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COMMENTARY

SPECIAL ISSUE

INTEGRATING BIOMECHANICS, ENERGETICS AND ECOLOGY IN LOCOMOTION

Integrating physiology into movement ecology of large terrestrial mammals

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ABSTRACT

Movement paths are influenced by external factors and depend on an individual's navigation capacity (Where to move?), motion capacity (How to move?) and are ultimately driven by internal physiological state (Why move?). Despite physiology underlying most aspects of this movement ecology framework, the physiology–movement nexus remains understudied in large terrestrial mammals. Within this Commentary, we highlight the physiological processes that underpin the movement ecology framework and how integrating physiological measurements can provide mechanistic insights that may enhance our understanding of the drivers of animal movement. We focus on large terrestrial mammals, which are well represented within the movement ecology literature but are under-represented in movement studies that integrate physiological state. Recent advances in biologging technology allow for physiological variables, such as heart rate and body movements, to be recorded remotely and continuously in free-living animals. Biologging of body temperature may provide additional insights into the physiological states driving movement. Body temperature not only provides a measure of thermal stress, but also an index of animal wellbeing through quantification of nutrition, hydration, reproductive and disease states that may drive animal movements. Integrating measures of body temperature with fine-scale GPS locations may provide insights into causality and improve our mechanistic understanding of animal movement, which is crucial for understanding population performance and monitoring reintroduction success. We recommend that baseline studies are undertaken, linking animal movement to the underlying physiological mechanisms, to allow for the development of realistic predictive models to improve conservation efforts in the Anthropocene.

KEY WORDS: Internal state, Navigation, Locomotion, Physiologging, Biologging, Body temperature

Introduction

Within the 'golden era of biologging' (Wilmers et al., 2015), we have unprecedented access to animal-borne sensors to gain insight into the biology of free-living animals (Ellis-Soto et al., 2023). Biologging, a term introduced to the literature only 20 years ago (Boyd et al., 2004), has made a remarkable contribution to our understanding of animals for more than half a century. In the 1960s, radio telemetry facilitated the first time–depth recordings of marine mammals (Kooyman, 1965) and allowed terrestrial animal locations to be determined through triangulation (Cochran et al., 1965). At the same time, pioneering studies were measuring heart rate and body temperature in unrestrained mammals (Essler and Folk, 1961) and blood flow through arteries of diving pinnipeds (Franklin et al., 1964). Since then, technological advances have expanded the range of variables that can be measured and improvements in memory and battery capacity have allowed miniaturization of devices, expanding the diversity of species studied and the time span of biologging studies (Williams and Hindle, 2021). Here, we use the term biologging to incorporate both biotelemetry (Cooke et al., 2004a), in which data are transmitted to a receiver, and biologging (Boyd et al., 2004), in which data are stored onboard and later downloaded. While the term physiologging (Hawkes et al., 2021) has been coined specifically for physiological metrics, we have chosen to use the broader term biologging as it incorporates the remote collection of movement, physiological, behavioural and/or environmental data (Rutz and Hays, 2009), using devices implanted or attached to animals.

With biologging presenting the opportunity to 'observe the unobservable' (Williams et al., 2020), studies on higher marine vertebrates spearheaded the development of biologging techniques (Ponganis, 2007), allowing researchers to monitor variables such as swim speeds and stroke frequencies, body temperatures and heat flux, heart rate and electrocardiography (ECG), blood flow and pressures, respiratory rates, blood and muscle oxygenation, prey ingestion, electromyography (EMG) and electroencephalography (EEG) in freely diving mammals and birds (Williams and Ponganis, 2021). In terrestrial systems, the uptake of biologging in ecological studies was initially slow (Cooke et al., 2004a), with the dominant biologging techniques focused on how animals move within their environment. Advances in global positioning system (GPS) technology allowed for animal movement studies to progress beyond simple home range estimates to assessing individual movement paths, creating a 'perfect storm of opportunity' to understand how and why animals move (Cagnacci et al., 2010), leading to a unifying conceptual framework (Nathan et al., 2008) and the rise of the field of movement ecology. However, to accurately assess the mechanisms of how and why large terrestrial mammals move, we need to incorporate physiological measurements into movement ecology studies, as done for other taxa (for reviews, see Cooke et al., 2022; Hays et al., 2016; Newton, 2023).

