SYMPOSIUM

Predicting the Movement Speeds of Animals in Natural Environments

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Synopsis An animal’s movement speed affects all behaviors and underlies the intensity of an activity, the time it takes to complete it, and the probability of successfully completing it, but which factors determine how fast or slow an animal chooses to move? Despite the critical importance of an animal’s choice of speed (hereafter designated as “speed-choice”), we still lack a framework for understanding and predicting how fast animals should move in nature. In this article, we develop a framework for predicting speed that is applicable to any animal—including humans—performing any behavior where choice of speed occurs. To inspire new research in this area, we (1) detail the main factors likely to affect speed-choice, including organismal constraints (i.e., energetic, physiological, and biomechanical) and environmental constraints (i.e., predation intensity and abiotic factors); (2) discuss the value of optimal foraging theory in developing models of speed-choice; and (3) describe how optimality models might be integrated with the range of potential organismal and environmental constraints to predict speed. We show that by utilizing optimality theory it is possible to provide quantitative predictions of optimal speeds across different ecological contexts. However, the usefulness of any predictive models is still entirely dependent on being able to provide relevant mathematical functions to insert into such models. We still lack basic knowledge about how an animal’s speed affects its motor control, maneuverability, observational skills, and vulnerability to predators. Studies exploring these gaps in knowledge will help facilitate the field of optimal performance and allow us to adequately parameterize models predicting the speed-choice of animals, which represents one of the most basic of all behavioral decisions.

Introduction

Movement is fundamental to animal behavior, governing the way animals use habitats, interact with conspecifics, avoid predators, obtain food, and even negotiate human-modified landscapes. A wide range of factors drive movement, including an animal’s internal state (why move?), motion (how to move?), and navigational decision-making (when and where to move?). The rapidly expanding field of the ecology of movement offers a unifying paradigm for the causes, consequences, underlying mechanisms, and patterns of movement-related phenomena (Nathan et al. 2008), but what determines how fast an animal chooses to move? This may seem like a simple question, but it is a key one: speed underlies the intensity of an activity, the time it takes to complete it, and the probability of successful completion. Despite the universal importance of speed and its central role in ecology, we still lack a framework for understanding and predicting how fast or slow animals should—or do—move through their environments. The goal of this article is to construct such a framework, and thereby facilitate studies of movement speed that integrate its biomechanical, energetic, and ecological foundations.

This kind of integration is not entirely new: the functional traits of individuals—such as morphology, physiology, and biochemistry—have long been linked...
with reproductive success and survival via whole-animal performance (Bartholomew 1966; Arnold 1983; Bennett and Huey 1990). Whole-animal performance is usually defined as the maximum speed or effort an individual can attain in a task relevant to their fitness. The integration of the function of whole-animal performance into studies of the evolution of form and function was initially driven by the realization that this level of function is more closely related to fitness than to lower-level traits (Huey and Stevenson 1979; Bennett 1980). However, the intuitive appeal of maximum performance as a critical link between the phenotype and fitness has led to an almost exclusive focus on maximal performances when studying the determinants of success (Jayne and Bennett 1990; Miles 2004; Irschick and Meyers 2007; Wilson et al. 2007a; Irschick et al. 2008). Some studies have provided clear evidence supporting this assumption. For example, faster juveniles and adults of the lizard *Urosaurus ornatus* were more likely to survive until the next sampling period than were slower individuals (Miles 2004; Irschick and Meyers 2007).

Despite the obvious appeal that higher performers should have greater fitness, field observations show that animals rarely move at their maximum capabilities in nature (Jayne and Ellis 1998; Irschick 2002; Husak and Fox 2006) (Fig. 1).

A common interpretation of the rare use of maximal capacities is that animals should only use these during rare fitness-defining activities like escaping predators or capturing prey (Hertz et al. 1988; Irschick et al. 2005). However, even during these infrequent events, when success really matters, maximal speeds rarely are used (Irschick et al. 2005; Wilson 2005; Husak and Fox 2006). For example, collared lizards (*Crotaphytus collaris*) use only 30–40% of their maximal capacity when trying to capture a simulated prey item and similar speeds when attempting to capture real prey in the wild (Husak and Fox 2006). Animals tend to use a greater proportion of their maximal capacity when running away from predators (Irschick et al. 2005; Husak and Fox 2006), but still it is often only 60–80% of their maximal capacity (Husak 2006a). The use of sub-maximal speeds when performing fitness-defining tasks is not just limited to lizards. Males of the eastern mosquitofish (*Gambusia holbrooki*) only obtain successful copulations using coercive swimming tactics in which they approach a female with stealth, place their intromittent organ (gonopodium) into the female's gonadopore, and release their packages of sperm (Wilson 2005). Obviously, the ability to obtain coercive matings is a critical determinant of a male’s reproductive success for *G. holbrooki*, but the approach speeds used by males to obtain copulations are only about 30% of their maximal speed of swimming (Wilson 2005). Rather than being surprised by the low speeds of animals during critical fitness-defining behaviors, we should ask ourselves why animals rarely use their maximal capabilities and how can we begin to predict the speeds they choose in natural environments?

