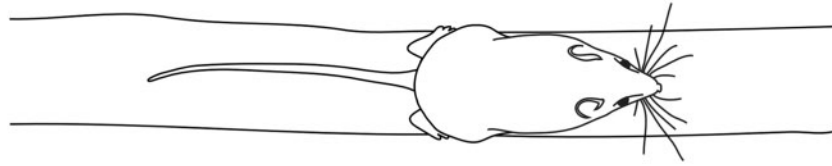


Fig. 1 An animal running along a branch to escape a predator (as viewed from above). The faster the animal runs, the more likely it is to outrun the predator; however the faster it runs, the less control it has over where it places its feet and the more likely it is to make a mistake and slip, which might result in its capture. To escape, it must therefore choose a speed that allows it to have the maximum probability of outrunning the predator, while minimizing its chance of making a large mistake. In other words, it must balance the trade-off between running speed and accuracy.

Because control and manoeuvrability declines as animals move faster, the speed that maximizes the probability of success often falls below the fastest possible speed (Wynn et al. 2015). As speed increases, so does physical resistance, or inertia, to changes in direction (Howland 1974). The faster an animal moves, the shallower it can turn without compromising stability (Howland 1974; Van Damme and Vanhooydonck 2002; Angilletta et al. 2008; Wilson et al. 2013; Wynn et al. 2015). Prey that have lower maximal speeds than their predators can take advantage of this constraint by rapidly changing direction when pursued (Howland 1974). Therefore, if a predator such as a cheetah is to catch its prey, it must pursue with a speed slow enough to mirror the prey's tight turns and complex manoeuvres. Consequently, cheetahs pursue their prey at speeds significantly slower than their maximum to compensate for the trade-off between speed and manoeuvrability (Wilson et al. 2013). Other predators use the same tactic (Howland 1974), meaning that the predator or the prey with the greatest locomotor capacity is not necessarily the most successful. But if animals should run slower than their maximum, how fast should they run when pursuing or being pursued?

The biomechanical trade-off between speed and accuracy also influences the success of the task. The faster or more powerfully an animal performs, the less effectively it controls its movement (Fitts 1992; Jayne et al. 2014). For example, consider an animal running along a branch to escape a predator (Fig. 1). The animal must run quickly enough to escape the predator while controlling the placement of its feet, because a mistake could result in its capture. The faster the animal runs without making a mistake, the more likely it is to escape. However, a faster speed reduces control and increases the chance of a mistake (Sinervo and Losos 1991). Thus, even from the prey's perspective, the fastest speed does not always result in the greatest chance of success. Functional trade-offs between speed and accuracy

are another reason why we must model the optimal level of performance for specific ecological scenarios (Howland 1974; Fitts 1992; Wynn et al. 2015).

Determining the optimal speed requires us to think in terms of successful performance rather than maximal performance (Howland 1974). Mathematical models provide us with concrete predictions that can be compared to values observed in nature (Crawley and Krebs 1992). Optimality models have been used extensively in theories that predict how an animal should balance the conflicting demands of predation, competition, and food availability when making decisions about foraging (Blanchard and Hayden 2015; Mohamad et al. 2015; Spiegel et al. 2015; Zimmermann et al. 2015). Despite the use of optimality models to solve a wide range of problems, they have not been used to understand how animals balance trade-offs in functional performance when selecting an appropriate speed for locomotion.

Here, we develop a simple model that predicts the optimal speed for an animal running from a predator along a beam (or branch). Modelling locomotion along a beam enables one to limit the trajectory of the animal to a straight line, thus exploring the trade-off between speed and accuracy without the confounding factor of manoeuvrability. Although many previous studies have quantified maximal speeds of animals during walking or running on beams (Losos and Sinervo 1989; Goldstein and Davis 1990; Llewellyn et al. 1990; Sinervo and Losos 1991; Losos and Irschick 1996; Speers et al. 1998; Buddeberg et al. 2004; Stanley et al. 2005; Vanhooydonck et al. 2006), none has attempted to predict the speeds that animals use when trading off speed and accuracy (Sinervo and Losos 1991).