Physiology underlies almost all aspects of animal movement. Integration of physiology into movement ecology analyses requires more than simply including body mass or age class in analyses (see for example, Joo et al., 2022). We need physiological measurements of energetics, nutrition, endocrinology and immunology, alongside

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ecological and environmental measurements, to provide a mechanistic understanding of animal movement (Goossens et al., 2020; Jachowski and Singh, 2015). Biologging provides an opportunity to measure body temperature (Hetem et al., 2016), microclimate selection (Hetem et al., 2007), heart rate (Signer et al., 2010), energetics (English et al., 2024) and behaviour-specific body postures and movements (Wilson et al., 2008) in free-living animals. A multisensor biologging approach optimized through an integrated biologging framework (Williams et al., 2021), complemented by isotope and hormonal analysis (Fleming et al., 2018), is required to improve our understanding of the relationship between physiology and movement (Goossens et al., 2020). Future technological developments may allow remote blood sampling for hormonal analyses (Takei et al., 2016) at set sampling intervals (Whitford and Klimley, 2019), but biologging currently provides the most appropriate toolbox for continually and remotely quantifying the physiology of free-living animals. In this Commentary, we unpack some of the physiological processes that underpin movement ecology and propose how integrating physiological measurements of these processes can provide mechanistic insights that are not feasible through standalone movement metrics. Physiological measurements are increasingly integrated into movement ecology studies of fish (e.g. Lucas et al., 1993; Cooke et al., 2004b) and birds (e.g. Ponganis et al., 2009; Bishop et al., 2015), but the integration of physiological measurements has been relatively slow in movement ecology studies of terrestrial mammals, despite mammals making up a third of all movement ecology papers (Joo et al., 2022). We focus specifically on large terrestrial mammals (>5 kg), which are less restricted by the mass of biologger placements than their smaller counterparts, based on the 3–5% body mass guideline (Wilson et al., 2021a), yet remain under-represented in studies of biomechanics and energetics of movement (Brown et al., 2013). We start by unpacking and expanding how physiology underpins each component of the movement ecology framework, then highlight how biologging physiological measurements in the field can enhance our understanding of movement ecology. We use body temperature variation as an example to illustrate the interconnectedness of physiological processes and movement ecology.

Physiology underpins movement ecology

External factors and internal state

The field of movement ecology was conceptualised succinctly by Nathan et al. (2008; redrawn and adapted in Fig. 1). Rather than merely representing a random walk through a featureless landscape, animal movements embody an interaction between behavioural, physiological and ecological factors (Getz and Saltz, 2008). Movement paths can be influenced by several external factors including both abiotic factors, such as celestial cues, weather, geographic obstacles or location of water sources or shelter, and biotic factors, such as foraging resources, inter- and intra-specific competitors, predators, prospective mates or kin. These external factors are inter-related, such that external factor dynamics (represented by the semi-circular grey arrow in Fig. 1) influence temporal and spatial variability in the landscape. For example, the consumption of food resources by conspecifics can directly impact the resource availability and therefore nutritional physiology of an individual animal. Movement paths are composed of a sequence of movement phases, each associated with fulfilling a set of goals. These proximate goals (e.g. to gain energy, drink water, seek shelter or safety, or reproduce) depend on the internal physiological state of

