

## REVIEW

# Jumping over fences: why field- and laboratory-based biomechanical studies can and should learn from each other

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## ABSTRACT

Locomotor biomechanics faces a core trade-off between laboratory-based and field-based studies. Laboratory conditions offer control over confounding factors, repeatability, and reduced technological challenges, but limit the diversity of animals and environmental conditions that may influence behavior and locomotion. This article considers how study setting influences the selection of animals, behaviors and methodologies for studying animal motion. We highlight the benefits of both field- and laboratory-based studies and discuss how recent work leverages technological advances to blend these approaches. These studies have prompted other subfields of biology, namely evolutionary biology and ecology, to incorporate biomechanical metrics more relevant to survival in natural habitats. The concepts discussed in this Review provide guidance for blending methodological approaches and inform study design for both laboratory and field biomechanics. In this way, we hope to facilitate integrative studies that relate biomechanical performance to animal fitness, determine the effect of environmental factors on motion, and increase the relevance of biomechanics to other subfields of biology and robotics.

**KEY WORDS:** Locomotion, Walking, Running, Swimming, Behavior, Methodology

## Introduction

In the pursuit of understanding how animals move, biomechanists have historically focused on one of two approaches (Fig. 1). Scientists either study animals in natural habitats, which limits the resolution or magnitude of data collection, or bring animal subjects into a controlled laboratory environment that permits detailed, repeatable observations. As such, our knowledge about animal locomotion (including the kinematics, muscle physiology, energetics and motor control) is separated from its ecological context. However, an animal's evolutionary trajectory was shaped by – and is therefore intrinsically tied to – interactions with its environment. Understanding biomechanical capabilities as adaptive traits requires both physiological and ecological context.

In the past decade, technological advances have spurred a growing capacity and interest in studying animals under more naturalistic conditions. To support this growing focus, we will discuss the advantages, disadvantages and integration of field and laboratory approaches in studying the biomechanics of locomotion. While these topics may apply more broadly, our discussion will involve moving through a given habitat (aquatic, aerial, terrestrial,

or at an interface) across scales from individual strides to migrations. Our Review examines the long history of animal locomotion as an example of this phenomenon because it spans several historical advances in experimental technology that facilitate both laboratory and field settings. By learning from these studies, we summarize a set of considerations for researchers planning future work on a variety of biomechanical tasks. We argue that mutual awareness of field and laboratory-based approaches enhances experimental design and expands the relevance of our results to other sub-disciplines of biology.

## Field- versus laboratory-based studies

At their core, the earliest observations and reports of animals moving may be considered field-based studies in animal locomotion. Informal reports of an animal's location, interactions and movement coordination date back to cave paintings (Bertram, 2016), but are especially documented in the writings of explorer naturalists (Mouillard, 1881; Hankin, 1914). Throughout history, these observations have been augmented by technology. Developed from eyeglass designs, the invention of the spyglass (a refracting monoscopic telescope) and the microscope expanded the spatial scale of perception to study animals too far (Bailey, 1889; Wood, 2006) or too small (Hooke, 1968) to be seen by the naked eye.

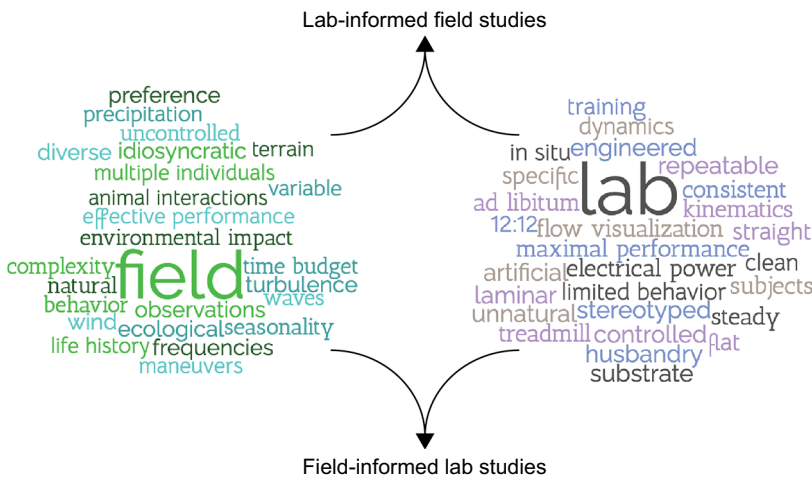
Temporal scales in field studies have also been limited by feasibility. Physical trap lines or mark-and-recapture studies reveal where and which animals are more likely to travel within a large swathe of an ecosystem, but the temporal resolution of these data is limited by how quickly these traps can be checked or the reliability of recapturing animals. These punctuated data points on animal survival have been shown to correlate with preferences for specific forms of locomotion (Brodie, 1992), but because animals rarely perform a behavior the same way each time (Irschick et al., 2008), it is difficult to find causal links between biomechanical performance and survival without directly observing predation events. The advent of tracking devices attached to an animal has improved temporal resolution at large spatial scales, but each methodological approach faces trade-offs. A radio-tracker can only record one animal at a time, so does not record interactions with other animals or the physical environment. GPS-based tracking can follow multiple animals simultaneously, but publicly available satellites have low spatial resolution, limiting studies to larger animals. All of these devices add mass to an animal, which may disrupt normal behavior, especially in considering the weight versus power capacity of a battery.