To help others adapt and apply our model, we use a top-down approach to describe the model and explain its derivation. First, we consider the broad factors that contribute to success (making it from one end of the beam to the other). Then, we deconstruct the model to explore its details. Our model predicts

the optimal running speed that will result in the highest probability of reaching the end of the beam unscathed, which can then be tested by seeing whether an animal chooses to perform at its predicted optimum under different conditions. A mismatch between our model's predictions and observed speeds would mean either of two things: (1) our assumptions are inappropriate for the system (Crawley and Krebs 1992), in which case the assumptions should be empirically tested and refined, or (2) the animal moves at a suboptimal speed, in which case the basis for this decision can be inferred by testing the model under different ecological conditions.

Description of the model

To determine the optimal running speed, we must first consider the factors that contribute to the success of the task. Here, we define "success" as reaching the end of a straight beam while running from a predator. To achieve this goal, the animal must run fast enough to escape the predator while avoiding a mistake (such as slipping or falling) that would compromise speed to the point of capture. Therefore, we develop the model in three stages. First, we consider how speed affects the probability of escaping the predator. Next, we look at the probability of making a mistake, the probability that the mistake will have consequences, and how likely it is that the animal will overcome these consequences. Finally, we evaluate the probability of success by combining components from the previous stages to complete the model.

Probability of escaping a predator

If an animal hopes to escape a predator without turning or manoeuvring, it must outrun the predator with speed. We expect that the probability of outrunning the predator follows a sigmoidal relationship with speed (Fig. 2), assuming negligible effects of acceleration or endurance. When the prey's speed (s) is much slower than the predator's maximal speed, the probability of outrunning the predator (p_{escape}) will be close to 0, because the predator can easily capture the prey. As the prey's speed increases, p_{escape} will gradually increase until the prey's speed approaches the predator's maximal speed, where p_{escape} will be close to 1. When the prey's speed exceeds the predator's maximal speed, p_{escape} will equal 1, because the prey can escape by running faster than the predator.

The relationship between the speed of the prey and the probability of escaping a predator running

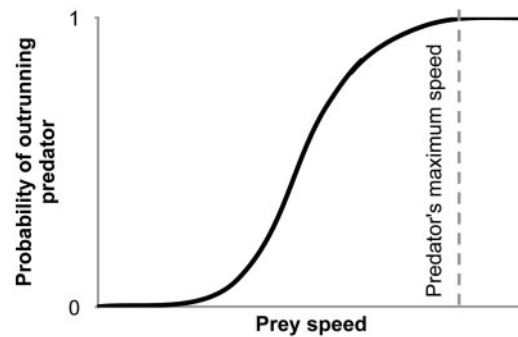


Fig. 2 Assumed effect of prey's speed on the probability of escape from a predator with a definable maximum speed. The solid line represents the probability of the prey's escape, whereas the dashed line represents the predator's maximum speed.

at a constant speed follows the function:

$$p_{\text{escape}} = \frac{Ke^{rs}}{1 + K(e^{rs} - 1)}, \quad (1)$$

where K and r set the speed at which survivorship equals 0.5 (Fig. 2), and therefore how rapidly an increase in speed improves the probability of survival.

Probability of overcoming a mistake

The probability of escaping the predator depends on more than their respective speeds. The faster an animal moves, the less effectively it can control its movements and the less accurately it places its feet (Fitts 1992; Jayne et al. 2014). Inaccuracy can lead to mistakes, which could trip or slow the animal, leading to injury or death. Different magnitudes of mistakes (or how badly the animal slips) have different consequences, ranging from minor mistakes that slow the animal to major mistakes that result in capture. The probability of success, then, depends not only on speed but also on the probabilities of making mistakes with minor to major consequences.

To visualize this problem, assume that the animal aims for the center of the beam, and imagine every possible placement of a foot (m) for a single step. When the animal runs slowly, it easily controls the placement of its feet, such that most steps land near the center of the beam and only a few miss by a small margin. When the animal runs quickly, it poorly controls the placement of its feet, such that some steps miss the center of the beam by a wider margin. The frequency distribution of all possible steps should approximate a symmetric distribution whose breadth increases with increasing speed (Fig. 3). Mathematically, we model this relationship with the probability density function for a Gaussian