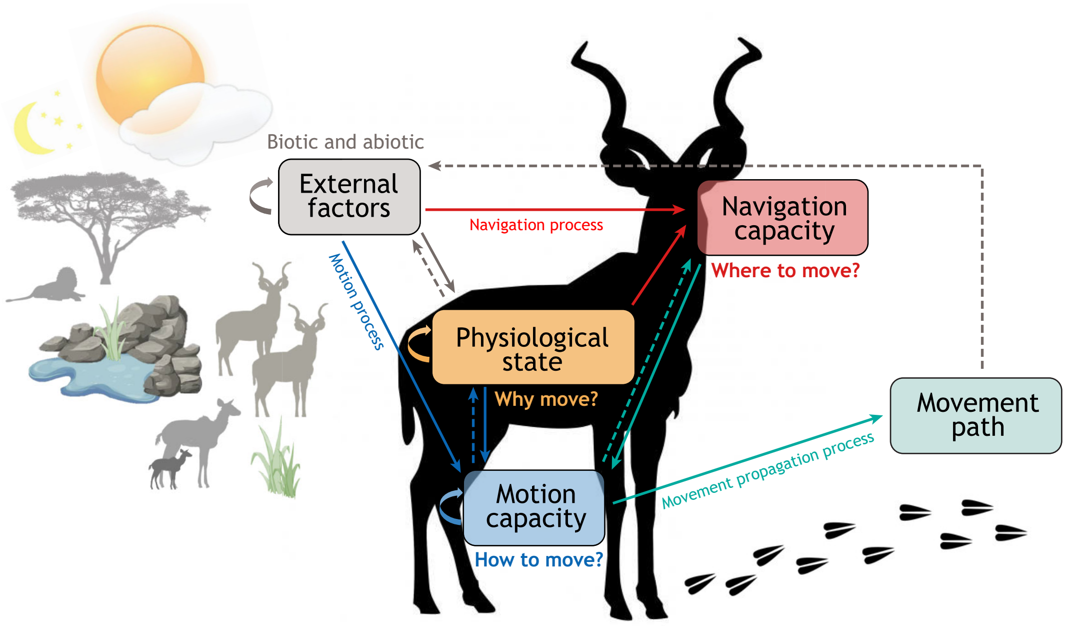

Fig. 1. Pictoral representation of the movement ecology framework. Both biotic (conspecifics, predators and food) and abiotic (weather, geographical barriers and celestial cues) external factors influence an animal's movement path, through direct effects on its motion capacity (How to move? e.g. biomechanical compensation to ensure stability on uneven terrain) or via navigation capacity (Where to move? e.g. integrating sensory cues and neurophysiological mechanisms) and physiological state (Why move? e.g. hormonal drivers to find a mate). The complexity of the feedback and feedforward control systems (dashed arrows) are represented by the addition of bidirectional arrows, with the movement path itself ultimately influencing the external factors to which the animal is exposed. Physiological state, as represented by a multitude of interrelated homeostatically regulated processes, drives almost all components of movement, yet it remains underappreciated in movement ecology literature. Figure adapted from Nathan et al. (2008), with graphics from Dreamstime (https://www.dreamstime.com).

the animal (e.g. hunger, thirst, cold, fear or hormonal cues) as the ultimate driver (why move?). This internal physiological state (*sensu* Jachowski and Singh, 2015) is influenced by abiotic and biotic external factors and self-regulated through homeostasis (represented by the orange semi-circular arrow in Fig. 1). Achieving homeostasis requires the integration of numerous physiological processes, such as thermoregulation, osmoregulation, digestion and reproduction, which act together like cogs in a machine (Fig. 2). Different physiological processes may be prioritized based on an animal's physiological state, which may in turn influence the nature of the external factors they experience (represented by dashed grey arrow in Fig. 1). For example, male fallow deer (*Dama dama dama*) during the rut may stand in open areas and experience high radiant heat loads while defending their territories, prioritizing acquisition of mates over thermal comfort or foraging (Clutton-Brock et al., 1988). Changes in physiological state, detected through interoceptive input and modulated through sensory perception of external factors (e.g. thermoreception, magnetoreception, visual, olfactory or auditory cues), and circadian and circannual rhythms (e.g. reproduction, moult or migration), will determine the timing and direction of an animal's movements (navigation capacity).

Navigation and motion capacity

Navigation capacity (where to move?) uses sensory cues to orient both spatially and temporally within a landscape. Navigation may depend on simply following sensory cues (beacon/gradient-based navigation e.g. following marked trails) or spatial memory that may be genetic (e.g. inherited predatory deterrence or migratory route) or learnt from prior experience or social transmission (Fagan et al., 2013; Jesmer et al., 2018), with some species thought to use complex cognitive mapping to locate resources (Toledo et al., 2020; Trapanese et al., 2019). However, spatial learning and memory need not involve complex maps or location-based navigation. For example, exposure to high radiant heat loads may stimulate thermoreceptors in the skin to elicit a movement response to a cooler microclimate. Across hierarchical levels of spatiality, navigation to a cooler microclimate may take place at a simple sensorimotor level, such as moving down a temperature gradient (e.g. altitudinal shift) or at a higher spatial level, such as moving to a preferred thermal refuge (e.g. tree or cave site). The precise mechanisms through which these different forms of spatial orientation translate into motion capacity (how to move?) are poorly understood (Jeffery et al., 2024), forming the most under-represented link within the movement ecology framework (Joo et al., 2022). Some of this under-representation may stem from the selection of keywords within systematic reviews, such as movement versus locomotion and biases in journal selection (Holyoak et al., 2008) that have tended to exclude a plethora of neuroscience literature. Yet, studies on the neuroscience of movement may provide crucial insights into navigation mechanisms underlying movement patterns.

For navigation to be effective, it must result in a motor response (motion capacity) through a movement propagation process (Fig. 1). Goal-directed behaviour and spatial planning rely on cognitive function within the forebrain (Grillner and El Manira, 2019), specifically the prefrontal cortex in mammals (Fine and Hayden, 2022). The primary motor cortex integrates information from various brain regions, including the thalamus that integrates sensory input, to initiate movement through a set of descending neurons within the corticospinal tract (Kiehn, 2016). We need to be cognisant of our anthropomorphic bias in inferring that conscious choice drives animal movement. Even humans are only conscious of their movement intentions after the motor cortex initiates its response