The expectation that faster is always better is overly simplistic. Maximum speeds are energetically costly (Hoyt and Taylor 1981; Steudel-Numbers and Wall-Scheffler 2009), constrain motor control and maneuverability (Alexander 1982; Wynn et al. 2015), and may affect visibility and safety (Bednekoff and Lima 1998; Treves 1998). Therefore, the speed of movement, even during extreme situations like escaping predation, should be based on a compromise between a range of factors. Such constraints on speed also impact humans’ behavior during everyday activities—intuitively, we are all aware of this. Humans rarely use their maximal speeds for common daily tasks because high speeds increase energetic costs (Steudel-Numbers and Wall-Scheffler 2009) and can decrease the control and accuracy of a movement (Fitts 1954). Just consider how one would approach typing out a text message if one were already late to an important meeting. We may not wish to be even later to the meeting—especially given the social costs of delaying colleagues—so getting the text message done without delay may make rapid typing favorable. However, typing requires accurate finger placement and a potential mistake, which is more likely at higher speeds, could be very costly, both because of the social

![Figure 1](https://example.com/figure1.png)

**Fig. 1** Distributions of speeds used by lizard species while capturing prey or escaping predators. Data compiled from Irschick and Losos (1998), Jayne and Ellis (1998), Irschick and Jayne (1999), Irschick et al. (2005), Husak and Fox (2006), and Muñiz Pagan et al. (2012).
embarrassment of sending a message that is full of mistakes and because it may be incomprehensible. Typing at a slower, more measured speed is likely to improve readability of the message and decrease any chances of having to retype a message. In this case, there may be an optimal speed for finger movement that is a compromise between speed, accuracy, and social constraints. We expect similar constraints to operate on the speeds of animals across natural ecological contexts, with the ultimate selection of speed based on a compromise between competing demands.

In this article, we develop a framework for predicting speed that is applicable to any animal—including humans—performing any behavior where choice of speed occurs. Testing these ideas will require a trans-disciplinary approach, incorporating expertise from the fields of metabolic physiology, neurophysiology, biomechanics, mathematical modeling, behavior, evolution, and ecology; in fact, the diverse expertise required to effectively study speed-choice is probably why the field has not progressed further. To inspire new research in this area, we will (1) detail the main factors likely to affect speed-choice, including organismal constraints (i.e., energetic, physiological, and biomechanical) and environmental constraints (i.e., predation intensity and abiotic factors); (2) discuss the value of optimal foraging theory in developing a model of movement speeds; and (3) describe how optimality models might be integrated with the range of potential organismal and environmental constraints to predict speed. We then consider how a framework for predicting speed-choice might be used in the fields of animal behavior, evolution, conservation biology, and sports science. Finally, we discuss the significance of predicting the movement speed of animals in studies exploring the ecology and evolution of organismal performance.

**Building a universal framework for predicting animal movement speeds: what factors affect speed-choice?**

Speed-choice is a complex trait, driven by an animal’s need for food and sociality but constrained by energetic costs and the risk of injury or death. In this section, we outline the factors that we expect to affect speed and the parameters that will form the basis of our predictive framework. Although this is certainly not an exhaustive list, we expect these to be the main drivers of speed-choice across most ecological contexts (Fig. 2). We have divided these factors into internal constraints, which include the morphological, physiological, and neurobiological features inherent to the individual and external constraints, which include the biotic and abiotic factors outside it.

**Internal factors affecting the choice of speed**

Increasing speed changes the biomechanics of movement and reduces an individual’s ability to observe their environment. Consequently, we expect speed-choice to be influenced by (1) the energetic costs of movement, (2) trade-offs between speed and maneuverability, (3) trade-offs between speed and motor control, and (4) the costs associated with detection of the environment (i.e., predators, prey, mates, or obstacles) during movement. The individual’s state—including its body size, mass, sex, condition, and life stage—should mediate these factors.

**Energetics of movement**

Locomotion is expensive, and the energetic costs of movement are likely to be a major driver of an animal’s choice of speed in nature. As an animal moves through a varied landscape, it expends energy differently, depending on how fast it is going and the characteristics of the terrain it is traversing. For many animals moving across level ground, the rate at which energy is spent increases in direct proportion to the speed of the movement (Schmidt-Nielsen 1972; Taylor et al. 1982). This would seem to suggest that individuals expend energy at the same rate when moving themselves, regardless of speed, and that there is no energetic advantage to moving slowly versus quickly. However, movement bears fixed costs not associated with speed: animals expend energy for facilities not related to movement—even as they move—and appear to pay an energetic price simply for striking a posture for locomotion (Halsey 2013) (Fig. 3A). Because of this, lower speeds are actually more costly per unit distance (net cost of transport or NCOT), as fixed costs must be paid over a greater period of time (Fig. 3A).

