# Integrating physiology into movement ecology of large terrestrial mammals

JOURNAL CLUB 2025

Luca Bortuzzo

# Physiology underpins movement ecology

- 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 are composed of a sequence of movement phases, each associated with fulfilling a set of goals**.

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-Brocketal.,1988).

# Physiology underpins movement ecology

- The **internal physiological state**(sensu Jachowski and Singh, 2015) is influenced by abiotic and biotic external factors and **self-regulated through homeostasis.**

- Achieving homeostasis requires the integration of numerous physiological processes, such as thermoregulation, osmoregulation, digestion and reproduction.

- **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).

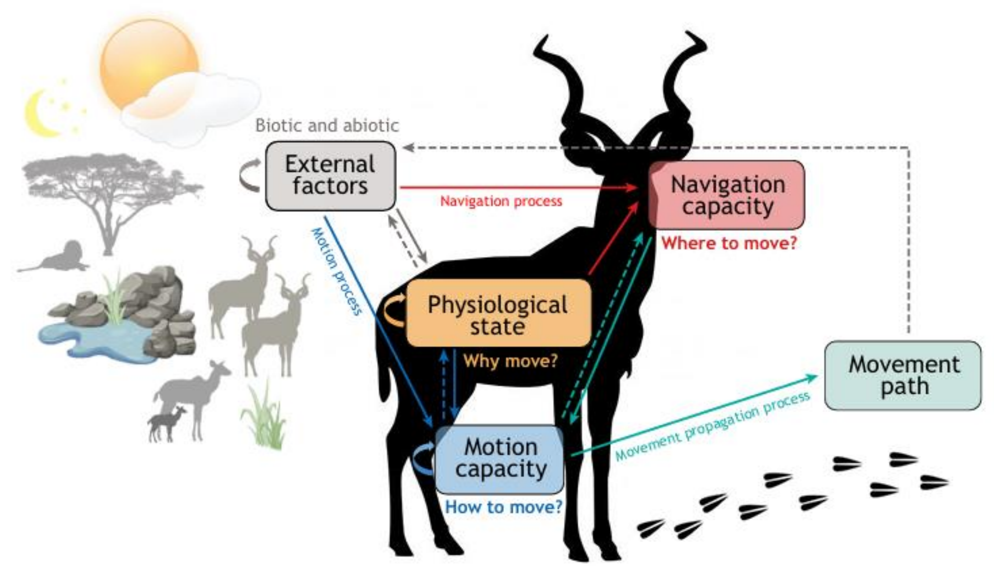



**Fig. 1. Pictoral representation of the movement ecology framework.** Both biotic (conspecifics, predators and food) and abiotic (weather, geographical barriers and celestial cues) external factors influence an animal's movement path, through direct effects on its motion capacity (How to move? e.g. 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).