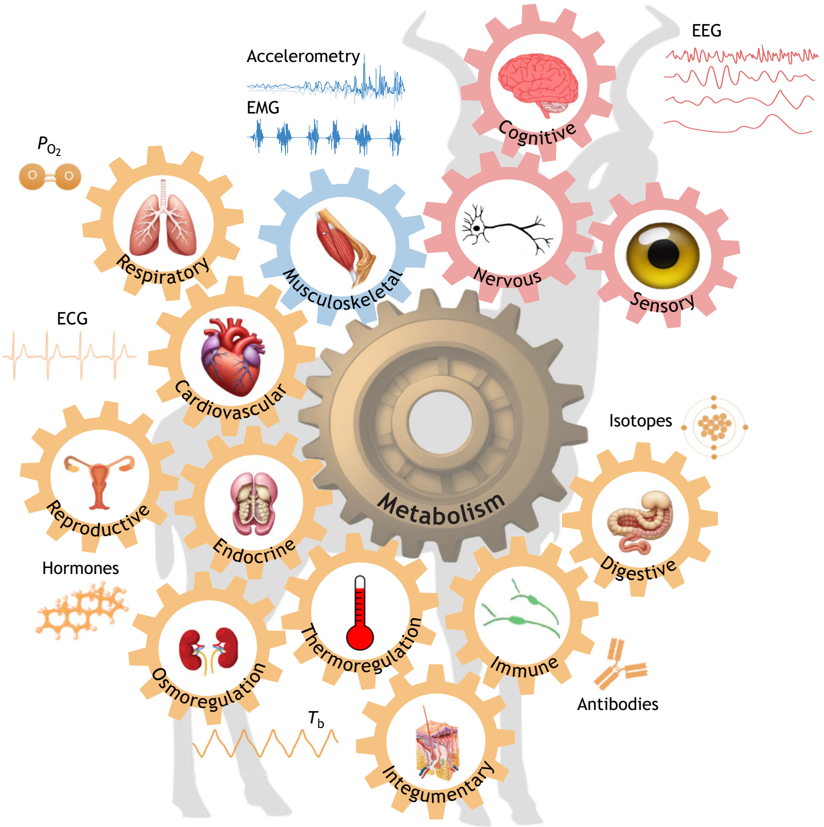

Fig. 2. Interconnected physiological processes drive the different components of the movement ecology framework. Organ systems and physiological processes continuously interact to form an integrated network, like cogs in a machine. Physiological processes provide insights into the causative mechanisms underlying the different components of the movement ecology framework, namely navigation capacity (red cogs), motion capacity (blue cog) and internal physiological state (orange cogs). Advances in biologging technology increasingly allow for the remote and continuous measurement of physiological variables in free-living animals, and may include brain waves through electroencephalography (EEG), activity (accelerometry) and electromyography (EMG), heart rate and electrocardiography (ECG), blood and muscle oxygenation (P_{O_2}), and body temperature (T_b). Isotope, antibody and hormonal analysis may complement biologging approaches by providing a snapshot into the physiological processes that drive animal movement. Organ graphics from AI Emojis (https://www.emojis.com/).

(Libet et al., 1983), highlighting the importance of unconscious neural processes. Most movements are achieved independently of the motor cortex, with the basal ganglia initiating movement or changing gait or speed via innervations to the locomotor regions in the midbrain. Once stimulated, locomotor regions activate neurons in the brain stem, which convey the excitation to activate spinal cord locomotor circuits (Grillner and El Manira, 2019), or central pattern generator (CPG) circuits, that produce repetitive rhythmic patterns of movement, such as walking, swimming or flying (Haspel et al., 2021). These neural networks innervate multiple muscle groups to control the timing of muscle contractions and are interconnected to allow for coordinated alternation between flexor and extensor muscles within each limb to produce movement.

Once movement has been initiated (motion capacity) several controls and feedbacks ensure coordinated movement (as represented by the addition of the dashed arrow of the movement propagation process, Fig. 1). At the neural level, the spinal locomotor circuits can function independently of brain and sensory input. However, they are generally modulated through somatosensory feedback (e.g. proprioception and cutaneous tactile afferents) and neuromodulators (e.g. noradrenalin). Further fine-tuning, based on feedback from the spinal locomotor circuits, the moving muscles themselves, and the somatosensory system, takes place in the cerebellum, which allows for the adaptation of coordinated movements over time through an error detection and correction learning process (Grillner and El Manira, 2019).

While navigating a goal-directed path, an animal must negotiate heterogeneous landscapes and adjust its trajectory in response to continuous sensory input that may or may not align with the original goal. Input from multiple sensory systems is received, integrated and processed relative to its spatial positioning in the orienting structures within the midbrain (Allen et al., 2021). The orienting structure also receives information from other brain regions, which allows it to build a map of the sensory environment and execute appropriate actions or behaviours, either orienting towards attractive stimuli or evading aversive ones (Isa et al., 2021). One of the best examples of an animal's physiological state modulating the approach or escape response (as represented by the lower red arrow in Fig. 1), is that of hungry zebrafish (*Danio rerio*) larvae, which were more likely to approach rather than evade larger moving items than their fed counterparts, thereby increasing their risk of predation (Filosa et al., 2016). Starvation decreased the larvae's aversion through decreased cortisol levels resulting in a downstream increase in the neuromodulator serotonin, which altered visual information processing in the midbrain and increased the size threshold for approach behaviour (Filosa et al., 2016). If these changes in the neural conformation of the midbrain also influence the fear response, via its connections to the amygdala (Isa et al., 2021), a similar mechanism may be responsible for large terrestrial mammalian herbivores foraging in riskier habitats when food resources are low (McArthur et al., 2014). Measuring the electrical activity of the brain may allow identification of the different brain regions associated with navigational cues and information processing (Fig. 2). For example, ambulatory EEG revealed landscape features of relevance to homing pigeon (*Columba livia domestica*) navigation (Vyssotski et al., 2009), and provided insights on sleep (Rattenborg et al., 2008) and welfare state (Stomp et al., 2021) of free-living, terrestrial mammals.