Tracking at finer spatial and time scales still presents challenges in the field. Scientists observing animals first-hand may disrupt natural behaviors, yet other methods may overlook important information about interactions with the environment and other animals. For example, one study used a spool of thread attached to a bandicoot (*Echymipera kalubu*) to reveal its pathway and time budget in various locations, but could not provide limb kinematics,

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**Fig. 1. Field studies and laboratory experiments present different opportunities for observing and quantifying animal movement.** Recent technological advances encourage more detailed measurement of movement patterns in the field, enable characterization of natural or laboratory conditions, and facilitate the analysis of larger, more variable datasets. We advocate that these advancements promote the development of field experiments that integrate laboratory approaches, as well as laboratory experiments inspired by field conditions. 12:12, 12 h of night and 12 h of day in laboratory animal conditions.

types of locomotory behavior (e.g. jump frequency or height) or interactions with other animals (Anderson et al., 1988). Today, videography from supervised cameras or camera traps helps document animal locations and movements while minimizing experimenter influence (Provini et al., 2023). The spatial resolution of these observations is determined by the number of cameras deployed and it is difficult to identify an individual across multiple data streams. Further, field conditions are often unpredictable and inhospitable to electronics, requiring robust equipment and frequent monitoring.

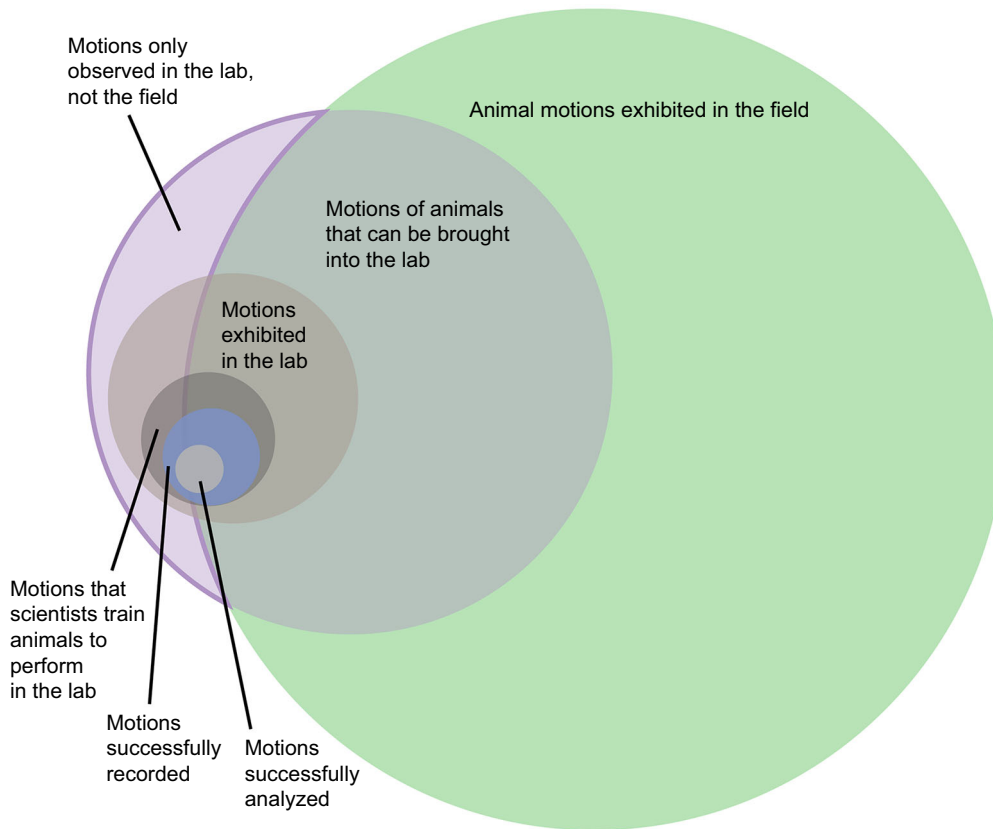
To summarize, field-based studies excel at observing animal locomotion under natural conditions, including complex interactions with the environment and other animals. In some cases, these studies track animal movements across long distances or durations, encompassing the inherent variability at this scope. These data can directly relate to an animal's ecological experience and, therefore, evolutionary fitness. However, many field techniques limit either the spatial or temporal resolution of the data and may only provide small sample sizes.

In comparison, laboratory-based studies have the advantage of being able to control environmental settings and use a suite of precise sensors to simultaneously record multiple forms of information. Environmental stimuli – such as temperature, sound and light – are significantly more controllable indoors than outdoors, reducing variability in locomotion patterns and measuring responses to specific, induced conditions (Anderson et al., 2007a; Mischiati et al., 2015; Christensen-Dalsgaard and Manley, 2005). However, laboratories are spatially constrained, permitting the recording of only a few representative animal movements. The use of a moving substrate – via treadmill, flume or wind tunnel – enables researchers to keep large, fragile, precise and power-hungry equipment in a single location while still recording multiple sequential gait cycles (Benedict and Murschhauser, 1915; Gray, 1957; Tucker and Parrott, 1970). This approach has made it possible to measure oxygen consumption (respirometry), 3D gait kinematics (motion tracking) and neuromuscular behavior (implanted sensors such as electrodes, sonomicrometry and tendon buckles) (Hoyt and Taylor, 1981; Kambic et al., 2015; Tobalske et al., 2010). Ground reaction forces are recorded using force plates for terrestrial animals (Alexander, 2003); however, fluid forces are more difficult to experimentally measure. An important technological innovation for studying movement in fluids was particle image velocimetry (PIV), in which a sheet of laser light illuminates neutrally buoyant particles that reveal the velocity of entire flow fields (Raffel et al., 1998). PIV

visually depicts the energy transferred to a fluid, enabling estimation of swimming forces and identification of vortex structures associated with anatomical structures and their material properties (Takagi et al., 2014; Curet et al., 2011; Zhong et al., 2021; Tytell et al., 2016). Compared with field studies, many laboratory studies on captive animals permit larger sample sizes (multiple strides of steady-state locomotion), and benefit from determining individual responses to conditions or across time.