For some species, the NCOT varies in a complex way with speed (Fig. 3B). Such species, which include humans, horses, ratites, salmon, and budgerigars, have also been observed to alter their speeds in ways that minimize NCOT while moving (Tucker 1968; Hoyt and Taylor 1981; Farrell et al. 2003; Steudel-Numbers and Wall-Scheffler 2009; Watson et al. 2011; Halsey and White 2012), by altering the length or frequency of strides (Zarrugh et al. 1974) and shifting their center of mass (Gordon et al. 2009). Although most animals select speeds that minimize total cost when moving extended distances (Culik and Wilson 1991; Wickler et al. 2000;
Minetti et al. 2003), they may move faster than their energetically most efficient speed when they are chasing or being chased, or slower than their energetically most efficient speed when actively scanning their environment (Wilson 2002).

Terrain also plays a major role in the energetic costs of locomotion (Rees 2004; Shepard et al. 2013). More energy is required to walk on sand than on grass (Pinnington and Dawson 2001), and the costs of movement increase with depth of snow (Pandolf et al. 1976; Fancy and White 1987; Crête and Larivière 2003). Inclines increase NCOT (Snyder and Carello 2008; Tullis and Andrus 2011; Lees et al. 2013), while declines require less energy for most animals (e.g., Armstrong et al. 1983; Fancy and White 1987), at least until the angle becomes steep (Minetti et al. 2002). Animals may change their style of locomotion and thereby take advantage of declines; for example, Adelie penguins use less energy moving downslope via tobogganing, compared with walking (Wilson et al. 1991).

Changing direction of travel also affects the energetics of movement (Wilson et al. 2013b; Amélineau et al. 2014) unless the animal is able to use its environment to facilitate the change (as in soaring on thermals; Shepard et al. 2013). A human walking in a straight line at 1.67 m s⁻¹ will increase his or her expenditure of energy by 18% by turning 90° every 10 s and by nearly 30% if they turn 90° every 6 s (Wilson et al. 2013b). Changing direction requires a force to exact change, as well as forces to accelerate and decelerate; animals on the move therefore do not change direction or speed without good reason.

Maneuverability

Animals must maneuver around obstacles in complex habitats and often use tight turns in predator/prey chases; yet few studies have directly modeled or measured the costs of maneuverability in terrestrial animals (but see Full et al. 2002). Early efforts in this field focused on turning gambits between predators versus prey in aerial animals. In a simulated turning game, Howland (1974) examined how forward speed and turning radius affected the ability to escape. His model predicted that an individual prey should escape when its normalized speed (prey’s speed/predator’s speed) is greater than the square root of its normalized turning radius (prey’s turning radius/predator’s turning radius). Although this simple model has been useful in predicting the probabilities of escape (Hedenstrom and Rosen 2001), it tells us little about how turning and escape happen.

Fig. 2 (A) The hypothesized relationship between lower-level structural traits (morphology, physiology, and biochemistry) with fitness via its effects on whole-animal performance (Arnold’s [1983] paradigm). This conceptual framework is based on the idea that organisms will utilize their capabilities for maximum performance during important fitness-defining activities related to energy, safety, and reproduction. (B) An hypothesized relationship between lower-level structural traits (morphology, physiology, and biochemistry) with fitness that places an emphasis on the importance of how animals choose the speed with which they perform important ecological tasks. An animal’s underlying morphology, physiology, and biochemistry affects their maximum capabilities for speed and also other critical traits that are compromised by high-speeds (energetics, maneuverability, motor control, and observation skills). Based on these trade-offs, the ecological context of the activity being performed, and the biotic environment, an animal’s fitness will be dependent on how fast they choose to move, which rarely will be at its maximum capability.
Fundamentally, maneuverability is constrained by the musculoskeletal system (Jindrich and Qiao 2009) and basic physics (Alexander 1982). Turning when running requires an animal to change the main vector of motion and rotate its body to the new orientation (Jindrich and Full 1999), meaning that a turning animal must overcome its inertia and undergo angular motion (Zollikofer 1994). To do this, it must produce greater stabilizing forces when turning than when running in a straight line. An animal running at a particular speed \( v \) around a curve of radius \( r \) can only continue forward motion as it changes direction if the coefficient of friction of its feet with the ground is at least \( v^2/rg \) (Alexander 1982). This means that an animal needs a larger coefficient of friction to turn at higher speeds or sharper angles, and implies that speed should compromise turning ability.

The risk of turning too quickly is skidding out, or sliding, which can increase the likelihood of injury, capture by predators, or loss of a prey item. Recently, Wynn et al. (2015) used wild northern quolls (Dasyurus hallucatus) to explore how the probability they crashed when running around corners was affected by their approach speed and turning angle. Quolls that ran faster into the turn were more likely to crash, and this probability was higher for tighter turns. As a result, quolls modulated their speeds: compared with straight-line running speeds (4.5 m/s), quolls approached 45° corners 33% more slowly and 135° corners 45% more slowly. A similar result was also shown for three different species of Anolis lizards, which modulated their speeds when running around corners of varying magnitude; lizards decreased their running speeds to about 48–79% of their straight-line speeds when negotiating turns of 90° (Higham et al. 2001).

Maneuverability can also be important for escaping predators by reducing the predictability of the trajectories of movement. Animals may choose to maximize either speed or maneuverability under different conditions to take advantage of the unpredictability of movement. In a study of leaf-cutter ants (Atta sexdens), Angilletta et al. (2008) found that individuals ran away from threats using straighter, more-predictable trajectories when they were faster at high temperatures, but when they were slower at lower temperatures they ran away using less-predictable trajectories. Thus, when it is not possible to move quickly, erratic maneuverable movements—referred to as protean behavior—may reduce the likelihood of predation (Humphries and Driver 1967; Driver and Humphries 1988).

