Introduction to the Symposium: Towards a General Framework for Predicting Animal Movement Speeds in Nature

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Synopsis Speed of movement is fundamental to animal behavior—defining the intensity of a task, the time needed to complete it, and the likelihood of success—but how does an animal decide how fast to move? Most studies of animal performance measure maximum capabilities, but animals rarely move at their maximum in the wild. It was the goal of our symposium to develop a conceptual framework to explore the choices of speed in nature. A major difference between our approach and previous work is our move toward understanding optimal rather than maximal speeds. In the following series of papers, we provide a starting point for future work on animal movement speeds, including a conceptual framework, a simple optimality model, an evolutionary context, and an exploration of the various biomechanical and energetic constraints on speed. By applying a cross-disciplinary approach to the study of the choice of speed—as we have done here—we can reveal much about the way animals use habitats, interact with conspecifics, avoid predators, obtain food, and negotiate human-modified landscapes.

You’re running late for work! Your important faculty meeting starts in less than 30 min and you definitely don’t want to be late for this one. So, what should you do? You could saunter out the door and start walking, but you’re going to be late and your colleagues aren’t going to be happy. Sauntering is a bad idea. Alternatively, you could sprint to your car, drive like a maniac and hopefully get to the meeting on time, but rushing can lead to a whole range of other problems; you might slip in the driveway (injuring yourself), crash your car (injuring your car, yourself, and others), or get a speeding ticket (injuring your wallet). Rushing is a terrible idea. It is clear that both of these solutions have their advantages and disadvantages—which is better? The answer is neither. Without even thinking about it, we select speeds that balance the benefits with the costs of moving too fast or too slow, and there is remarkable consistency in the speed at which we perform specific functions—whether it is how fast we drink our coffee or type a text message.

Much like academics, wild animals must also make decisions about how fast to move in their natural environments. Just watch any animal look for food, display to a mate, or avoid danger and it is quickly apparent that selection of movement speed is a fundamental behavior. As an example, let’s consider a predator stalking its prey—in this case, a lizard stalking an insect. Ultimately, the lizard will strike out to capture the insect with its mouth; before then, it has to get within striking distance. To do so, the lizard must move at a speed that balances the conflicting costs of time (i.e., the insect might fly away) and detection (i.e., the lizard might draw attention to itself). Under these constraints, a predator is likely to be most successful if it moves within a certain, optimal range of speeds—yet we lack a general framework for understanding and predicting what this range should be. It was the goal of our symposium and its associated papers to begin developing a predictive framework for the speeds at which animals move. By defining the
“rules” whereby animals choose speeds we hope to provide a more holistic and definitive understanding of animal behavior and a new pathway for exploring the ecology and evolution of animal performance.

The movement of animals historically has been studied within the context of the evolution of form and function rather than of behavior. The functional traits of individuals—such as morphology, physiology, and biochemistry—have long been linked with reproductive success and survival via the performance of whole-animals (Arnold 1983). The performance of whole organisms generally is viewed as an important target of selection, shaping the phenotype (Huey and Stevenson 1979; Lailvaux and Husak 2014) via its role in fitness-related tasks (Bennett and Huey 1990; Irschick and Garland 2001; Husak et al. 2008; Careau and Garland 2012). The intuitive link between performance and fitness has led to a number of studies centered on the eco-morphological paradigm (Arnold 1983), in which variation in morphology drives performance, which in turn drives variation in fitness (e.g., Bartholomew 1966; Huey and Stevenson 1979; Pough 1989; Bennett and Huey 1990). The eco-morphological framework has given us novel insights about the way selection operates, but in measuring how well individuals perform a task and describing the mechanistic bases of their capacities, researchers have largely ignored how they do it—namely, how animals decide to perform and the various constraints affecting these decisions.

Over the last 40 years the study of animal performance has been biased towards measuring maximum capacities—including sprint and burst speeds—with less consideration of how animals select their speeds under natural conditions (Irschick et al. 2008; Lailvaux and Husak 2014). In nature, animals rarely move as fast as they can, even when trying to escape predators, catch prey and obtain matings (Irschick et al. 2005; Wilson 2005; Husak and Fox 2006; Wilson et al. 2013). This is because speed is costly—using more energy (Hoyt and Taylor 1981; Steudel-Numbers and Wall-Scheffler 2009), constraining motor control and maneuverability (Alexander 1982; Wynn et al. 2015), and reducing visibility and safety (Bednekoff and Lima 1998; Treves 1998). Multiple biotic and abiotic factors contribute to what speed an animal can and does use in a given instance (Wilson et al. 2015). Some factors impose physical constraints on speed, whereas others influence decisions made by individuals in specific situations (Moore and Biewener 2015). Environmental characteristics such as temperature (Angilletta 2009; Dell et al. 2011), substrate (Losos and Sinervo 1989; Jayne and Irschick 2000; Higham et al. 2001), and obstacles (Kohlsdorf and Biewener 2006; Jones and Jayne 2012; Sathe and Husak 2015) are known to affect speed, as do internal factors such as energetics (Halsey and White 2012; Halsey 2013; Wall-Scheffler 2015) and biomechanics (Clemente and Wilson 2015a; Wynn et al. 2015). Aside from these constraints, an individual’s choice of speed is further influenced by the behavior and performance of its predators (Jayne and Ellis 1998; Irschick and Jayne 1999; Husak and Fox 2006; Moore and Biewener 2015) and prey (Husak and Fox 2006; Wilson et al. 2013; Moore and Biewener 2015), and the presence of potential mates or rivals (Husak and Fox 2006; Nilsson et al. 2014). Therefore, choice of speed is a compromise between numerous costs and benefits of moving fast, and to predict speeds we must consider:

1. the energetic costs of movement across natural substrates (energy),
2. vulnerability to predation (safety),
3. performance of controlled and directional movement (biomechanics),
4. ability to detect food or predators (observation), and
5. the social constraints of the species (social).

This kind of general framework will be broadly applicable across speed-choice situations, making it relevant to understanding the speed of any animal, including humans, even in the context of vehicular movement (Graves et al. 1989; Kockelman 2006; Archer et al. 2008).

In recent years, the new field of “movement ecology” has tried to fill some of these gaps, integrating studies of movement and ecology under a unifying paradigm. Movement ecology considers how external and internal factors affect animals’ movements, including motivation (why move?), motion (how to move?), and navigational decision-making (when and where to move?) (Nathan et al. 2008). Speed provides a demonstrable link between each of these mechanistic tenets of movement ecology—the why, how, when, and where to move—yet we need a testable, predictive framework to understand it. Luckily, the models of foraging ecology can be used to make a start in this direction. These models examine the decision-making processes of animals as they seek and acquire food and other resources, including mates (Stephens and Krebs 1986; Ydenberg et al. 2007), showing how behavior affects fitness (e.g., Carrete and Donázar 2005; Ale and Brown 2009). Foraging theory has provided numerous insights into animal behavior and ecology, and the rich diversity of mathematical approaches in foraging theory will undoubtedly help researchers explore the selection of speeds by animals in natural environments.

In this symposium, we began working toward a general framework to predict the movement speeds
of animals. The variety of perspectives we used to approach the issue—including those from modelers, physiologists, biomechanists, ecologists, and evolutionary biologists—highlight the importance of a cross-disciplinary collaboration in achieving this aim. A fundamental difference between previous approaches and those presented here is the move toward understanding optimal rather than maximal speeds. Studies of optimality consider the constraints on speed using mathematical functions to hypothesize what an animal should do (in this case, how fast it should go) to give it the best chance of succeeding. This is in sharp contrast to the heavy emphasis on maximal locomotor performances that have dominated the biomechanical and eco-morphological literature in recent decades. In the first paper in our symposium, Wilson et al. (2015) describe a conceptual framework for understanding the rules used by animals in selecting their speeds, and discuss how an approach using optimality theory can help develop quantitative predictions of speeds across ecological contexts. Clemente and Wilson (2015b) then use a tablet-based game to show how the optimal speeds for escape are likely to be dependent on the nature of the trade-off between speed and maneuverability. Wheatley et al. (2015) develop a simple mathematical model to explore the optimal speeds of animals when running from a predator along a straight beam—in this case, the running speeds that maximize success in escape are dependent on the trade-off between speed and the accuracy of placement of the feet. Cespedes and Lailvaux (2015) use models based on individuals to simulate the evolution of speeds over a range of selective contexts, and explore the factors that affect the evolutionary relationships between optimal and maximal performance. Wall-Scheffler (2015) explores how the role of energetics, the cost of transport, and sex influence the preferred walking speeds of humans. Finally, Moore and Biewener (2015) explain how unpredictability in an animal’s locomotor strategy may help to offset some of the locomotor constraints on speed in the context of escape from predators.

By providing a conceptual framework (Wilson et al. 2015), a simple optimality model (Wheatley et al. 2015), an evolutionary context (Cespedes and Lailvaux 2015), and an exploration of the various biomechanical and energetic constraints on speed (Clemente and Wilson 2015b; Moore and Biewener 2015; Wall-Scheffler 2015), these papers provide an exciting starting point for explorations of a fundamental question in animal behavior—why do animals choose the speeds they do in nature? By embracing a cross-disciplinary approach to this question, researchers will undoubtedly reveal much about the way animals use habitats, interact with conspecifics, avoid predators, obtain food, and negotiate human-modified landscapes.

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References