Working in laboratories necessarily comes with some restrictions, especially in the types of animals selected for study. The size of the lab and animal care facilities enforces an upper limit on the size of animals that can be examined. Most university research labs are unable to accommodate large vertebrates, such as elephants, condors or whales (although some leverage collaboration with zoos or wildlife facilities; Langman et al., 1995; Shine et al., 2015). Other animals are difficult (but not impossible) to bring into the lab because of health concerns or safety regulations; for example, bats and venomous snakes (Dickson and Green, 1970; Santos et al., 2021). Even when animals can be brought into the lab, the range of behaviors they perform may differ greatly from what they exhibit in more naturalistic conditions (Fig. 2). This may be because of the physical differences between lab and field environments (summarized in 'Towards field-informed laboratory studies', below). Similarly, the uncharacteristically straight, steady-state locomotion exhibited in labs often differs vastly from the motions animals exhibit in the wild. For example, bipedal hopping rodents, jerboas, are capable of running, hopping and skipping down a straight trackway. However, complex trajectories with many accelerations and decelerations are the norm, for both predator evasion and foraging (Moore et al., 2017; Schröpfer et al., 1985). A lack of variability in animal motion may also be due to the enforced consistency of the locomotor matrix. Flumes and wind tunnels generally generate laminar flow, which is rarely experienced by animals outside of laboratory conditions. Similarly, some behaviors only emerge with a critical number of individuals interacting together, which becomes less tenable with larger animals. Small social organisms such as volvox, fish or bees may be feasibly studied as groups in a lab (Goldstein, 2015; Peters et al., 2019; Katz et al., 2011), and some research suggests that these smaller groups are representative of larger assemblages in more naturalistic environments (Romenskyy et al., 2020). However, a murmuration of starlings or cooperative hunting in whales can only occur with numbers of individuals that are impossible to keep in a lab (Goodenough et al., 2017; Domenici et al., 2000). Because indoor

**Fig. 2. A conceptual diagram of the subset of animal motions that can be studied in the context of a laboratory.**



conditions can only recreate a subset of (or are entirely different from) field conditions, laboratory-based studies gain precision, constraint, control and multi-sensory capabilities at the cost of losing the natural variability exhibited by animals under natural conditions.

While the advantages and disadvantages described above have shaped how we approach the design of biomechanical studies, we argue that recent technological advances reduce the severity of these trade-offs. The following sections will outline how to integrate field and laboratory approaches to promote evolutionarily and ecologically relevant biomechanical experiments.

### **Towards laboratory-informed field studies**

As described in the previous section, there are some forms of data and some animal behaviors that only exist outside of laboratory environments. Although field-based data collection includes significant challenges, advances in sensors, power sources, actuators and wireless communication have helped bridge the gap between field and lab approaches. To highlight how laboratory studies can inspire field-based experiments, this section will discuss two topics focusing on how the measurement of a biomechanical metric has been expanded to natural environments. A detailed discussion of a third metric, video-based kinematics recordings, can be found in Provini et al. (2023).

### **Energetics of locomotion**

Determining how locomotion influences metabolic costs remains a fundamental question in biomechanics. One of the most popular ways to estimate energy use is by measuring oxygen consumption via respirometry, often using a mask or enclosed chamber. Because it is sensitive to small environmental changes and requires both

electricity and air pumps, respirometry equipment has historically been kept stationary. Thus, these studies have generally depended on treadmills (although an experiment with the oxygen apparatus carried by a golf cart driving ahead of a masked elephant is a notable exception; Langman et al., 1995). Recent work has extended respirometry measurement outside of the laboratory, using portable respirometers and logging overall movements.

Portable respirometry has become increasingly popular in human sports training and healthcare monitoring (Macfarlane, 2017). A common non-human model is horses on racetracks, as these animals are already trained to carry loads in semi-controlled outdoor environments (van Erck et al., 2007). Because fish and other aquatic animals use gills for respiration, oxygen depletion from the water around the animal can be measured to estimate energy expenditure without an enclosure (Byrnes et al., 2020). Respirometry tunnels are deployed in the migration paths of salmon to test how energy consumption relates to ambient temperature, photoperiod and differences in water content (Farrell et al., 2003). Respirometer chambers have also been successfully deployed for invertebrates, such as those placed over the known paths of unrestrained harvester ants (Lighton and Duncan, 2002). Because of the constant power consumption and localized sampling required by field respirometry, this methodology has been most successful for animals that move in predictable paths or that can carry the respirometry equipment themselves. In aquatic animals without gills, respiration only occurs at the surface of the water, so recording the location and timing between surfacing reveals a respiration rate. In orca whales, theodolites (mounted scopes to measure angles in horizontal and vertical planes) have been used to correlate respiration rate with speed and path complexity (Williams and Noren, 2009). Researchers recorded the timing of surface breathing as well as the swimming

motions of free-ranging penguins to estimate the cost of transport during dives (Sato et al., 2010).