# Physiology underpins movement ecology

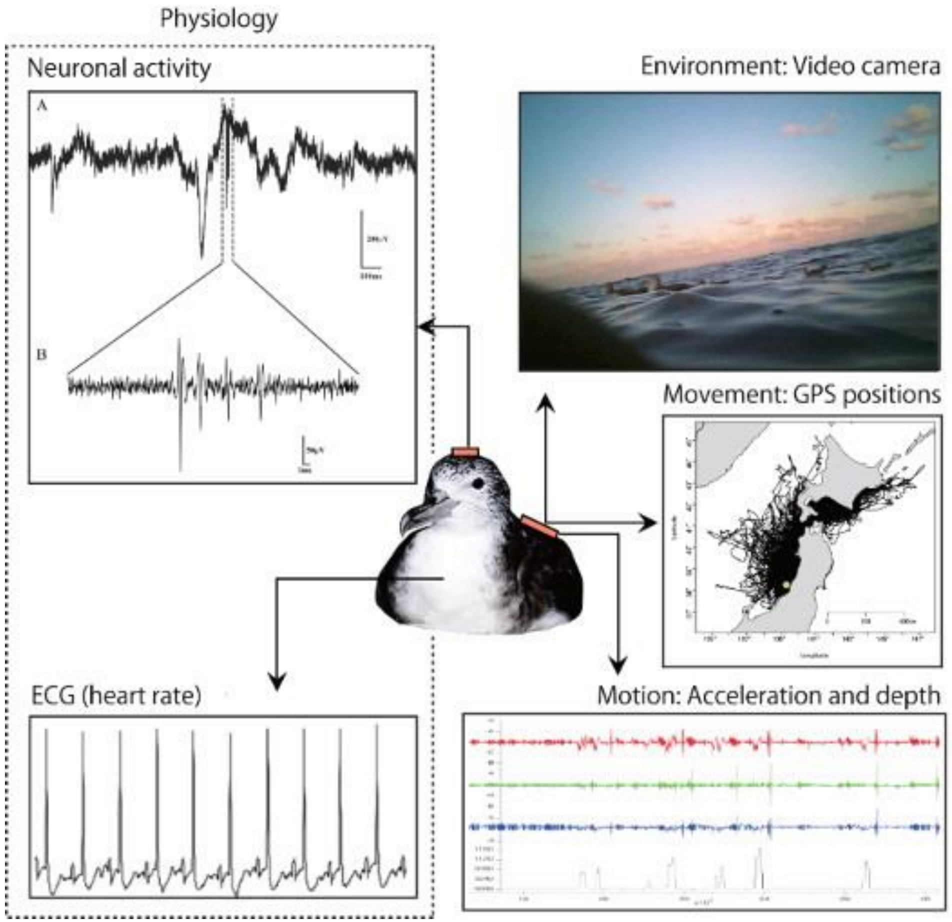
- Movement paths are influenced by external factors and depend on an individual's **navigation capacity** (Where to move?), **motion capacity** (How to move?) and are ultimately driven by **internal physiological state** (Why move?).
- Despite physiology underlying most aspects of this movement ecology framework, the physiology movement nexus remains understudied in large terrestrial mammals (>5 kg).

↓

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).

# The golden era of biologging

- Since the 1960s, technologies like radio telemetry and heart rate monitoring have evolved, allowing researchers to measure a wider range of variables and study more species.
- The article uses 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.
- **Biologging presents the opportunity to 'observe the unobservable'** (Williams et al., 2020) and currently provides the most appropriate toolbox for continually and remotely quantifying the physiology of free-living animals.