Because of the complexity of neurophysiological mechanisms, electrophysiological and neuroimagery studies are traditionally undertaken in a laboratory setting, where confounding factors can be carefully controlled to elucidate mechanisms. We now need to take these measurements to the field to understand how real-world navigation integrates multifaceted cues within a complex ecological context (Park et al., 2018). The complex integration of navigational capacity, neurophysiological mechanisms and context-dependent information results in neural impulses being sent via motor neurons to stimulate muscles to contract to execute the movement (motion capacity). The musculoskeletal system (bones, muscles and joints) integrates neuronal and mechanical feedback, with feedforward control, to facilitate stable movement through complex natural environments (Dickinson et al., 2000). Ambulatory EMG may provide further insight into muscle function, locomotor biomechanics and kinematics (Struble and Gibb, 2022) of large terrestrial mammals. The end result, movement, is comparatively easy to measure and quantify in the field. A review of movement literature at the time the unifying conceptual framework was proposed revealed that most papers on movement published in the preceding decade were narrowly focused on documenting movement pathways or showing how external factors influenced motion capacity (Holyoak et al., 2008). Yet, external factors seldom affect motion capacity directly, as they need to be sensed and integrated within the individual's prevailing physiological state to allow initiation of an appropriate movement response. Despite calls for integrative approaches and interdisciplinary collaboration, a decade later, the majority of the 8000+ papers published on movement ecology still focused on environmental factors driving movement and behaviour (Joo et al., 2022), potentially because of an underappreciation of the critical role that physiological processes play in movement responses and perceived difficulties in the measurement of physiological variables.

Movement tracks

Over the past decade, significant technological advancements have allowed the recording of high-resolution movement tracks (Nathan et al., 2022) and the development of statistical analytical tools for quantifying movement (see for example, Joo et al., 2020). Movement paths can be broken down based on a hierarchical scale, with lifetime movement tracks made up of several movement phases (e.g. escaping a predator or searching for food), each of which is likely to be driven by underlying physiological processes (Fig. 2). Movement phases are made up of a number of canonical activity modes (CAMs), like standing, walking or running (Nathan et al., 2008). These activity modes can be summarized into diel activity regimes to quantify movement responses to changes in landscapes or climates (Getz, 2022, 2023). Traditional analyses of movement tracks defined these activity modes based on vector dimensions, i.e. a combination of distance (step-length) and direction (turning angle) between consecutive GPS locations (Getz and Saltz, 2008). Because of the initial coarse temporal resolution of GPS fixes (in the order of hours), which likely include a combination of short-duration activity modes (e.g. resting and foraging), behavioural states were classified based on the likely dominant activity mode occurring between fixes. Finer resolution GPS fixes allow for more accurate classification of dominant behavioural states, with sufficiently high-resolution GPS fixes (in the order of fractions of a second) detecting individual repetitive body movements or fundamental movement elements (FMEs), such as single steps or wing beats (Getz, 2022). Individual movement elements are seldom discernible from GPS fixes alone but can be inferred through the integration of data from biologging sensors (Williams et al., 2020). For example, audiologgers can be used to record individual steps and bites of ungulates (Northrup et al., 2019), or GPS fixes can be combined with data from an inertial measurement unit (IMU), which integrates data from tri-axial accelerometers, magnetometers and occasionally gyrometers, to allow for fine-scale path reconstruction through dead reckoning (Bidder et al., 2015).

Integrating high-throughput technology for more accurate path reconstruction allows greater insight into the drivers of animal movement (Nathan et al., 2022), movement speeds and associated energetic costs. To achieve energetically optimal movement, animals should travel at a speed that allows them to maximize their energy gains while minimizing energy expenditure rate (Pyke, 1981). However, animals seem to only select optimal speeds when travelling extended distances in their natural environments. They generally travel faster than their optimal speeds when evading predators or chasing prey, which may increase the risk of injury, and slower than optimal speed when foraging to increase the detectability of potential food items (Wilson et al., 2015b). While searching for food within a patch, energetic gains may be enhanced through increased path tortuosity, with greater turning angles. However, frequent turns are energetically costly (Wilson et al., 2013), prompting animals to further reduce their speed to achieve cost-effective locomotion (Wilson et al., 2021b). Indeed, lower-speed hunts favour prey survival, as prey can maximize their turning manoeuvrability to evade predators (Wilson et al., 2018). Therefore, realized movement speeds represent a complex interaction between an individual's morphology, behavioural context, environmental constraints (Jahn and Seebacher, 2022) and physiological capacity (Wu and Seebacher, 2022).