Energy expenditure is often considered an important metric of human health, leading to consumer demand for indirect ways to measure locomotor energetics. For example, wearable exercise loggers use a combination of heart rate monitors and accelerometers to estimate energy expenditure throughout a variety of outdoor conditions and tasks (Kowalsky et al., 2021; Villars et al., 2012). Accelerometers have also been added to biologgers to characterize the energetics of non-human animals. Biologging tags attached to dolphins and whales with suction cups were combined with physics-based models of drag along the body to build energy budgets and estimate cost of transport for a variety of daily activities (Allen et al., 2022; Watanabe and Goldbogen, 2021). Another study attached accelerometers to Malayan colugos to compare the energetic cost of gliding and walking (Byrnes et al., 2011). When using biologgers with wild animals, challenges include (i) reducing the weight and therefore influence of the sensor on animal behavior while having enough power to record for the desired amount of time, (ii) restraining wild animals and attaching the sensor securely, (iii) recovering the sensor to obtain the collected data, and (iv) maintaining precision of the measurements, which may drift over time (Williams et al., 2020).

Field-based energy estimates are strengthened by comparison with laboratory-based respirometry, demonstrating the importance of combining the two approaches. Future developments in the design of portable respirometry equipment and bio-loggers may reduce the size and enable sampling from within the body, expanding this approach to additional animals and behaviors.

### Ethology of locomotion

Laboratory-based methods that isolate animals and present highly controlled stimuli provide incredible insight into the sensory capabilities of animals and the feedback control laws used to control changes in direction or acceleration (Stöckl et al., 2017; Catania, 2009; Sponberg et al., 2015). An exciting new area of field-based biomechanics research investigates how animals use sensory cues to regulate locomotion in more complex, naturalistic environments.

#### Collective motion

Animals that congregate in moving groups must coordinate with their conspecifics to regulate spacing and respond to obstacles in the environment. Observations of smaller groups operating in controlled laboratory conditions have informed mechanistic hypotheses and models for emergent group dynamics that can be tested in the field. For example, tracking and modeling studies of laboratory fish schooling have revealed that these patterns emerge from collision avoidance, directional orientation and cohesion (Lopez et al., 2012). However, lab-based studies on collective motion are often limited to small group sizes and species that will congregate under experimental conditions.

Empirical field-based studies are necessary to analyze collective dynamics in larger groups, non-captive species or environmental factors (Hughey et al., 2018). These studies have become more accessible with the development of field-portable multiple-camera recording protocols (Jackson et al., 2016) and wearable sensory technology. For example, an array of GoPro cameras was used to record swift flocking flight (Evangelista et al., 2017). Studying larger or less accessible animals benefits from lightweight sensors and software to synchronize multiple forms of data, such as in studies of ibis V-formation flight (Portugal et al., 2014) and wildebeest migrations (Torney et al., 2018). Other techniques have

also been deployed, such as the use of multi-beam sonar to examine how large fish schools respond to perturbations in natural environments (Fréon et al., 1992).

#### Moving through complex or variable environments

Natural habitats vary temporally and spatially, presenting disruptions and challenges for animal locomotion. Studies associating animal movements with environmental features require both detailed animal tracking and characterization of the habitat. While laboratory-based studies offer the opportunity to directly probe how animals respond to spatial structures (Wang et al., 2022), these conditions differ from natural habitats. Some hybrid studies build portable labs taken to the field for observation of wild animals in otherwise natural environments (Hunt et al., 2021). Characterizing field conditions reveals how material properties, resource distributions and spatial organizations affect animal movement. For example, empirically testing the flexural stiffness of natural grasses and twigs revealed that *Anolis* lizards prefer to jump from sturdier perches and land on more compliant perches (Gilman and Irschick, 2013). Using an acoustic Doppler velocimeter to map out the turbulence intensity of a stream revealed that trout prefer to stay in lower turbulence regions (Cotel et al., 2006). Quantifying physical aspects of the environment has made it possible to determine animal preferences in ways that were previously only possible in laboratories.

The introduction of engineered structures to a natural environment provides the opportunity to observe changes in locomotion in response to a controlled perturbation with otherwise naturally behaving animals. For example, offering honeybees artificial nest boxes identified cavity volume and entrance size as the dominating factors in nest quality assessment (Seeley and Buhman, 2001). Anthropogenic urbanization offers an extreme opportunity for this approach, which is especially important for understanding how habitat shifts may influence animal movement patterns (Winchell et al., 2020). Some habitat changes drive away animals, such as cheetahs and *Colobus* monkeys that avoid visiting human farmland (Van der Weyde et al., 2017; Anderson et al., 2007b). In contrast, humanmade structures placed in the ocean often attract fish, acting as artificial coral reefs (Layman and Allgeier, 2020).

In summary, lab-inspired field experiments studying motion through complex natural environments might develop field-portable 'labs', induce discrete changes within a habitat or analyze animal responses to uncontrolled habitat disruptions. These approaches provide a unique opportunity to quantify animal locomotion biomechanics and movement preferences in non-captive animals.

### Towards field-informed laboratory studies

Laboratory experiments permit detailed quantification of animal movement under controlled conditions, which is important for mechanistic studies. However, to contextualize animal movement in terms of evolutionary fitness or ecology requires directly connecting lab conditions to an animal's natural environment and behaviors. We advocate that laboratory studies can bridge this gap (i) through awareness of contributing factors during experimental design, (ii) by measuring and reporting laboratory conditions, and (iii) by directly testing how these factors influence animal movement.