# Navigation and motion capacity

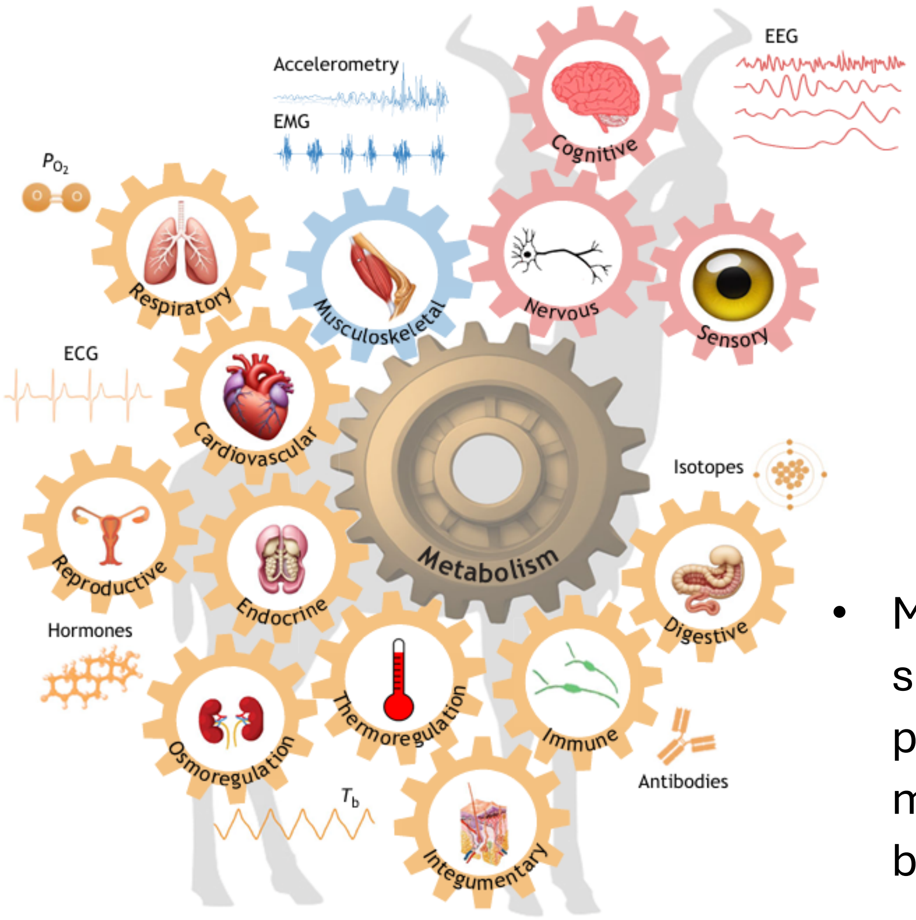



**Fig. 2. Interconnected physiological processes drive the different components of the movement ecology framework.** Organ systems and physiological processes continuously interact to form an integrated network, like cogs in a machine. Physiological processes provide insights into the causative mechanisms 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/).

- **Animal navigation involves using sensory cues** to orient themselves in both space and time, which can be based on simple cues (like following a gradient) or more complex cognitive processes such as spatial memory. These can be inherited or learned.

- Movement is controlled by the brain's motor systems, which integrate sensory information and initiate motor responses through complex neural processes. While conscious choice is often assumed to drive movement, much of it is unconscious, driven by structures like the basal ganglia and brainstem.
- **Feedback mechanisms involving proprioception and neuromodulators fine-tune movements.**

# Navigation and motion capacity

- 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 so, its **physiological state can affect navigation**.

One of the best examples of an animal's physiological state modulating the approach or escape response 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(Filosaetal.,2016).

- Understanding movement requires field studies that integrate neurophysiological data with real-world contexts.

# Movement tracks

- **Movement paths can be broken into phases**, such as escaping predators or searching for food, with each driven by underlying physiological processes.

- These phases consist of **canonical activity modes** (CAMs), like walking or running, and can be analyzed in relation to changes in landscapes or climates. **Higher-resolution GPS fixes now allow for more precise tracking of movements**, including repetitive body movements, by combining data from biologging sensors like accelerometers. This integration provides deeper insights into movement drivers and energetic costs.

- **Animals aim to move energetically optimally**, balancing speed and energy expenditure, **but this varies with context**.

For example, animals move faster when escaping predators or chasing prey, potentially increasing injury risk, while they slow down when foraging to detect food more easily. Moreover, the cost of transport varies with terrain and conditions, influencing movement paths.

Lewis G. Halsey, Terrestrial movement energetics: current knowledge and its application to the optimising animal, J Exp Biol, 2016, Fig. 4.

# Movement tracks

- So, animals often prioritize other factors over energy efficiency, influenced by their physiological state, navigational capacity, and environmental constraints.
- Their "**individual energy landscape**" depends on factors like thermoregulation, muscle morphology, and nutrient levels. These physiological processes, such as muscle fatigue or hormonal changes, are interdependent and must be prioritized under stressful conditions, highlighting the complex trade-offs that influence animal movement.