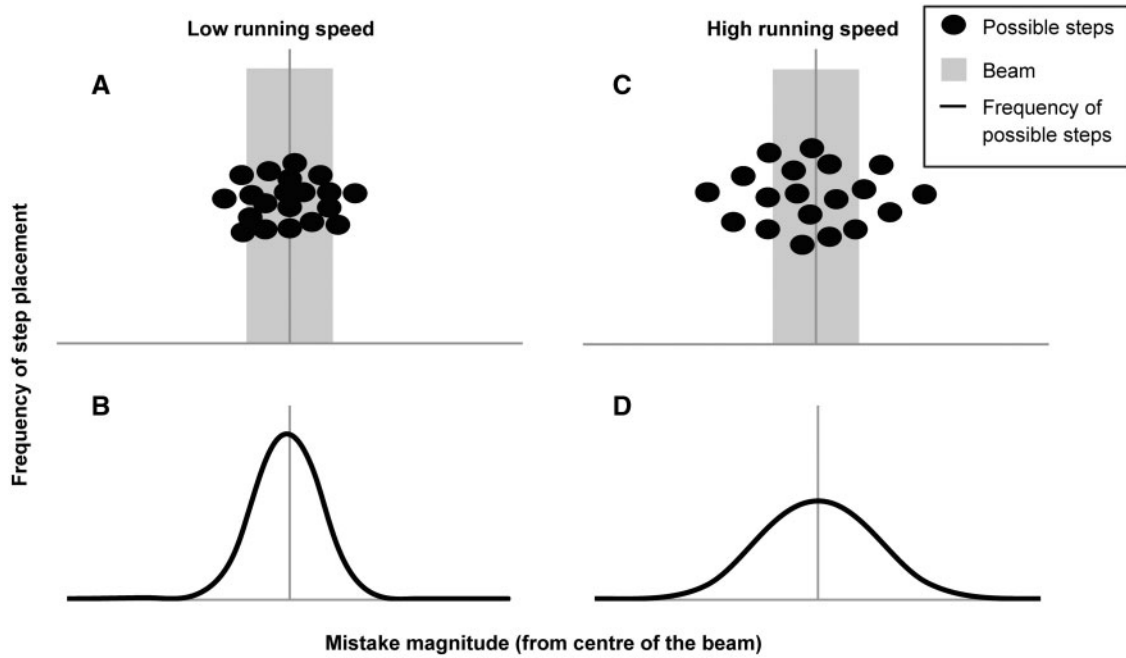


Fig. 3 An example of the frequency of foot-placement positions for a single step at a given running speed. In each case, the intersection of the axes is assumed to be the center of the beam, where the animal is aiming to place its feet. **(A)** Replicates of the foot's placement for a single step when the individual is running at a low speed; **(B)** Corresponding frequency distribution of step placements when the individual is running at a low speed. **(C)** and **(D)** are the corresponding graphs for an individual running at a high speed.

distribution centered about the y -axis (equivalent to the center of the beam):

$$f_m = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{m^2}{2\sigma^2}}, \quad (2)$$

where m is the magnitude of mistake (or the placement of the foot in relation to the center of the beam) and σ is the standard deviation, which represents the average magnitude of a mistake. By making σ a function of speed, we enabled a faster speed to cause a greater probability of a major mistake:

$$\sigma = c\sqrt{s}, \quad (3)$$

where c is an index of the animal's degree of coordination. Specifically, c equals the variation in foot placement, which is directly proportional to the variance of f_m . Individuals with a high value of c suffer a greater risk of mistakes when running at a faster speed than do individuals with a low value of c (Fig. 4). We assume that the variation of an individual's placement of feet has a positive linear relationship with speed. By substituting Equation (3) into Equation (2), we predicted the frequency of a mistake of each magnitude at any given speed.

We assume that, in every step, the animal aims to place its foot in the center of the beam; however, the animal makes mistakes when its feet miss the beam. Depending on the width of the beam, some mistakes

have no consequence since the animal's feet still land on the beam. For a beam of width (w), a mistake of zero magnitude occurs when the animal's foot hits the center. Since no mistake was made, the probability of continuing to run after that step equals 1 (Fig. 5). Moreover, a mistake $\leq 0.5w$ has no effect on the probability of continuing the run as the animal's foot is still on the beam. If the mistake causes the animal's foot to miss the beam by a small amount, we assume that the animal will right itself quickly and continue running, such that the probability of continuing to run is still close to 1. As the animal's foot misses the beam by a wider margin, however, we assume the animal requires more time to right itself and continue running, such that the probability of continuing decreases. If the animal's foot misses the beam by such a large margin that it falls, its probability of continuing to run equals 0.