This section will outline factors that may modulate an animal's movements under laboratory conditions. We categorize these factors into two groups: (i) the media that animals directly contact, which influences the physics underlying movement, and (ii) environmental factors, whether abiotic or biotic, that affect an animal's behavior. Importantly, these factors vary over time. Diurnal changes, seasonal fluctuations and learning may, often unknowingly, influence biomechanics findings. This section will



not provide a comprehensive review of all animal locomotion research that addresses these behavioral modulators, but instead will highlight studies that demonstrate the importance of controlling for or directly testing these factors.

## Media

The media that an animal directly contacts, sometimes called a locomotor matrix (Anderson et al., 2007b), dynamically interacts with the animal to determine any resulting motion. Although laboratory experiments may attempt to replicate natural substrates, variation in this media can fundamentally change how an animal moves.

Most terrestrial locomotion studies are performed on flat, level and stiff ground. But natural terrain is inherently rough with 3D features that influence ground contact dynamics (e.g. friction, adhesion), constrain foot placement and destabilize the body (Clifton et al., 2023). Further, the composition of a soil and the interaction of its component liquids and gases leads to a broad range in soil compaction level and compliance (Burland, 1990). Granular media also demonstrate non-linear dynamics (Askari and Kamrin, 2016), which has been an active focus for recent studies on animal locomotion. Animals interact with granular media using self-propulsive slithering (Goldman, 2014), burrowing/digging (Dorgan, 2015, 2018; Hosoi and Goldman, 2015) and walking (Li et al., 2013). Natural sands often contain particles of multiple sizes and shapes (Fonseca and Koehl, 2006), with the proportions of these components influencing friction and therefore media deformation (Mostefa Kara et al., 2013). Most laboratory studies use either commercially available sand, which differs from natural sand because it has undergone sieving to standardize particle size, or manufactured glass spheres, which possess a precise particle size and shape while being permeable to X-rays.

As the influence of natural versus laboratory sediment has become more broadly acknowledged, biomechanics studies are increasingly testing animals in the field (Moore et al., 2017) and/or using media collected from an animal's natural environment (Collins et al., 2013). A few studies have directly compared terrestrial locomotion under field and lab conditions. A ground bird species walking over snow versus on a treadmill uses relatively similar gait phasing but shorter stride lengths (Marmol-Guijarro et al., 2019). Dogs running on uneven fields prefer trotting gaits, which increase body stability (Wilshin et al., 2017, 2020). However, with relatively few studies on walking and running over natural terrain, the extent of kinematic divergence between laboratory and field conditions remains to be tested for most species.

Fluids can be characterized by several properties, including density, viscosity, surface tension and composition. These properties influence how fluid particles move in response to an applied force, which determines how an animal within or at the boundary of a fluid will experience fluid forces (such as drag, buoyancy and lift). Sea water density varies from 1.02 to 1.03 g cm<sup>-3</sup> globally at the sea surface as well as with depth (Webb, 2021). Variations in water density may greatly influence swimming animals (Fuiman and Batty, 1997), especially low-Reynolds number swimmers (Doostmohammadi et al., 2012), yet few empirical studies measure the influence of these factors.

Density varies more dramatically in air than in water, with bar headed geese flying at 9000 m (28,000 feet) experiencing an air density of 0.02 kg m<sup>-3</sup> versus the 1.2 kg m<sup>-3</sup> experienced at sea level (Hawkes et al., 2011). Several studies have experimentally altered air density and recorded flight kinematics; however, only for hummingbirds (Altshuler and Dudley, 2003) and bees (Altshuler

et al., 2005; Dudley, 1995). Radar recordings of wingbeat frequencies in migrating birds (Schmaljohann and Liechti, 2009) and video recordings of hummingbirds translocated to high elevations (Segre et al., 2016) have confirmed laboratory observations that flying animals increase flapping rate in lower density air. Not only can biomechanical studies varying air density elucidate how extant flying animals contend with elevational gradients but these findings also explore how extinct animals could have evolved under historical atmospheric conditions (Dudley and Chai, 1996). Despite the influence of air density, the majority of laboratory experiments on flight occur at approximately sea level elevations and at standardized temperatures.

A desired feature of laboratory equipment designed for testing animal flight or swimming (such as wind tunnels and flow tanks) is low-turbulence, laminar fluid flow. However, velocity gradients and vortices are commonplace in natural environments. Water turbulence has been measured within stream beds (Dey et al., 2012), resulting from waves (Burchard et al., 2008) and surrounding vegetation or other sessile organisms (Thomas and McLelland, 2015; Boothroyd et al., 2017). Air flow is turbulent around vegetation (Baldocchi and Meyers, 1988), near slopes (Belcher and Hunt, 1998) and due to thermal gradients (Lenschow and Stephens, 1980) including diurnal temperature variations (Zardi and Whiteman, 2013). This turbulence can dramatically alter the generation of fluid forces in flying and swimming animals (Liu et al., 2017). Several studies have directly observed animal flight in turbulence, including in bumblebees (Crall et al., 2017; Combes and Dudley, 2009), honeybees (Burnett et al., 2020), flies (Ristoph et al., 2010; Vance et al., 2013), hawkmoths (Ortega-Jimenez et al., 2014a, 2013) and hummingbirds (Ortega-Jimenez et al., 2014b; Ravi et al., 2015). Studies of fish swimming in turbulent flows (Liao, 2007) have identified an influence on body stability and orientation (Tritico and Cotel, 2010; Heatwole and Fulton, 2013), muscle activity (Liao et al., 2003a), energetics (Enders et al., 2003; Taguchi and Liao, 2011), kinematics (Liao et al., 2003b) and location preference within streams (Cotel et al., 2006). These studies highlight the importance of an animal's ability to adjust to spatial and temporal changes in turbulent flow structures in natural environments.