The cost of transport varies across an energy landscape and increases with higher substrate penetrability (e.g. soft snow or sand), uneven terrain (limbs need to be lifted higher) and inclines (Shepard et al., 2013). Both cervids (Newmark and Rickart, 2012) and elephants (*Loxodonta africana*, Wall et al., 2006) avoid steep inclines, presumably because of higher energy costs, providing a direct example of external factors influencing motion capacity to direct a movement path (Fig. 1). While some landscape features may remain constant, an animal may not always prioritize energy expenditure economy, and the selected movement path will likely be influenced by trade-offs between physiological state (e.g. athletic ability or nutritional wellbeing) and navigational capacity (e.g. past experience of resource locations) to create the 'individual energy landscape' (Halsey, 2016). How an individual experiences the energy landscape also depends on its thermoregulation, body maintenance and muscle morphology (Amélineau et al., 2018). Based on functional requirements, muscle fibres themselves can be remodelled and the relative contribution of the major components can change in response to use (represented by the addition of the semi-circular blue arrow in Fig. 1) and physiological state, such as nutrition or hormonal influences (Schaeffer and Lindstedt, 2013). The working muscles themselves modify 11 homeostatically regulated variables (represented by the addition of the dashed blue arrow from motion capacity to physiological state in Fig. 1), including blood pressure, blood gases, glucose and ion concentrations, plasma osmolarity and body temperature (Notley et al., 2023), with disruptions in these variables likely to cause muscle fatigue (Schaeffer and Lindstedt, 2013). Because these homeostatic processes are not independent, they may come into conflict and require hierarchical ranking for prioritization under physiologically stressful conditions (Notley et al., 2023). It is therefore crucial to gain insight into multiple competing physiological processes (Fig. 2) to gain a better understanding of the trade-offs that underpin animal movement.

Insights from physiological measurements

Energetics

Ecologists have long recognised the value of metabolism (represented by the central cog in Fig. 2) as the 'fundamental biological rate' governing energy flows underlying ecosystem processes (Brown et al., 2004). Yet, measuring metabolic rate in the field is challenging. The doubly labelled water technique is the gold standard for estimating daily energy expenditure in the field, as it quantifies carbon dioxide production based on the dilution rate of isotopically labelled water between two time points (Speakman, 1997). There are, however, limitations to this technique. For example, multiple samples would be needed to break down individual components of the energy budget. The logistical challenges associated with animal recapture and the high cost of the technique have limited its application for large terrestrial mammals (Butler et al., 2004). Biologging heart rate in free-living animals offers a proxy for energy expenditure at higher temporal resolution. However, estimating metabolic rate from heart rates requires calibration against oxygen consumption in a laboratory setting (Green and Frappell, 2007), across a range of conditions likely to be experienced in the field, as the same heart rate can correspond to very different rates of oxygen consumption depending on body temperature and activity level (Butler et al., 2004). To overcome these limitations, accelerometry was proposed as a method to quantify the activity-specific metabolic rate of free-living animals. Following initial proof of concept (Wilson et al., 2006), the predictive relationship between dynamic body acceleration (DBA) and oxygen consumption was confirmed in numerous species (Halsey et al., 2009), leading to its rapid expansion in ecological applications (Brown et al., 2013). Estimates of daily energy expenditure were further improved when accelerometry was combined with measures of heart rate (Green et al., 2009), behavioural-time budgets (Jeanniard-du-Dot et al., 2017) and allometrically adjusted (Chakravarty et al., 2023), potentially reducing the need for laboratory calibration (Halsey et al., 2011). Further refinement of the technique requires appropriate placement and calibration of the device (Garde et al., 2022) and the incorporation of non-movement-based contributions to metabolic rate (Wilson et al., 2020), such as thermogenesis or pregnancy. Biologging of body temperature in large terrestrial mammals has the potential to address these gaps and provide additional insights, yet temperature is seldom integrated into accelerometry studies (<15% of studies in Brown et al., 2013).

Body temperature

Body temperature was one of the first physiological variables assessed through biologging (Bligh and Harthoorn, 1965) and holds tremendous promise for elucidating the internal physiological state of an animal that mechanistically drives its movement path. It is more than simply a measure of heat stress or heat generated by working muscles; body temperature is a regulated physiological variable and should not be dismissed as simply 'the output of an underlying physiological alteration' (Williams et al., 2021). Given its interactions with multiple physiological systems (Fig. 2) and its tendency to be given lower priority in the hierarchy of regulated physiological processes, fluctuations in body temperature can provide insight into the physiological wellbeing of free-living endotherms in terms of nutrition, pregnancy, hydration, and disease state (Hetem et al., 2016). For example, large terrestrial mammals display a lowered nychthemeral trough of body temperature rhythm, associated with reduced food availability, during periods of drought (Boyers et al., 2021) and low levels of green vegetation (Weyer et al., 2020), when body condition is poor and plasma leptin low (Botha et al., 2023). Indeed, the hypothermia of northern-temperate mammalian herbivores during winter may be more related to food restriction than low ambient temperatures (Turbill et al., 2011). Similar low troughs of body temperature are evident in summer during periods of high energy expenditure or hypophagia, such as those observed in male camels (*Camelus dromedarius*) during the rut (Grigg et al., 2009). Lowered troughs of body temperature may therefore allow quantification of nutritional wellbeing that drives large mammalian herbivores to seek more productive foraging patches (Fig. 3B) or large carnivorous mammals to seek successful hunting opportunities. Incorporating body temperature metrics into movement analyses may aid the interpretation of movement responses by quantifying nutritional wellbeing, thereby facilitating the assessment of the effectiveness of selected movement paths to buffer variability in external factors.