Motor control
Movement—particularly that which requires precision and control—occurs via a complex interplay between the central nervous system and the musculoskeletal system, known as motor control. Motor control is constrained by biomechanical trade-offs that reduce the accuracy of limb placement at high speeds and is especially important as animals move across uneven substrates, over rocks, through trees or anywhere that falling presents a serious risk. Work to-date has focused mainly on its physiological and neural pathways (Daley and Biewener 2006; Kohlsdorf and Biewener 2006; Toro et al. 2006), and more recent studies have explored the evolutionary consequences of motor skill (Byers and Kroodsma 2009; Byers et al. 2010; Barske et al. 2011). Previous studies have not attempted to quantify how the speed of movement affects the motor control of animals in natural environments. However, a recent re-analysis of data from Husak and Fox (2006) revealed that the
faster that collared lizards (C. collaris) ran, the more likely they were to inaccurately strike at a prey item and miss it, demonstrating how speed can constrain motor control in an ecologically important task. Interestingly, the function of this relationship between speed and accuracy was logistic whereby there was a rapid decrease in accuracy above a critical running speed (Fig. 4).

Early studies of the speed-accuracy trade-off were based on Fitt’s law (1954), which posits that the time it takes to move accurately to a target depends on the size of the target and the distance between the individual and the target. Accurate movement takes longer when the target is smaller or farther away. Taken one step further, we can see that hitting the target becomes less likely when the individual moves quickly or is particularly uncoordinated (Fig. 5A). For example, consider a hunter attempting to spear a fish: the harder the individual throws the spear, the faster the spear moves between the hunter and the fish and the more likely he or she is to hit the fish before it swims away. Although faster throws should be less accurate they do not necessarily miss the target (fish) completely—the likelihood of doing so is simply lower. The spear either misses the fish or it doesn’t, and by how much it misses is almost irrelevant. This emphasizes the point that we need to calculate how speed affects the probability of accuracy, rather than the average miss-distance (Fig. 5B).

Detection of food and danger
Speed is also likely to affect an animal’s ability to observe its surroundings and detect the presence of predators, mates, and food. Intuitively, we know that moving slowly increases sensory resolution—imagine a driver slowing down to look for house numbers—but we find no studies exploring this relationship in animals. Foraging animals routinely pause to scan their environment for danger (Bednekoff and Lima 1998; Treves 1998), but what about when they are moving? The shape of the function between speed and ability to observe could dramatically affect an animal’s behavior and movement. For example, if small increases in speed (even at low speeds) decrease the ability to observe, then animals in risky environments might favor short, rapid movements interspersed with quick scans (Fig. 6). An extreme example is found in tiger beetles. These beetles are capable of running so fast that their vision cannot cope with the detection of light at these high speeds. To deal with the blurred vision at high speeds, they run in a staccato fashion of stops and starts to allow their vision to become clear (Gilbert 1997). Tiger beetles also incorporate mechanosensory input while running, rigidly holding their antennae forward and slightly downward to detect obstacles (Zurek and Gilbert 2014).

If an animal’s ability to observe begins to decline only at moderate speeds, then animals might favor low to moderate speeds of movement, even when predators are common or food is inconspicuous. The relationship between speed and the ability to observe could be measured by manipulating the density or conspicuousness of food in the wild, in semi-natural arenas, or along a treadmill in the laboratory. In these cases, the proportion of food detected and the rate of detection over time can be compared with the animal’s selected speeds in the wild. This is a key area requiring more research on behavior and performance.

External factors affecting speed-choice
Abiotic factors such as slope and type of substrate and habitat are likely to affect movement speeds via their influence on the internal factors governing the choice of speed (i.e., energetics of locomotion, maneuverability, motor control, and ability to observe). For example, animals may be more likely to make mistakes when running over uneven or low-friction surfaces, and they may modulate their speeds to account for these risks.

The threat of predation is one of the most powerful selective forces acting on animal behavior, yet we know little about how speed changes the risk of
predation. Movement can make animals more conspicuous to predators, depending on the size and coloration of the moving animals, their style of movement, and even the noise they make as they move, and different habitats offer predators or prey better places to hide or to blend with their surroundings (Brown and Kotler 2007). Quantifying the relationship between speed, pattern of movement, and

Fig. 5 (A) The faster an individual performs a movement the lower the accuracy of the movement, which will be manifest in a greater average distance away from the target. In addition, the average accuracy of un-coordinated individuals when performing an action toward a target will be more affected by increases in speed than for coordinated individuals. When performing a task like throwing a spear at a fish, then, we would expect a more coordinated individual to have a higher probability of hitting the target than an uncoordinated individual. (B) The faster an individual performs a task the greater is the increase in the variance in the accuracy. This change in the variance in accuracy with increasing speed of movement needs to be quantified in order to model an individual’s optimal speed for a task that is affected by the trade-off between speed and accuracy. When throwing a spear at the fish then we would expect slower throws to have a higher probability of hitting the target than faster throws, assuming the fish does not swim away.