## Abiotic influences

Physical aspects of a natural environment that do not mechanically contact an animal may still influence its biomechanics, physiology and behavior. These factors include temperature, humidity, light levels, noise and fluid composition. Conservation-focused, ecological and behavioral studies have long examined the influence of these conditions; however, relatively few biomechanics studies directly address or account for these factors.

### Temperature and humidity

As ambient temperature is easy to control, numerous studies have explored its influence on physiological processes (Angilletta, 2009), including enzyme activity, cell membrane mechanics, aerobic metabolism, muscle function and animal locomotion. Because ectothermic animals do not maintain a consistent internal body temperature, they are more likely to be influenced by ambient temperatures. Indeed, environmental temperature increases stride frequency and walking speed in ectothermic invertebrates, including cockroaches, spiders and crabs (Full and Tullis, 1990; Booster et al., 2015; Claussen et al., 2000; Augustin et al., 2020). This pattern of increased maximal performance at higher temperatures also extends to vertebrate ectotherms, including lizard running speeds (Lailvaux and Irschick, 2007; Lailvaux et al., 2003; Zajitschek et al., 2012),

rattlesnake strikes (Whitford et al., 2020), crocodile swimming (Elsworth et al., 2003) and turtle head movements (Vervust et al., 2011). However, temperature-induced effects have not been observed during jumping by insects (Snelling et al., 2013; Deban and Anderson, 2021) or tongue projection in reptiles and amphibians (Olberding and Deban, 2021; Anderson and Deban, 2012), which are movements relying on elastic energy storage.

Most fish species are ectothermic, and a large body of research has investigated the influence of temperature on fish swimming. In warmer waters, fish generally swim at faster speeds (Dickson et al., 2002; Claireaux et al., 2006); however, tests of greater temperature ranges show speed declines at both temperature extremes (Wakamatsu et al., 2019). The effects of water temperature can also persist throughout a fish's lifetime. Zebrafish that developed in warmer water continue to demonstrate faster maximum swimming speeds (Sfakianakis et al., 2011) and escape responses (Ackerly and Ward, 2016) even after a month of acclimation at a common temperature. Numerous studies have measured the metabolic cost of swimming at varying temperatures (Guderley, 2004; Norin and Clark, 2016), showing that thermal effects vary across species and experimental conditions.

In contrast, investigation of thermal effects on endotherm kinematics is extremely limited. To the best of our knowledge, the only studies measuring the effect of temperature on kinematics in mammals or birds focus on hummingbirds. These studies find that despite maintaining similar flapping frequencies, hummingbirds decrease stroke amplitude at cold temperatures (Chai et al., 1998; Evangelista et al., 2010). By nature of regulating internal temperatures, endothermic animals are less likely to demonstrate temperature-dependent locomotion. However, this assumption has yet to be rigorously tested in most endothermic species, and extreme heat and cold events due to anthropogenic climate change will likely pose significant challenges to endotherms as well as ectotherms.

For a closed system of air, absolute humidity ( $\text{mass}_{\text{water}}/\text{mass}_{\text{air}}$ ) is independent of temperature and pressure. However, most hygrometers (and therefore studies) measure relative humidity (actual water content/maximum water holding capacity), making it difficult to isolate the effects of humidity. Relative humidity is known to impact heat and moisture exchange processes in animals (Wolkoff, 2018; Ludwig, 1945), influencing the body's water content, internal temperature and susceptibility to infections. Humidity has also been shown to influence walking kinematics in crabs (Weinstein, 1998; Claussen et al., 2000) and the flight performance of some insect species (Zhang et al., 2008; Rowley and Graham, 1968). Overall, very few studies on animal locomotion control for – or even measure – humidity.

#### Light and noise

The 'visible spectrum' of light is based on human vision; however, many (if not most) species are sensitive to ultraviolet light (Cronin and Bok, 2016) with a few documented cases of infrared light sensitivity (Goris, 2011). Several species, including birds and amphibians (Horváth and Varjú, 2004) can see light polarization, which is often used during navigation (Webb and Wystrach, 2016). Light sensed by an animal may be used to localize objects in their surroundings, identify nearby conspecifics and prey (Garm and Nilsson, 2014), or provide a temporal signal (diurnal or seasonal light fluctuations).

Given the influence of light on perception as well as on physiological processes (Hanifin et al., 2019), it is no surprise that light intensity has been shown to influence animal locomotion and behavior both in the field and in the laboratory. Lion hunting

behaviors depend on the moon cycle (Packer et al., 2011). Dragonfly prey capture rates and fruit fly speed vary with light intensity (Combes et al., 2012). Some species of *Daphnia* increase swimming speed with more light exposure (Dodson et al., 1997). Despite this influence, few studies on animal movement measure or control for light level. This is likely because of the complexity of measuring light. Photometers record electromagnetic radiation intensity, but only for specific wavelengths, which are often tuned to human-centric ranges. Isolating the intensity of individual colors using a spectrometer poses even greater challenges (Johnsen, 2016). While using this equipment may be outside the scope for many studies, we encourage researchers to describe details of all light sources.