Body temperatures may also provide insights into reproductive status, which may in turn alter movement paths (Malagnino et al., 2021). During pregnancy, body temperatures are tightly regulated (Schmidt et al., 2020) and may progressively decline throughout gestation, termed gestational hypothermia, to maintain a thermal gradient for heat loss from the growing foetus (Laburn et al., 2000). Remote identification of pregnancy may allow for insights into reproductive success and abortions (e.g. through the Bruce effect, Trethowan et al., 2016), not easily observable in the field. Integrating temperature sensors into vaginal implant transmitters, used for the detection of birth sites to monitor neonatal survival (Dion et al., 2019), would also expand insights into maternal effects (Cheynel et al., 2021), since body temperature is more variable when gestation or lactation coincides with resource limitation during droughts (McFarland et al., 2024). Body temperatures may therefore infer effectiveness of selective movement paths, such as ruminant preference for foraging areas with higher protein content in late gestation, switching to areas with reduced predation risk immediately post-parturition (Blum et al., 2023), but increasing selection of greener patches (Heffelfinger et al., 2020) and access to water (Long et al., 2009) as energy and water costs of lactation increase.

Regulating a high and stable body temperature (homeothermy) not only requires extra energy when ambient temperatures are low, but also involves loss of body water through evaporative cooling (panting or sweating) to prevent an excessive increase in body temperature when ambient temperatures are high (Fig. 3A). However, when water is limited, endotherms prioritize conserving body water over regulating body temperature. When dehydrated, osmoreceptors in the hypothalamus switch off panting and sweating resulting in higher nychthemeral peaks of body temperature rhythm (McKinley et al., 2008), such as those observed in desert antelope (Hetem et al., 2010). If distant surface water is available, these high peak body temperatures may drive movement to water sources to replenish body water lost through evaporative cooling (Fig. 3C) at the cost of increased energy expenditure and reduced foraging time. Indeed, long movements to water may provide a strong selective pressure for efficient muscle fibres to reduce the thermoregulatory challenges of movement (Curtin et al., 2018). Seeking thermal refuge (e.g. shade) during the heat of the day would reduce radiant heat loads, reducing reliance on evaporative cooling, and possibly extending the time between trips to water (Fig. 3C), but may come at a cost of reduced foraging time (Hetem et al., 2012). The outcome of those trade-offs may differ depending on resource availability, predation pressure and individual reproductive or disease states. Sustained upregulation of body temperature rhythms is indicative of a febrile response (Hetem et al., 2008). The resultant sickness behaviours may alter an individual's motivation to forage (anorexia), move (lethargy) or engage in social activities, and may even alter the outcome of social interactions. For example, febrile vervet monkeys (*Chlorocebus pygerythrus*) experienced increased aggression from conspecifics and injury compared with their afebrile counterparts (McFarland et al., 2021), which may result in avoidance