To represent this relationship mathematically, we used two logistic functions: one for mistakes on the left side of the beam (from $-\infty$ to 0) and another for mistakes on the right side (from 0 to ∞). To scale these functions according to the width of the beam, we modified the generic logistic function as follows:

$$p_m = \frac{1}{1 + e^{\theta - \theta e^{-0.5w(\pm m) + (0.6w)}}}, \quad (4)$$

where p_m is the probability of continuing to run after a mistake of magnitude m , and θ is a constant that affects

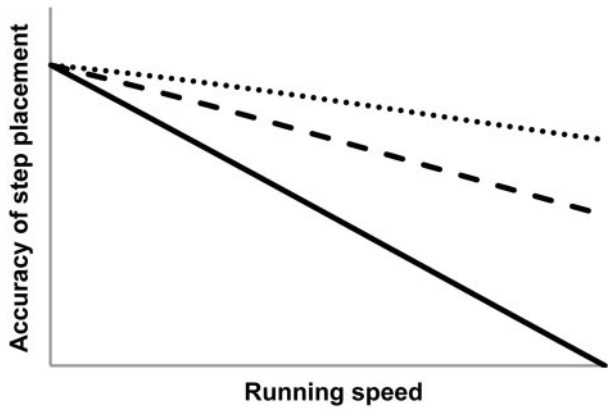


Fig. 4 An example of the effect of running speed on the accuracy of step placement for three different individuals. Speed has a strong effect on individual **A**'s accuracy (solid line), whereas it has a smaller effect on individual **B**'s accuracy (dashed line), and an even smaller effect on individual **C** (dotted line). We are assuming that speed has a negative linear effect on accuracy; and, inversely, a positive linear relationship with the variation in an individual's placement of steps.

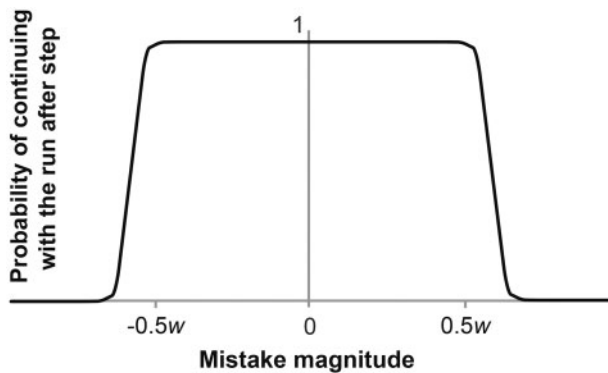


Fig. 5 Assumed effect of a mistake for any placement of a foot on the probability of continuing with the run after that step on a beam of constant width (w). The y -axis is assumed to be the center of the beam where the animal is aiming to place its foot. A mistake only affects the probability of continuing with the run if the animal's foot misses the beam (i.e., the mistake has a magnitude of $\pm 0.5w$).

how steeply the function rises or falls as it passes through its midpoint. Thus, θ determines the point where a mistake of unrecoverable magnitude occurs.

We now have functions for the frequency of making a mistake of magnitude m , f_m (Equation (2)), and the probability of continuing to run after that mistake, p_m (Equation (4)). However, we still must calculate the probability of continuing to run after any given step. Importantly, the integral of f_m equals the probability of a step falling somewhere along the distribution of possible placements, or 1

(Patel and Read 1996). To calculate the probability of making a mistake of magnitude m , we integrated f_m between points at minute distances on either side of m (Fig. 6A). The area beneath the curve between these points approximates the probability of making a mistake of magnitude m . If we multiply this area by the probability of continuing to run after a mistake of magnitude m , given by p_m (Fig. 6B), we get the probability of the animal continuing to run after that step. To obtain the probability for an individual continuing with the run after any given step, we repeat this process for every possible foot placement and then sum the results as follows:

$$p_s = \int_{-\infty}^0 f_m(-p_m) + \int_0^{\infty} f_m p_m, \quad (5)$$

Probability of success

Equation (5) yields the probability of continuing to run after a single step. However, depending on the length of the beam (l) and the animal's length of stride (l_s), numerous steps will be required to reach the end of the beam. Although the length of the beam remains constant, the animal's length of stride depends on the length of its limbs and the speed at which it runs (Rocha-Barbosa et al. 2005; Herbin et al. 2006; Maes et al. 2008; Hudson et al. 2012; Shapiro and Young 2012). The faster the animal runs, the longer its stride becomes; but every individual has a maximal stride length ($l_{s \text{ max}}$) set by anatomical constraints such as the length of the limb (Fig. 7). Therefore, we expect the stride length to have a bounded logistic relationship with speed:

$$l_s = l_{s \text{ max}} - (1 - \delta)e^{-\delta s}, \quad (6)$$

where δ is the rate of increase in stride length with increasing speed, and thus affects the smallest stride length at the slowest speed. The number of steps, then, simply equals the length of the beam divided by the length of each stride at the chosen speed, assuming no acceleration phase:

$$\text{steps} = \frac{l}{l_s}, \quad (7)$$

Assuming that the probability of continuing after any given step is independent of that for previous steps, we can calculate the probability of reaching the end of the beam by raising p_s to the number of steps:

$$p_{\text{continue}} = p_s^{\text{steps}}, \quad (8)$$

We now have the probability of escaping the predator (p_{escape}) and the probability of reaching the end of the

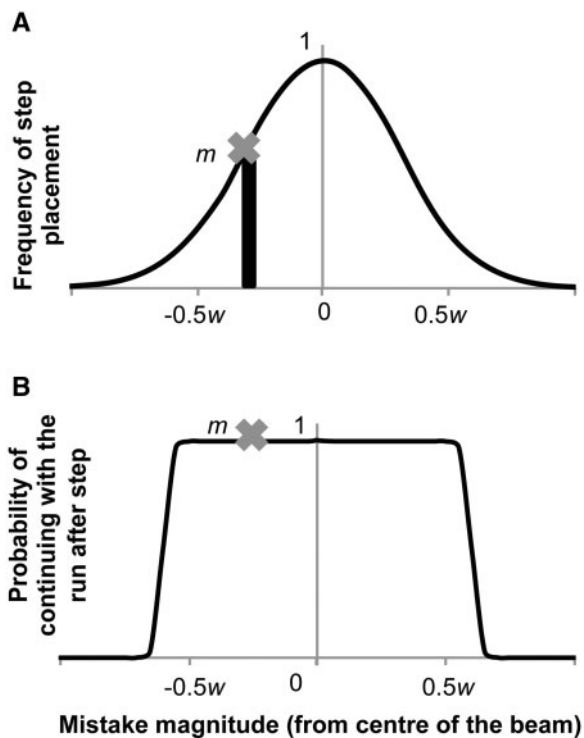


Fig. 6 Process of calculating the probability of continuing with the run after any given step for an animal running along a beam. (A) If we integrate under our frequency distribution of possible placements of steps, f_m , between points at minute distances on either side of the magnitude of mistake in which we are interested (m), the resulting area approximates the probability of making a mistake of that magnitude. Multiplying this area by (B) the probability of continuing with the run after a mistake of magnitude m , given by p_m , will result in the probability of continuing with the run after that step. If we repeat this process for all possible values of m and sum our results, we have the probability of continuing with the run after any given step.

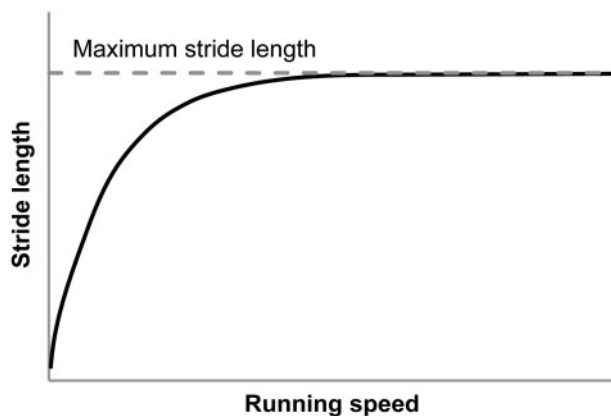


Fig. 7 Assumed shape of the effect of running speed on the length of stride. The solid line represents the stride's length as it changes with speed, whereas the dashed line represents the individual's maximum length of stride (constrained by anatomical properties such as the length of the limb).

beam, given all steps (p_{continue}). The probability of success (reaching the end of the beam without being captured; p_{success}) equals the product of p_{escape} and p_{continue} :

$$p_{\text{success}} = p_{\text{escape}}p_{\text{continue}}, \quad (9)$$

Implementing the model

To assess whether our model generated plausible outcomes based on our assumptions, we fitted hypothetical values to K , r , θ , and δ (0.0001, 0.01, -3.5 , and 0.04, respectively), which we estimated for a small quadruped. However, to generate numerical estimates comparable to a real animal's performance, a set of preliminary data would have to be collected and appropriate values fitted for K , r , θ , and δ such that the shape and scale of the relationships defined in the model accurately represents those for the species of interest.