A growing number of studies aim to characterize the soundscape of natural habitats (Merchant et al., 2015) and identify the influence of noise on animal behavior (Kunc et al., 2016; Kight and Swaddle, 2011; Shannon et al., 2016; Rutz et al., 2020; Southall et al., 2016; Jézéquel et al., 2022; Lillis and Mooney, 2022; Suca et al., 2020). In the field, anthropogenic noise has been tied to shifts in flight pathways for bats (Schaub et al., 2008) and birds (Ortega, 2012; Ware et al., 2015), as well as to changes in behavior (e.g. predation efficiency) for many terrestrial and aerial species. Underwater environments are far from silent (Slabbekoorn et al., 2010), with noise disrupting normal behavior in fish, marine mammals and aquatic invertebrates. These studies examine the influence of large-scale anthropogenic noise pollution, such as traffic, vessels, aircraft and fracking. Smaller-scale noises (e.g. equipment, researchers) likely also influence observed animal movement (von Kortzfleisch et al., 2022); however, this remains broadly untested.

#### Fluid composition

All animals live surrounded by some fluid, most notably air or water. The composition of this fluid directly influences an animal's physiology through the availability of metabolic nutrients or exposure to noxious chemicals. Swimming animals are influenced by dissolved levels of oxygen (Kramer, 1987; Nudds et al., 2020), carbon dioxide (Pörtner et al., 2004) and in some cases nitrogen (Hansen et al., 2013). Salinity also influences swimming speeds (Yu et al., 2010; Li et al., 2019), likely as a result of the cost of osmoregulation and the stimulation of growth through food intake and conversion (Bœuf and Payan, 2001).

Besides changing the density of air, relative oxygen and carbon dioxide levels influence flight or terrestrial respiration and energetics (Harrison and Roberts, 2000; Lombardi et al., 2020). Inversely, the presence of pollutant chemicals in air or water may disrupt normal physiological processes or injure the body (Xia et al., 2014). All of the above factors likely differ under laboratory conditions compared with natural environments, influencing how an animal moves.

#### Biotic influences

Biotic factors also affect the behavioral expression of motion and should be explicitly considered during experimental design. We present these factors in categories, although we note that some behaviors may be modulated by interactions between factors. We are categorizing factors that occur within the body of the individual as 'intrinsic' (e.g. age). We are categorizing factors that occur as a result of interaction with other plants, animals or signals produced by other animals as 'extrinsic' (e.g. pheromones).

#### Intrinsic factors

Development and growth can affect both the physical capabilities and the cognitive preferences for locomotion. In some animals with

large post-natal changes in body proportion, gaits used by young might not be used in adults. For example, as jerboas experience rapid postnatal elongation of metatarsals, they progress from creeping on forelegs only, to quadrupedal trotting, and finally bipedal walking on hindlimbs only (Cooper et al., 2013; Eilam and Shefer, 1997). Some behaviors may be affected by environmental changes during ontogenetic development. For example, butterflies that experience a lack of water as larvae have significantly lower quality wing aspect ratio and higher mortality, despite no changes in take-off performance (Lailvaux et al., 2017).

Animals might also have innate preferences for specific patterns of locomotion. Lateralization, or ‘handedness’, is exhibited by bipedal marsupials and dolphins (Giljov et al., 2015; Bandyopadhyay et al., 2013). Individuals of the same species exhibit ‘personalities’ (e.g. shy versus bold) that are associated with a preference for certain types of locomotion (Hall et al., 2019; Toms et al., 2010). These locomotor personalities also affect higher-level exploration and foraging strategies (Patrick et al., 2017). Some animals use prior experience to inform future behaviors (Freymiller et al., 2017; Frost et al., 2007), which may be modulated by personality.

Body condition and motivational state can also affect animal locomotion and behavior. Limb loss is common in many spider species, which may constrain them to hunting smaller prey and reducing speed while climbing inclines (Brueseke et al., 2001; Gerald et al., 2017). Furthermore, spiders shift to a novel gait following limb loss to enhance stability and maintain speed (Wilshin et al., 2018; Escalante et al., 2020). Gravity greatly reduces locomotor performance in most animals, but in reptiles this effect may be similar to the ingestion of a large meal (Shine, 2003). The effects of body condition on expression of motion provide opportunities to explore the neural and endocrine basis of these patterns. In zebrafish, hunger enhances the response to *d*-amphetamine, which causes significant increases in swimming distances and tail activity (Bansal et al., 2022 preprint). In *Drosophila* fruit flies, hunger increases locomotion by interacting with the AKHR receptor, but the downstream neuronal mechanisms are still being investigated (Lin et al., 2019). Host manipulation is a common strategy in which parasites might increase, decrease or redirect host locomotor activity to benefit the parasite (Ni and Doherty, 2022; Lafferty and Shaw, 2013; Goodman and Johnson, 2011; de Bekker et al., 2021). Especially for wild-caught animals, recording the presence, absence or degree of infection may provide critical context for interpreting biomechanical data.

Extrinsic factors

Interactions between organisms have great potential to influence the behavioral expression of motions in animals. Dogs are more likely to explore a novel object when conspecifics are nearby, potentially to minimize individual risk (Moretti et al., 2015). Mating and courtship displays often include exceptional divergence from

non-mating behaviors, which are summarized elsewhere. As one brief example, male–female pairs of mosquitoes harmonize, while same-sex pairs diverge in their wingbeat frequencies (Gibson et al., 2010).

For many species in captivity, the behavior of free-living individuals has not yet been characterized, so it is difficult to measure the influence of captivity on locomotion. In general, captive animals tend to be less active or exhibit repetitive behaviors (‘stereotypy’) as a consequence of having a smaller and less complex environment available for them to explore (Bennett et al., 2015). Despite this difference, captive dolphins maintain the same capability for maximum swimming speeds compared with free-living individuals (Rohr et al., 2002). In some animals, changes in locomotor activity as a result of captivity are highly plastic and do not persist in free-living offspring (Stoinski et al., 2003).