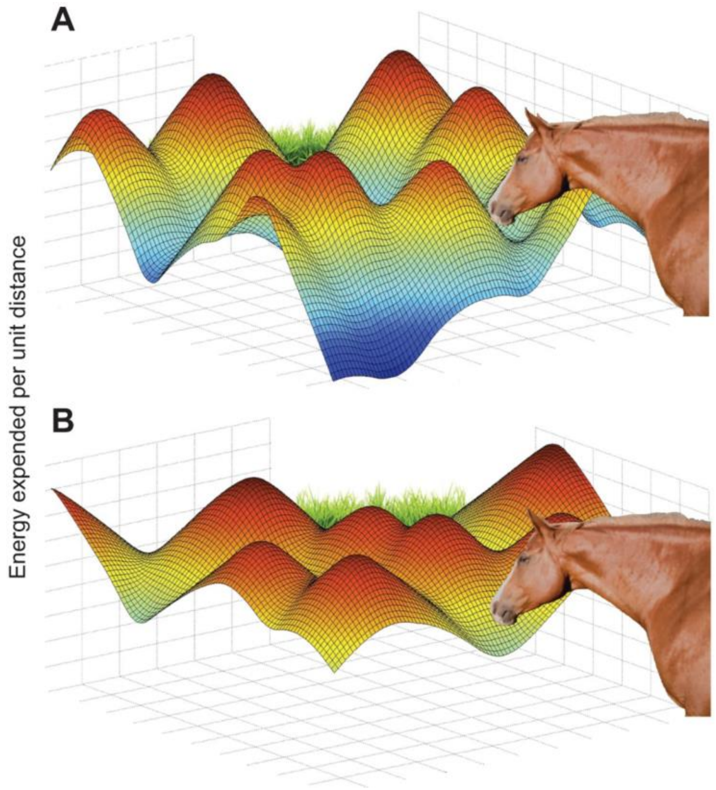
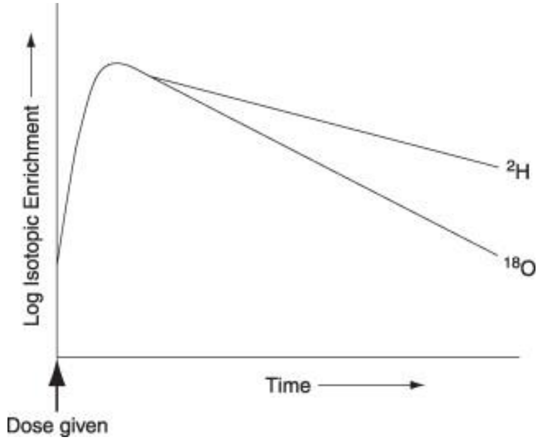



**Figure Caption:**
The concept of the individual energy landscape. This landscape represents variation in space in the energy cost to move a unit distance; reds indicate high costs and blues represent low costs. The minimum energy costs that can be incurred by an animal to move across a geographical landscape by a given route are defined by physical factors such as the substrate and slope of the terrain. However, the energy costs actually incurred by that animal can differ depending upon the decisions it makes predominantly about the speeds at which to traverse the landscape. An animal may wish to minimise its costs to move in order to maximise energy available for reproduction or to minimise the effects of fatigue. For example, if a horse intends to move to a food patch but is not under a time constraint, it may opt to walk at an average walking speed, which is likely to be energetically economical for the given terrain (Hoyt and Taylor, 1981) (A). It may also choose an indirect route across its individual landscape that is nonetheless energetically more economic than the most direct route such that the energy spent to reach the food patch is further reduced. (B) In contrast, if, for example, the horse opts to trot at a high speed (less economical for horses) in order to reach the food patch quickly, then all routes to cross the landscape, at least on average, become more energetically expensive. The energy expended to get to the food might be further increased if a direct route is taken to further reduce the time taken (for example, if the direct route included inclined terrain). Because of possible interactions between, for example, movement speed, slope angle and the substrate underfoot, we would typically expect the landscape to vary in response to movement speed in a more nuanced fashion than simply raising or lowering a consistent amount across the surface. For instance, in the present example, although the majority of the landscape is raised in B, indicating higher energy costs to cross the landscape at a high trotting speed, there are nonetheless a number of peaks in A where that point on the landscape cannot be traversed more economically by moving at slower speeds. This could be the case, for instance, when moving into high winds or travelling downhill.

# Insights from physiological measurements: Energetics

- Ecologists have long recognized metabolism as a key factor driving energy flows in ecosystems, but measuring metabolic rate in the field remains difficult.
- The **doubly labelled water technique** is considered the gold standard for estimating daily energy expenditure by measuring carbon dioxide production, though it **requires multiple samples** and the logistical challenges associated with **animal recapture and the high cost of the technique** have **limited its application for large terrestrial mammals** (Butleret al., 2004).