Once we were satisfied that the model produces realistic outcomes, we explored the sensitivity of optimal running speed to changes in running speed ($10\text{--}200\text{ cm s}^{-1}$), individual coordination (variation in step placement of $0.025\text{--}0.175$), and beam width ($2\text{--}12\text{ mm}$). To determine the optimal speed for a given scenario (parameter values), we calculated the probability of success for every possible speed to identify the speed that yielded the maximal probability of success. All calculations were made by a computer program written in Python (Python Software Foundation, Python Language Reference, version 2.6.5). Finding the solution for each scenario took $\sim 12\text{ s}$. The computer code is available as supplementary material.

Results

We explored the effects of the width of the beam and individual coordination on optimal running speed (Fig. 8). Optimal speed is slower on narrower beams, because only smaller mistakes are tolerated as the room for error decreases. Similarly, when the placement of step varies more (a reflection of poor coordination), animals should run slower to avoid missing the beam. Hence, the fastest runners should be those animals with the greatest coordination running on a wide beam.

We also examined how the degree of coordination and the width of the beam interact to determine the optimal running speed (Fig. 9). On a narrow beam, coordinated individuals have a higher optimal speed than do uncoordinated individuals; in other words, individuals who step more accurately perform better

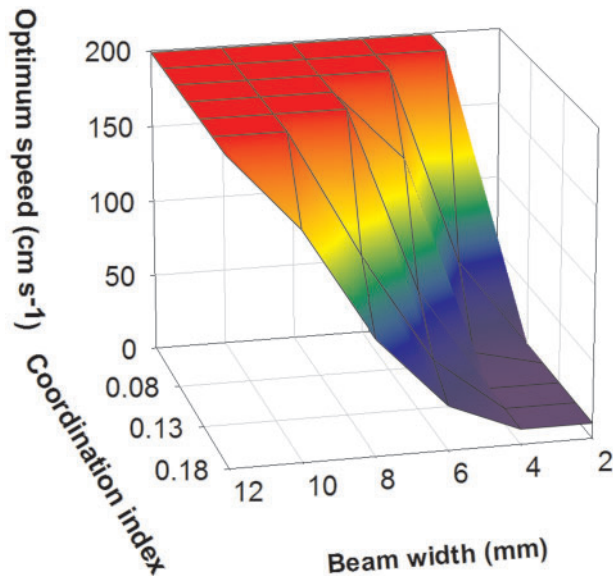


Fig. 8 Simulated effects of width of the beam and an individual's coordination on the optimal running speed for individuals with the same maximal speed. Warm/light tones represent fast optimal running speeds, and cool/dark tones represent lower optimal running speeds. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

at high speeds. As the width of the beam increases, optimal speed also increases. This effect of beam width occurs regardless of the animal's coordination, because slipping becomes less likely on wider beams (Losos and Sinervo 1989; Losos and Irschick 1996). Therefore, all individuals should run fast on the widest beams.

Discussion

The ability to perform tasks adequately to acquire resources, avoid predators, and reproduce is essential for all animals (Irschick et al. 2008). Despite this realization, we still cannot predict the levels of performance that give an animal its best chance of success in a given task. Given functional trade-offs, the optimal performance is not always maximum performance (Howland 1974; Fitts 1992; Wynn et al. 2015) and likely depends on the ecological context (Wynn et al. 2015). To encourage a quantitative exploration of optimal locomotor performance, we created a model that predicts the optimal speed for an animal running along a beam. By parameterizing the model for a small quadrupedal animal, we examined the behavior of the model in relation to our expectations. As we expected, the optimal speed decreased as the difficulty of the task increased (as the width of the beam became thinner), and as the animal's coordination decreased. Because of the vast

range of situations in which such trade-offs are likely to constrain performance, we wanted to develop a model that could easily be modified to suit different systems or scenarios. Obviously, the model applies to studies of animals walking or running on beams (Losos and Sinervo 1989; Goldstein and Davis 1990; Llewellyn et al. 1990; Sinervo and Losos 1991; Losos and Irschick 1996; Speers et al. 1998; Buddeberg et al. 2004; Stanley et al. 2005; Vanhooydonck et al. 2006), but the model is not limited to these situations. Width of the beam can be set as constant for studies that do not vary the width of the substrate; similarly, the runway need not be a beam. We constructed the model as if the individual were evading a predator, but one can modify the model to focus on a predator pursuing prey, merely by changing the relationship defined by Equation (1). The model can be parameterized for any animal running in a linear dimension when a trade-off between speed and accuracy exists.