Closely related to captivity is the influence of experimenters and zookeepers. Repetitive pacing behaviors in captive okapi decrease as the number of zookeepers they interact with increases (Bennett et al., 2015). In humans and other animals, experimenter sex and/or gender has significant effects on cognitive, behavioral and physical tasks (Chapman et al., 2018), but this factor is often undocumented and uncontrolled in many studies.

Pheromones and other scent cues have the potential to affect locomotor behaviors, whether they are left by conspecifics, predators, prey, parasites or hosts. The neuromechanisms of aquatic chemical sensory cues that trigger fish motor behaviors have been well documented (Daghfous et al., 2012). For example, short-term cortisol increases locomotion activity in trout, while long-term exposure inhibits locomotion (Øverli et al., 2002). Reptiles, their competitors and their prey are also sensitive to chemical cues (Wasko et al., 2014; Amo et al., 2004; Halpin, 1990). Thus, it is important to clean and remove potential scent cues between trials (Davis Rabosky et al., 2021).

Temporal fluctuations

An animal’s behavior changes over time as a result of learning, aging and varying environmental conditions. Many of these factors have been discussed above; however, it is important to reiterate that media properties and both biotic and abiotic environmental conditions vary temporally and interact with each other, producing diurnal or seasonal patterns. For example, foraging Argentine ants slow down only marginally under dark versus light conditions; however, repeating measurements after 3 months showed a 30% reduction in all average walking speeds (Clifton et al., 2020). This dramatic shift likely corresponds to seasonality within Argentine ant colonies (Markin, 1970), with changes in caste composition and activity. In fact, many animals demonstrate behavioral and physiological changes across time, at both shorter time scales (e.g. throughout a day) and longer time scales (e.g. mating seasons, migrations). Yet, few studies on animal movement repeat data collection under identical conditions across time.

Table 1. Factors to consider while designing field-informed laboratory studies

Media properties	Abiotic factors	Biotic factors
3D terrain structure	Temperature	Age
Substrate compliance	Humidity	Behavioral preferences (e.g. handedness)
Granular media composition	Light	Body condition (e.g. limb loss, gravity)
Flow turbulence	Noise	Motivational state (e.g. hunger)
Fluid properties (e.g. density, viscosity, temperature)	Fluid composition (salinity, dissolved gases, air proportions, pollutant levels)	Conspecific interactions
		Experimenter Influence

←Temporal fluctuations: time of day, seasonality, climate patterns (e.g. El Niño, climate change)→

We advise that researchers (i) choose experimental conditions that base these factors on real-world conditions, (ii) explicitly test how animal movement depends on variability in these factors, and/or (iii) measure and communicate relevant factors used in experimental set-ups.



## Conclusions and outlook for the future

We agree that ‘the importance of studying intact, behaving organisms under a broader range of locomotor conditions (other than steady state) and in the context of their natural environment remains a critical need for vertebrate biologists’ (Biewener, 2002). Both laboratory and field experiments are crucial in biomechanics, contributing detailed knowledge about how an animal moves and how these movements relate to its daily life and survival. Technological advances bolster our ability to combine these approaches by developing techniques for measuring intricate kinematic features under field conditions. We advocate studying organisms in their native habitats as some confounding factors cannot be standardized or may be yet unrecognized within the scientific community. In designing laboratory experiments, we encourage investigators to consider, measure and standardize factors that may modulate animal behavior and performance as summarized in Table 1. Further, designing studies to directly test the influence of these conditions will enable us to best evaluate how past and future lab studies differ from natural behavior.

The guidance presented in this Review is intended to inspire and inform future studies. However, we acknowledge that the inherent complexity of this outlook may be daunting to those interested in animal movement through naturalistic environments. We believe that research at any point along the lab–field spectrum contributes meaningfully to understanding animal locomotion, and hope that future studies will explore locomotion under field conditions, report environmental factors controlled under laboratory conditions, and directly test how relevant factors impact animal movement.

Pursuing field studies on animal movement and quantifying the influence of modulating factors under lab conditions will improve how biomechanics interfaces with the fields of evolution, ecology, conservation and robotics. Investigating biomechanics in natural habitats enables the association of movement performance with life history, therefore better contextualizing the evolution of animal locomotion. Ecologists require standardized metrics of performance in natural environments that are straightforward to obtain in field conditions and can therefore be used for taxonomically broad comparative studies (Losos and Sinervo, 1989). Biomechanists endeavoring to understand movement in the context of ecology and evolution can continue to develop broadly informative metrics that can be used by experts in each of these fields. Conservation efforts may also benefit from identifying field-relevant measures of animal performance. Urbanization and the introduction of novel structures to outdoor environments dramatically alter an animal’s habitat and may inconsistently influence different species (Winchell et al., 2020). Lastly, robotics faces significant challenges in developing both hardware and controllers suitable for real-world exploration (Torres-Pardo et al., 2022). Analyzing animal motion under variable, naturalistic conditions will inspire robotic innovations, which may also help inform our biological understanding (Gravish and Lauder, 2018).

No animal is an island. To fully understand how an animal moves entails incorporating the complexity of its environment, either by extending biomechanical studies to field conditions or by bringing relevant aspects of natural environments into the lab. Focusing on biomechanics under naturalistic conditions has the potential to foster interdisciplinary research and accelerate findings in multiple fields.

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## ECR Spotlight

This article has an associated ECR Spotlight interview with Talia Moore.

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