Fig. 6 The function describing the relationship between an animal’s speed and their probability of detecting a predator per unit time (p/time) will have implications for optimal speeds when animals are foraging and traveling between patches. The possible functions could show: (A) Individuals will have a high probability of spotting danger unless they are traveling at high speeds, (B) there is a threshold speed after which animals are unlikely to detect a threat, (C) a linear decrease in the probability of detecting a predator, and (D) a rapid decrease in the probability of detecting a threat, even at low speeds of movement.
Optimality theory as a framework for predicting animals’ speeds

Optimality theory is an ideal framework for new models exploring the speed choices of animals. For 40 years, optimality theory has distilled the decision-making processes of animals into their competing demands: energy, time, safety, and social interaction (Krebs and Kacelnik 2007). At the heart of this approach is the assumption that evolution selects for approximating efficiency in behavior (i.e., maximizing net gains). Models approach problems by considering an animal’s (1) objective or goal, (2) available choices, and (3) constraints on these choices (e.g., physiological limitations on behavior). Ultimately, we can predict behavior by showing how constraints affect decision-making; for selection of speed, these are likely to include energy, safety, biomechanics, and social interactions. Although many have criticized the assumptions underlying optimality in studies of animal behavior, it is clear that our understanding of the factors governing the decisions of animals and the constraints acting upon behavior have been enlightened using optimality theory (Stephens et al. 2007).

To illustrate the utility of optimality for understanding the behavioral choices of animals, let us consider one of the most basic concepts in optimality theory, the marginal value theorem (MVT). The MVT is an optimality model that describes the decision that maximizes the gain of resources per unit time in systems in which resources—and thus, the rate of returns—decrease with time (Charnov 1976). For example, in areas where food is located in defined patches across the landscape, animals must consider food intake, travel time, and foraging time as they decide where to go and how long to spend there; the MVT can then be used to predict when an animal should give up foraging where they are and move to another patch, given these factors.

The value of these models is that they can be applied to any situation with diminishing returns. Consider, for example, copulation by yellow dung-flies (Scathophaga stercoraria): in this species, male flies gather on cow droppings and wait for females to arrive in smaller groups to lay their eggs. The longer a male copulates with a female, the more of her eggs he can fertilize—but by doing so, he misses out on copulations with other females. How long should a male spend with each female? MVT predicts that a male should copulate with a female just long enough to fertilize about 80% of her eggs (~41 min), because after that point he will fertilize more eggs per unit time by copulating with a new female rather than staying with the initial one (Parker 1970); there are diminishing returns to mating with the same female. In fact, male flies copulate on average for very close to the predicted time—about 36 min (Fig. 7) (Parker 1970).

An optimality approach has already been used to predict speed by flying animals and by those chosen by drivers of automobiles, although neither case is easily generalizable. According to aerodynamic theory, the total mechanical power needed to propel a bird through the air is characterized by a U-shaped curve (e.g., Pennycuick 1969, 1975; Rayner et al. 2001), in which there are high energetic costs at high and low speeds. This means that the energetic costs of flight can be minimized in two ways: either by selecting the speed that minimizes the power required to fly a given time (Vmp), which reduces expenditure of power, or the speed that minimizes the expenditure of energy per distance traveled (Vmr) (Pennycuick 1975; Rayner et al. 2001). Small migrating birds seem to fly at their predicted Vmp when they perform song flights and are “flying nowhere” (Hedenström and Alerstam 1995), while higher speeds at about Vmr are used when migrating (Hedenström and Alerstam 1995).

Like studies of flight, research has examined the factors that influence selection of speed by the drivers of automobiles, although in this case the goal is manipulating speed to enhance public safety (Graves et al. 1989; Rodriguez 1990; Andersson and Nilsson 1997). Drivers seem to choose speed based on their perceptions of safety on a road and the designated speed limit, and manipulations of speed-choice usually are attempted by increasing the costs of speed via enforcement (Graves et al. 1989; Rodriguez 1990; Andersson and Nilsson 1997; Kockelman 2006; Archer et al. 2008). Drivers do respond to enforcement by reducing their speed—but only when they perceive the speed limit as appropriate (see e.g., Shinar and McKnight 1985)—and the effect of enforcement seems confined to the particular site and nearby locations and times (Graves et al. 1989; Rodriguez 1990; Andersson and Nilsson 1997; Kockelman 2006; Archer et al. 2008). Research is now being directed toward changing drivers’ perceived speed of travel, for example by using patterned road surfaces that make it appear that they are driving faster than they are.

From these studies, we know that chosen speed reflects the balance between energy consumed and
distance moved (in flight) or between travel time and safety (in driving), but these examples have little relevance for understanding how terrestrial animals move in nature. They focus primarily on directional travel between two distant points, when most movements by animals (e.g., foraging, escaping predators, interactions with conspecifics) vary over short scales of time and distance. To predict these moment-to-moment choices, we must extend models to incorporate threats of predation, abilities to detect food or mates, motor control, and maneuverability.