$^2$H label from DLW mixes with the body water and is eliminated as water in the urine. Similarly, $^{18}$O label from DLW is eliminated as water, but it is also utilized in bicarbonate synthesis and hence is also eliminated in the breath as $CO_2$. The difference in turnover rates of isotopic $^2$H-H and $^{18}$O-labeled water is proportional to $CO_2$ production. Energy expenditure, oxygen consumption, water intake, and metabolic water production can be calculated using standard indirect calorimetry equations with an estimated RER

# Insights from physiological measurements: Energetics

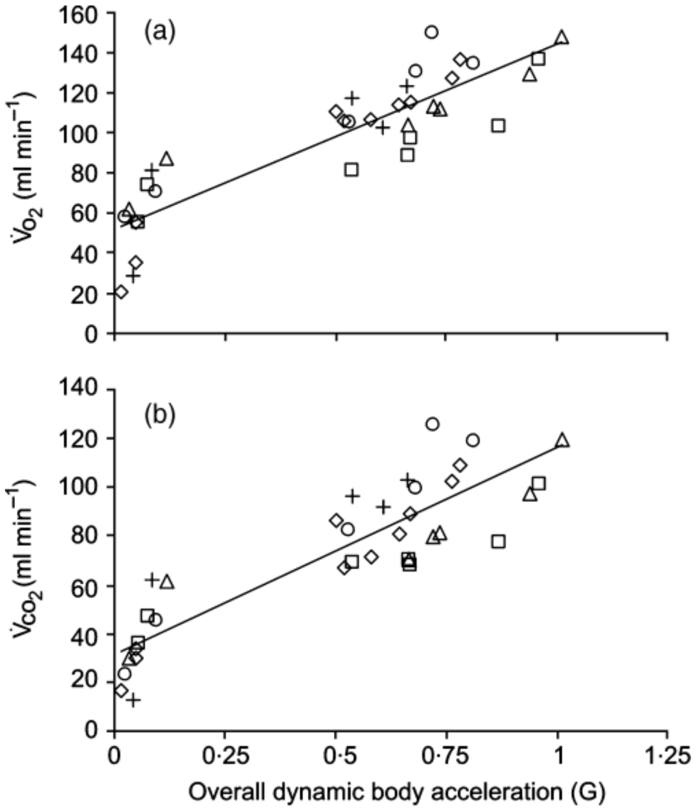
- **Biologging heart rate offers a proxy for energy expenditure**, but it requires calibration with oxygen consumption under various conditions, making it challenging to apply directly in the field.

- To overcome this, **accelerometry** was introduced as a method to quantify activity-specific metabolic rates, with **dynamic body acceleration** (DBA) shown to correlate with oxygen consumption in various species.

- 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).

- However, refining this technique requires **proper device placement and calibration**, and the **integration of non-movement-related metabolic contributions**, such as thermogenesis or pregnancy, remains underexplored.

**Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant (Wilson et al., 2006)**



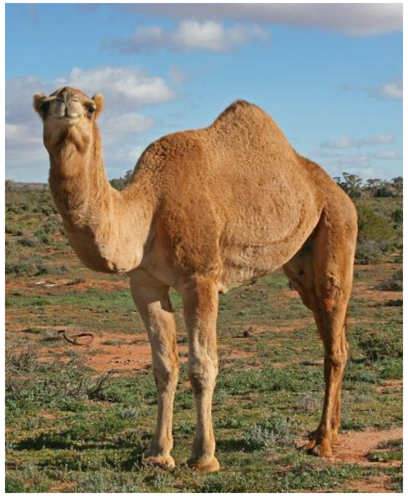

Relationship between overall dynamic body acceleration and (a) oxygen consumption and (b) carbon dioxide production for five great cormorants resting and walking at different speeds on a treadmill.

# Insights from physiological measurements: Body temperature

- Body temperature 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).

- 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 mammals may experience reduced body temperature during droughts due to food scarcity or during periods of high energy expenditure like in male camels (*Camelus dromedarius*) during the rut.



# Insights from physiological measurements: Body temperature

- Monitoring body temperature can help **assess nutritional wellbeing and movement paths**, as animals may seek areas with better food or water resources depending on their physiological needs.