The relationships described by our model are essential for calculating an animal's optimal performance. However, the shapes of these functions are largely hypothetical, because they have never been quantified empirically. Although we assumed a sigmoidal relationship between the prey's speed and its probability of escape (Equation (1)), this relationship may not hold for real animals. To predict an animal's optimum speed while fleeing a predator, we must also know how speed affects its probability of making a mistake (Equation (2)) and the relationship between the magnitude of these mistakes and the prey's speed (Equation (4)). Since these functions have not been measured empirically but have the potential to influence optimal speeds, researchers should quantify the shape of these functions if they wish to predict optimal speeds for real animals. Many factors could influence the shape of these relationships, but we cannot include them in our model without some estimates of their importance. These factors include whether mistakes with different feet have equal costs (e.g., forelimb versus hind limb), whether missing the beam completely impedes recovery more than a slip does, and whether substrate or style of gait affects any of these relationships. To achieve a theory of optimal performance that makes accurate predictions, we encourage empiricists to quantify these relationships in a variety of species and contexts.

Differences between simulated and observed values are interesting, because they can reflect decisions the animals make in different circumstances (Motta and Pappalardo 2013). Whether an individual chooses to perform at its optimum across contexts depends on a

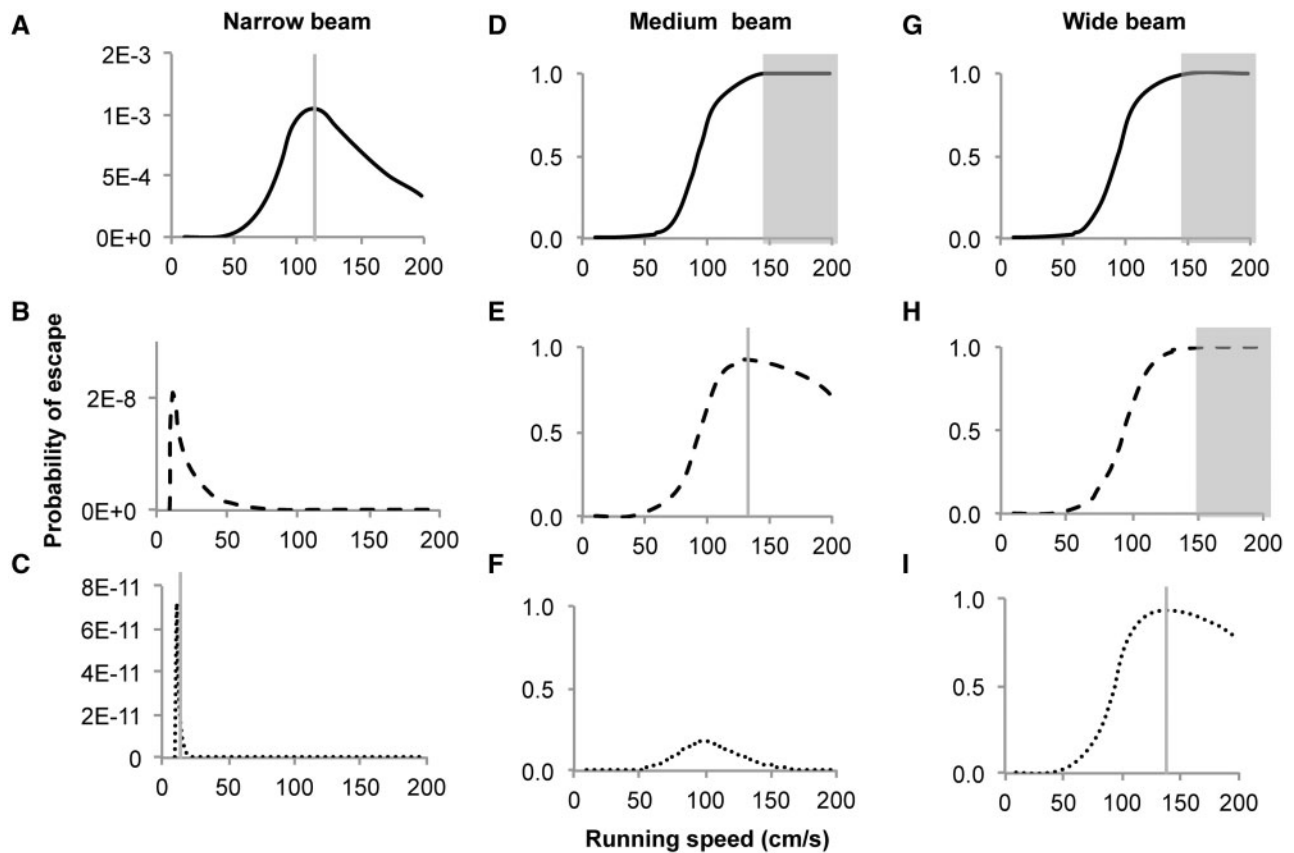


Fig. 9 Simulations showing the effect of running speed on the probability of escape from a predator when running down a beam of length 180 cm and width of 2 mm (**A, B, C**), 7 mm (**D, E, F**), and 12 mm (**G, H, I**) for three individuals with different coordination. One individual has low variation in step placement (good coordination) of 0.025 (solid line), another has medium variation (average coordination) of 0.1 (dashed line), and the last has high variation (poor coordination) of 0.175 (dotted line). The optimal running speed, which results in the highest probability of escape (or the peak in each curve), is dependent both on width of the beam and on the individual's coordination, and is represented by a gray line or bar.

variety of factors, such as the energetic cost of optimal movement (Bennett 1986), the individual's condition or capabilities (Wilson and Nussey 2010; Lailvaux and Kasumovic 2011; Wilson et al. 2014), and the cost of failure (Metcalf and Ure 1995; Carrascal and Polo 1999). If the cost of failure is low and the energetic cost of optimal movement is high, an animal may choose to risk failure rather than perform optimally. Similarly, if the perceived cost of failure