**Predicting the speeds of animals when traveling between patches, foraging, and during risks to survival**

We have now highlighted a range of factors likely to affect speed and have shown how optimality theory can use these constraints to predict animals’ decision-making. Below, we discuss how this knowledge can now be applied to the study of animals’ movement across three important ecological contexts: (1) traveling between foraging patches, (2) during foraging, and (3) during survival situations like escaping predators and capturing prey.

**Speed when traveling between foraging patches**

As shown in studies of avian migration (Hedenström and Alerstam 1996; Nilsson et al. 2013, 2014), travel between foraging patches is likely to be driven by the energetic efficiency of movement—minimizing the expenditure of energy per unit time or per unit distance. However, two other constraints must be considered: the way that speed affects the likelihood of spotting, or being spotted by, a predator and the loss of foraging time during travel. Thus, we would expect the selection of speeds by animals moving between feeding patches to be affected by: (1) the energetic costs of movement per unit time and/or per unit distance, (2) the probability of detecting predators, (3) the probability that predators detect them, and (4) the energetic costs of lost feeding opportunities when traveling.

One of the main issues with multi-factor models is that each parameter must be incorporated into models in the same units. In the case of optimal foraging theory, both the benefits of energy consumption and the costs of predation are translated into a life-history framework—as energy and predation both impact survival and reproductive success, or fitness (Ydenberg et al. 2007). We must be able to translate the costs and benefits of speed in a similar way.

Urban koalas are ideal for studies of speeds between foraging patches, and information on their decision rules would also aid conservation efforts. Koalas are common in southeastern Queensland, where they spend most of their time foraging in particular types of *Eucalyptus* trees—preferentially selecting larger foraging trees and leaves of low toxicity, high digestibility, and high nutritive value (Hindell and Lee 1987; Lawler et al. 2000; Moore and Foley 2005; Moore et al. 2010; Ellis et al. 2013). The most dangerous time of a koala’s life is when it is on the ground moving between trees; between 1997 and 2011, more than 5200 koalas were killed by dogs or cars in southeastern Queensland alone, and nearly 6000 additional koalas died from a combination of cars, dogs, and/or disease during this time.

Given that koalas are relatively safe in trees but vulnerable on the ground, how fast should they move between their foraging patches? A model of koalas’ transit speeds would need to incorporate (1) the energetic costs of movement over distance and time, (2) the link between speed and detection of, and detectability by, dogs and drivers, and (3) the energetic costs of lost foraging time, estimated via the nutritive value of local *Eucalyptus* trees. Each of these factors can be empirically determined, allowing us to develop a model of optimal movement speeds for koalas that can be tested against observations in the wild. Ultimately, this work could facilitate habitat...
management that minimizes the koalas’ movements—particularly through dangerous areas—and encourage safer driving during times when koalas are most likely to be on the ground.

**Speeds during foraging**

Foraging animals must obtain enough energy for growth and reproduction while minimizing the risks of encountering predators, so we expect the selection of speed to reflect (1) the energetic costs of movement per unit time, (2) the rate of encountering food, (3) the probability of detecting food when it is encountered, (4) the probability of being detected by predators, and (5) the ability to spot predators while foraging. Again, we must translate the costs and benefits of speeds into units of fitness, using a life-history framework.

Consider an actively searching forager, like a monitor lizard—the faster it moves through its environment, the greater number of food items it is likely to encounter per unit time, but a fast-moving lizard may also detect fewer food items, so the speed that maximizes net energy intake is likely to be intermediate (Fig. 8). To the best of our knowledge, no studies have explored these competing demands on the foraging speeds of animals, although they could be easily conducted by manipulating the openness of the habitat. We expect that animals should move more quickly in open habitats or where food items are large—that is, where food is easier to spot—than in cluttered habitats or where food items are small or camouflaged (Fig. 8). Because high speeds are also energetically costly, they should rarely be used by actively foraging animals, although in some cases safety may play a prominent role in the choice of speed.

**Speeds during risky situations**

How fast should animals move during situations affecting survival, that is, when attempting to escape predators or to capture prey? Failure has a high cost, particularly for those animals attempting to escape predators, so we do not expect energetic costs to drive speed-choice in these circumstances; prey will go as fast as they need to in order to escape. The stakes for predators are lower than for prey, but predators’ speeds should still be determined by biomechanical trade-offs between speed, maneuverability, and motor control, and largely ignore the energetic costs. Thus, in order to predict speeds during the capture of prey or escape from a predator we need to quantify: (1) how speed affects success in the task when free of mistakes, (2) the nature of trade-offs between speed, maneuverability, and motor control, (3) how maneuverability and motor control each affect the task’s success, and (4) the costs of mistakes. Obviously, the importance and relevance of each factor will be associated with the species and the task that the animal is performing. For example, the rapid strike of a sit-and-wait snake toward a mouse is likely to depend more on speed and accuracy than on maneuverability, and the capture of a gazelle by a cheetah should depend more on speed and maneuverability than on motor control, because of the fast speeds and rapid turns in these chases (Wilson et al. 2013a). Unlike models predicting the movement speed of animals traveling between patches or when foraging, the competing costs and benefits during situations risking survival should be modeled using probabilities of the task’s success.