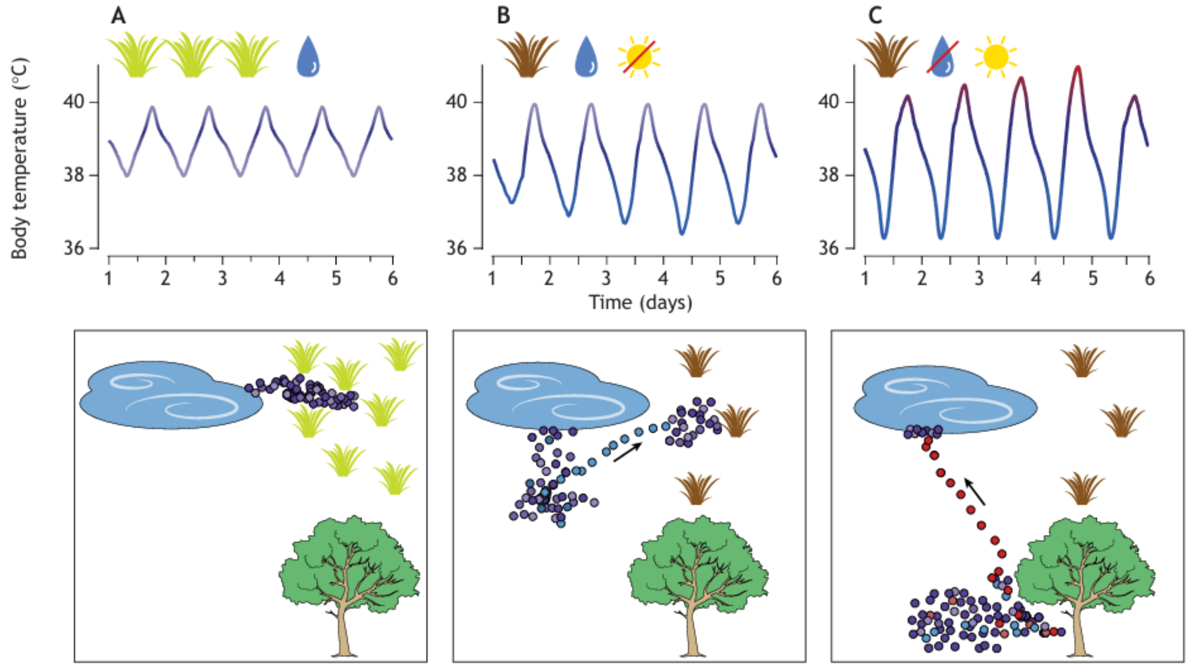



**Fig. 3. Biologging body temperature of free-living endotherms may provide insight into the mechanistic drivers of animal movement paths.** (A) When a large mammalian herbivore has access to sufficient food and water it will maintain a narrow rhythm of body temperature and move little in search of resources (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).

# Insights from physiological measurements: Body temperature

- Temperature also provides insights into **reproductive status**, such as during pregnancy when body temperature may decrease (gestational hypothermia) to maintain a thermal gradient for the fetus or to identify abortions.
- Body temperature data also help identify **sickness behaviours**, as fever can alter an animal's foraging, social behaviour, and interactions with others.

For example, febrile vervet monkeys (*Chlorocebus pygerythrus*) experienced increased aggression from conspecifics and injury compared with their afebrile counterparts (McFarlandetal.,2021), which may result in avoidance of conspecifics.

# Conclusions

- It is important to understand the connection between physiological processes and animal movement, focusing on how internal states influence mobility at various scales, from immediate physiological responses to longer-term behaviours like seeking water.
- The use of internal biologgers, rather than external devices, can provide valuable insights and be ethically feasible, offering potential breakthroughs in understanding the effects of thermal stress from climate change.
- Integrating physiological data with movement ecology could revolutionize conservation management by revealing causal mechanisms behind observed movements. Biologging can aid in species management and recovery efforts, such as improving reintroduction success and identifying critical habitats.

# Reference


- Hetem, Robyn & Haylock, Kiara & Boyers, Melinda & Parrini, Francesca & Owen-Smith, Norman & Beytell, Piet & Strauss, W. Maartin. (2025). Integrating physiology into movement ecology of large terrestrial mammals. The Journal of experimental biology. 228. 10.1242/jeb.248112.