is high, such as when the beam is thin or high above ground, an animal may run slower than the optimal speed because of the perceived risk of running faster. In poor condition or with limited experience, an animal might be incapable of running at the optimal speed without paying some cost beyond the risk of predation. When running at the optimal speed yields only a small chance of survival, an animal may adopt a different strategy entirely such as jumping from the beam.

Mathematical models of biological systems have limitations (Motta and Pappalardo 2013), and no

model will predict the exact performance of animals in nature. However, large discrepancies between predicted and observed speeds would tell us that important factors are missing from the model. Our model can be refined if any assumptions are shown to be invalid. Depending on the locomotory task, the effect of coordinating limbs is likely to be significant for certain animals (Corbetta and Thelen 1996; Reisman et al. 2005). If the effect were significant for the system under observation, the model could be modified to account for this effect. Similarly, several studies have found reaction times and acceleration, rather than speed, to be important for escaping predators (Webb 1976; Elliott et al. 1977; Huey & Hertz 1984). Although our model assumes no acceleration phase, this assumption is likely to be violated by real organisms. We encourage others to modify our model to explore the effects on optimal performance, as optimization has proven a valuable technique for understanding the movement of animals (Crawley and Krebs 1992; Czaczkes 2014; Janssen and Hill 2014;

Blanchard and Hayden 2015; Mohamad et al. 2015; Spiegel et al. 2015; Zimmermann et al. 2015). By developing and applying optimality models, we can understand why animals move at the speeds they do in nature and infer the consequences for interactions within and between species.

Acknowledgments

We would like to thank Chris Brown from the Global Change Institute for recommending literature regarding modelling techniques; all members of the Wilson and Angilletta research groups for input and advice during the derivation and writing; Andrew Maynard for allowing us to use his artwork in Figure 1; the Society for Integrative and Comparative Biology for allowing us to present this work in the symposium; Company of Biologists for financial support to attend the conference; and our various funding sources for making this work possible.

Funding

This work was supported by an Australian Postgraduate Award from the Australian Federal Government to RW, an Australian Research Council Discovery Grant to RSW (DP150100198), an Australian Research Council Discovery Early Career Research Award to ACN (DE130101410), and the Society for Integrative and Comparative Biology.

Supplementary data

Supplementary data available at *ICB* online.

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