As an example, let us consider a mouse running away from a cat (Fig. 9). First, we must describe the relationship between the mouse’s straight-line running speed (assuming no errors) and its probability of escape (Fig. 9A). Is the likelihood of escape best described as a linear function, or as a logistic function—where there is little improvement in escape probability above a critical speed? Although no studies have quantified the shape of the function between speed and the escape from predators under natural conditions, Clemente and Wilson (2015) did so using a tablet-based game in which human subjects were asked to “capture” moving prey items (dots on screen) by touching them as they passed over the screen. They found a logistic relationship between speed of the prey and its probability of escape: at low speeds of the prey, most prey were captured but the probability of escape rapidly increased over intermediate speeds to a high speed at which probability of escape was high (Clemente and Wilson 2015) (Fig. 9A). The shape of this function has profound implications for understanding the running speed selected by escaping prey.

We must then quantify the relationship between the mouse’s maneuverability and its probability of escape. In other words, how does the magnitude of the turn a mouse can make affect its probability of getting away from the cat? Clemente and Wilson (2015) found a linear relationship between the sharpness of the turn and the probability of escape—this can be used as a starting point for predicting escape-speeds in our mouse example (Fig. 9B). Next, we need to incorporate biomechanical constraints between speed and maneuverability into our model; in other words, how does speed change the magnitude of turns the mouse can produce and its likelihood of slipping during a turn? It is important to
note that the magnitude of this trade-off will be affected by the substrate on which the animals are running; a grippy surface will allow much sharper turns to be made at higher speeds than a slippery surface (Fig. 9C). By incorporating the costs of any mistakes (slips or falls)—in this case, how mistakes would affect the probability of capture—then it is possible to construct an optimality model of escape probability based on speed, maneuverability, trade-offs between speed and maneuverability, the probability of mistakes, and the cost of mistakes. This model allows us to quantitatively predict how fast the mouse should run away from a predator. Manipulations of substrate should change the optimal speed for escape by modifying the trade-off between speed and maneuverability.

As part of this symposium, Wheatley et al. (2015) developed a simple mathematical model that predicted the optimal speed for an animal running away from a predator along a straight beam. The straight beam was used as a proxy for straight-line running that required accurate placement of the feet in order to avoid mistakes. Although faster speeds without mistakes were assumed to increase the probability of escape, higher speeds were also more likely to result in inaccurate placement of the feet, thereby leading to higher frequencies of mistakes. Their model predicted that animals should run slower when the beam was narrower—with greater costs for missteps—or when an animal’s coordination is worse. This simple model, consistent with empirical studies of arboreal lizards on different-sized substrates (Losos and Sinervo 1989; Irschick and Losos 1998, 1999; Spezzano and Jayne 2004; Mattingly and Jayne 2005; Jones and Jayne 2012), emphasizes the point that speeds of escape are unlikely to be
maximum speeds across all contexts and that it is possible to develop quantitative predictions for optimal speeds for escape.

One could similarly apply this framework to tasks that are associated with social contexts such as sexual displays or fighting, though the costs and benefits would be different. For example, males may take more risks for mating success benefits (Snell et al. 1988; Magnhagen 1991; Andersson 1994). The cost of rivals usurping mates may also result in higher movement speeds in order to oust intruding rivals (Husak et al. 2006, 2008). The same constraints associated with making mistakes would apply if the goal is simply to chase away a rival, but the probability of making a costly motor mistake may be much lower.

**Discussion**

Movement speed affects all behaviors and can determine the fate of individuals across all ecological contexts. In this article, we set the foundations for understanding the speed-choices of animals, but more importantly, we outlined a framework for predicting animals’ speed-choices. By utilizing optimality theory, we show it is possible to provide quantitative predictions of optimal speeds across different ecological contexts. However, the usefulness of any predictive model is still entirely dependent on it being able to provide relevant mathematical functions to insert into the model. We still lack basic knowledge about how an animal’s speed affects its motor control, maneuverability, observational skills, or vulnerability to predators. Studies exploring these gaps in knowledge will help facilitate the field of optimal performance and allow us to adequately parameterize models for predicting speeds.

One important factor that complicates our ability to predict the speeds of animals in nature is determining whether an animal’s speed is because they choose that particular speed or because they are forced to use that speed because of some external environmental constraint. For example, the incline, compliance, and rugosity (the amount of unevenness) of the substrate on which animals run can dramatically affect the maximum speeds attainable. For terrestrial organisms, moving on soil, sand, or rocks presents challenges and potential constraints to

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**Fig. 9** The hypothesized relationship between the speed (without mistakes) (A) and maneuverability (B), of a prey species and their probability of escape from a predator based on the work of Clemente and Wilson (2015). If the ability of the prey to make sharp, rapid turns (maneuverability) is affected by the friction of the substrate upon which they are running (C), then the optimal speed for successful escape would differ between low-friction and high-friction substrates (D). Assuming that the friction of the substrate only influences the prey’s turning ability and not that of the predator.
For example, Sathe and Husak (2015) found a three-fold decrease in speed when green anole lizards (Anolis carolinensis) ran on a racetrack with pegs (a cluttered environment) compared with the same racetrack without pegs (an open environment). When determining the extent to which abiotic factors limit speed, one must first determine an animal’s maximum capabilities under the relevant conditions. For example, when wishing to predict an animal’s selected speed when running along a beam of a certain width, one must determine an animal’s maximum capabilities when running along this beam while subjected to encouragement by the experimenter when running freely and without any mistakes. By then measuring how speed along the beam affects the animal’s energetic costs of movement, probability of mistakes, ability to observe their surroundings, and vulnerability to predators we can then parameterize any model predicting optimal success.