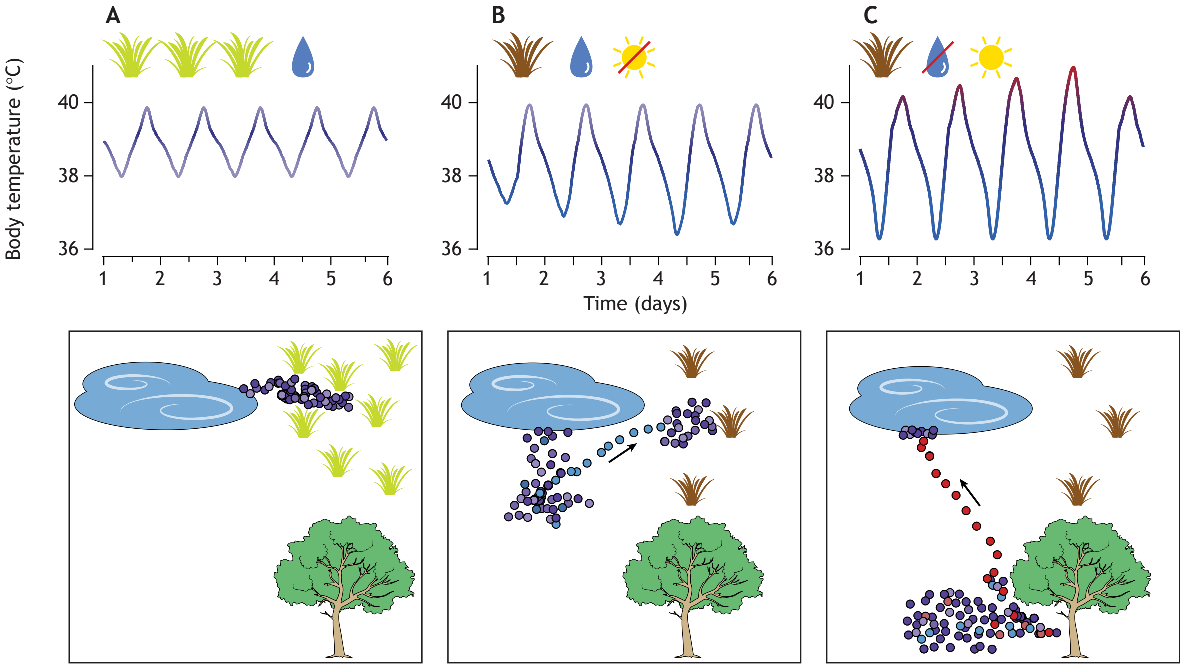

Fig. 3. Biologging body temperature of free-living endotherms may provide insight into the mechanistic drivers of animal movement paths. (A) When a large mammalian herbivore has access to sufficient food and water it will maintain a narrow rhythm of body temperature and move little in search of resources (shades of purple dots correspond to daily peaks and troughs of body temperature rhythm). (B) When forage quality/quantity is limited, but the herbivore is able to maintain body water balance either through access to water or low reliance on evaporative cooling, daily troughs of body temperature progressively decline (blue shades in body temperature plot) as energy stores are depleted and may ultimately drive the animal to search for higher quantity/quality forage (blue dots correspond to low body temperatures and increased searching movements represented by the arrow). (C) In hot and dry conditions, peak body temperatures increases (red shades in body temperature plot) as dehydration switches off evaporative cooling to conserve body water and may drive movement to known water sources (red dots correspond to high body temperatures and increased movements towards water).

of conspecifics. As such, biologging body temperature can provide insights into the internal physiological state underpinning the movements of large terrestrial mammals.

Conclusion

We have provided examples of how physiological processes underpin movement ecology at two spatiotemporal scales, from immediate physiological processes to the drivers and outcomes for longer-term mobility, such as travel to seek water. Both physiologists and ecologists have embraced biologging and the technological advances that have enhanced remote measurements of physiology and movement in free-living animals, yet the physiology–movement nexus remains understudied for large terrestrial mammals. The small (2%) increase in movement ecology studies integrating internal physiological state over the last decade likely stems from the increased use of accelerometry tags (Joo et al., 2022). While accelerometry can identify behavioural states and, through careful placement and calibration, correlate with activity-related metabolic rates, it is ultimately a metric of fine-scale movement. But the underlying physiological states that drive movement need not be indirectly inferred through micro-movements (Wilson et al., 2014) or increasingly sophisticated analyses (Getz and Saltz, 2008); they can be directly quantified through biologging physiological variables, such as body temperature. Rather than being a 'major barrier' to biologging physiological variables (as suggested by Williams et al., 2021), the internal placement of biologgers can be both ethical and feasible in the field, possibly even preferable to external devices (Forin-Wiart et al., 2019), paving the way for novel insights into the direct and indirect consequences of the extreme thermal stress anticipated from rising global temperatures.

Incorporating physiological insights could revolutionize conservation management through identification of causal mechanisms underlying observed movements. Biologging is an essential part of a conservationist toolbox (Wilson et al., 2015a), enabling innovative and interdisciplinary research to improve the management of endangered species (Cooke, 2008) and translocation success (Tarszisz et al., 2014). For example, biologging heart rates of scimitar-horned oryx (*Oryx dammah*) may improve reintroduction success by identifying duration, timing and location of stressors, thereby defining thresholds for management (Leimgruber et al., 2023). Movement ecology (Fraser et al., 2018) and physiology (Madliger et al., 2022) data are increasingly integrated into species management and recovery plans, with combined insights likely to be synergistic. With unprecedented changes in climate predicted in the near future, we need baseline information on how physiology integrates with movement ecology in both migratory (Lennox et al., 2016) and non-migratory species to inform conservation planning. For example, identification of stopover sites that act as physiological refuges along the migratory routes of mule deer (*Odocoileus hemionus*) allowed key areas to be prioritized for wildlife corridors (Jachowski et al., 2018). We advocate for collaboration between physiologists and ecologists, to break down historic disciplinary silos and move beyond simply inferring causality through intuitive correlations. Combining biologging technologies to confirm causality through underlying physiological processes will enhance our understanding of the mechanistic drivers of animal movement in the face of climate change and anthropogenic disturbance.

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Competing interests
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ECR Spotlight
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Special Issue
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