Increased probabilities of mistakes represent one of the most important costs for high-speed movements. Mistakes can be manifest as slippages when trying to turn too quickly, tripping when approaching an obstacle too fast, or an inability to accurately control placement of the limbs at high speeds. Mistakes make success in any task less likely, but despite the importance of mistakes, biologists rarely quantify such mistakes. In order to advance our ability to predict the speeds of animals, we need to begin to study their mistakes. Because mistakes can also vary in their costs—or probability of leading to failure of the task—we need to understand the relationship between the types and magnitudes of mistakes and how they affect success. For example, errors in the placement of limbs may have very different consequences for quadrupedal animals if they involve the hind limb rather than the forelimb. In addition, the costs of crashing could substantially differ between small and large prey running away from a predator. A loss of footing and a crash for a larger animal may have much greater costs if it takes longer to recover and a greater chance of severe injury, and these costs may be enhanced in arboreal species. Smaller animals can have spectacular crashes but recover almost immediately and with little chance of injury.

Our framework for predicting optimal speeds also has the potential to add to the fields of sports science, conservation biology, and human health. Improving the performance of athletes in tasks that require both power and accuracy for success offers an obvious extension for studies of optimal performance (Lailvaux et al. 2014; Wilson et al. 2014). Whether it is kicking a football, serving in tennis, or throwing a ball, success requires both speed and accuracy. Our framework for studying optimal performance could be used to identify the optimal efforts supporting an individual’s peak success in performing a task and provide pathways for better protocols of training (Wilson et al. 2014). In addition, by understanding an animal’s “decision rules” for selecting speeds in nature we could begin to provide a mechanistic understanding of how an animal uses its home range. Management strategies for most threatened species focus on when and where animals move, and the types of habitats they select, but this ignores how an animal moves through a landscape and why it chooses to move the way it does. Our work could enhance conservation efforts by providing a mechanistic understanding of an animal’s use of its home range and how this use varies as a result of environmental—and anthropogenic—modifications.

In the context of predator–prey contests it is important to acknowledge that the best strategy for the predator is going to depend on the strategy used by the prey. This means a game-theoretic approach would be best under these circumstances, but simple models that just consider the behavior of either the predator or the prey, independent of the other, will still undoubtedly enhance our understanding of the speed-choices of animals. In addition, we should acknowledge that there is unlikely to be just a single optimum value for success in any task. There may be a variety of speeds for which success is identical (multiple optima) or a range of speeds over which success varies little (performance range). For example, an individual hunter attempting to spear a fish may be extremely accurate at low throwing speeds but lose accuracy rapidly at intermediate speeds before his accuracy plateaus again at high speeds (logistic relationship). This may mean that the hunter’s ability to hit the fish may have equally high probabilities at specific low speeds and specific high speeds, thus providing multiple optima. In contrast, another hunter may lose accuracy at a rate that is proportional to increases in throwing speed, which effectively results in a very consistent rate of success (probability of hitting a fish) across all speeds of throwing (wide performance range). By quantifying the shape of any function that describes the relationship between speed and success at a task should reveal how variance in selected speeds can affect overall success (Huey and Stevenson 1979; Bennett 1980).
How does the expectation that animals will rarely use their maximal capabilities, even during escape from predators or capture of prey, affect our interpretation of Arnold’s (1983) eco-morphological paradigm? It is clear that there are many cases in which variation in survival and reproductive success are associated with maximum whole-animal performance (Miles 2004; Husak 2006b; Irschick and Meyers 2007; Wilson et al. 2007b; Irschick et al. 2008), suggesting maximum performance is still important in some circumstances. We should also still expect maximum performance to be closely linked with success for any activity for which maximum performance is positively associated with optimum performance. However, when one considers tasks performed by humans and for which success is dependent both on power and accuracy (e.g., tennis serve), it is clear that the fastest or strongest individuals are not necessarily going to be the best performers. There is no reason to expect this will be any different for non-human animals. The connection between variation in form and fitness is going to be a lot more complicated than just via the impacts of form on maximum capacity for performance—and this may be an important reason why variation in individual maximum capabilities often explains limited variance in success. Our understanding of how animals select their speeds of movement in nature is clearly in its infancy, but studies exploring their speed-choice offer exciting opportunities for learning more about a basic decision made by all animals across almost all behavioral contexts. To move this research program forward, we need further empirical and theoretical studies exploring the relationship between variation in an animal’s maximal capabilities with the magnitude of their optimum performance and ability to accurately select their optimum. We believe that now is an exciting time for studies exploring the relationship between form, performance, and fitness.

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