Making movement ecology into a predictive science

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Abstract

1. Movement allows animals to change their environmental surroundings and remain in suitable conditions. As environments shift, e.g. through predictable seasonal progression, individuals can adapt their movement strategies accordingly. However,

novel climate change introduces unpredictable, atypical conditions (e.g. droughts, floods), which may drive distinct movement responses. Predicting how future conditions will affect these movement decisions requires a better understanding of how such environmental variability shapes animal movements.

2. Gaining predictive power in movement ecology requires establishing a baseline understanding of movements during typical conditions and responses to within-the-norm shifts in conditions. We propose that animals respond along different axes to changes in conditions, adjusting *when*, *where*, and *how* they move as different components of their environment change. Integrating responses across these three movement axes provides a powerful framework for identifying when change occurs (e.g. animals moving outside of their typical movement 'envelope') and for inferring the type of environmental change based on which axes are affected.
3. We propose a framework to detect ecologically meaningful environmental shifts, identify the type of change, and use animals as sentinels of novel environmental conditions. By comparing movement responses under predictable and unpredictable conditions, this framework enables the identification of key environmental elements or habitat features that are critical for survival. Such insight improves our ability to predict how species will be affected by—and respond to—future climate change.
4. Coupling large-scale, real-time animal tracking with our predictive movement ecology framework unlocks the potential to use animals as sentinels for detecting rapid and unpredictable environmental changes. Advancing movement ecology into a predictive science is essential for addressing questions about the impacts of novel environmental conditions on animals.

Keywords: animal movement, animal tracking, climate change, environmental variability, habitat shifts, long-term studies, movement ecology

1. Introduction

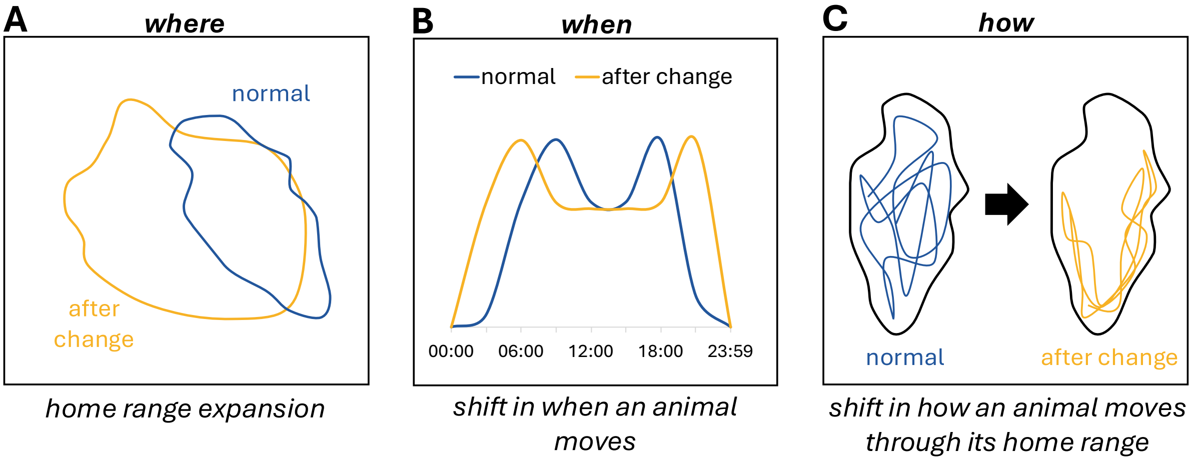
Movement, driven by factors such as temperature, resource availability, predation risk, reproduction, and interactions with others, is a primary strategy for adapting to dynamic landscapes and environmental fluctuations (1,2). For example, movement allows animals to remain within their thermal tolerance range (3) and to find food, water, and other resources (1) that are essential for survival. Nearly all mobile species have evolved strategies to cope with such variabilities in their environment, reflecting trade-offs such as the balance between the time spent extracting resources versus the time spent searching for new resources to maximise overall energy budgets (e.g., optimal foraging theory (4–6)). Consequently, movement provides a window into the environment that animals experience.

Environmental factors, such as temperature and resource availabilities, shape animal movement and distributions at multiple spatial and temporal scales (1,7). Daily, these factors influence how animals navigate and use (micro-) habitats, with recurring needs for food and shelter driving the establishment of limited movement ranges—such as a territory or home range—within which they must meet survival requirements (8,9). Across longer time periods, predictable, seasonal shifts can often lead to changes in movement behaviours. Such changes might include a temporary expansion or contraction of home ranges (e.g., (10)) or a move to an entire new range (such as migratory (11,12) and nomadic (13,14) movements). These are typically expressed within the set of responses that species are adapted to make. Increasingly, however, animals are confronted with novel and (from their perspective) unpredictable changes, such as sudden or extreme alterations in weather or resource distributions. A key question is how animals might respond to such events. Understanding how animals adjust their movements and space use in response to expected daily and seasonal variation is critical for predicting their responses to novel conditions (15,16). This knowledge will not only help us predict their future trajectories and space use (17), but can also allow us to infer environmental conditions from observed changes in movements and detect when novel conditions arise.

Our aim is to present a framework for capturing animal behavioural responses (movement and habitat selection) to different types of environmental shifts as a means of predicting future effects of environmental changes. We begin by reviewing commonly used methods for assessing and interpreting animal movements. We then outline and organise existing work on how animals alter their space use and move in response to (generally predictable) fluctuations in environmental conditions. While our review focuses on the use of biologging, similar principles could be applied to studies that use camera trap data, transect surveys, and other methods for studying animal movements. Finally, we propose that by understanding how fluctuations in environmental conditions drive variations in movement and space use, we can infer the ecological conditions that animals—and their populations—are experiencing. In doing so, our framework provides a complimentary movement guide to recent perspectives on anthropogenic effects on animal movements (18) and the use of "animal tracking as an eye on life and planet" (19).

2. Detecting shifts in animal movements

To accurately infer behavioural responses to environmental conditions from movement data, it is important to consider how movement can change along multiple axes (*when*, *where* and *how;* i.e., habitat selection and use, **Fig. 1**). These responses can involve both larger-scale and local adjustments and each axis can change independently from another. For example, as the environment changes, an animal's overall space use may be unaffected (*where* the animal is), while a specific metric (e.g., step length) changes (*how* the animal moves). Similarly, an animal's step length (*how*) may remain consistent, yet it moves out of its previous home range (*where*), resulting in altered space use but consistent movement metrics. Alternatively, an animal could remain consistent in *where* and *how* it moves, but change *when* it moves (e.g., a shift from late to early morning). These changes may also occur at various time scales, including changes in daily movement patterns, seasonal shifts, and responses to unpredictable events outside of what would be expected under baseline conditions, such as extreme weather events (**Fig. 2**). Given that such changes can co-occur in various combinations, studies should ideally attempt to capture all three aspects across longer temporal scales (but see *Section 8*) to fully understand how animals are responding to environmental changes.



home range expansion

shift in when an animal moves

shift in how an animal moves through its home range

Figure 1. Animal movement split across three axes: where, when and how to move. *In response to environmental shifts, animals may change A) where they move (e.g. home range expansions or contractions), B) when to move (e.g. changes in when animals are active, such as avoiding strenuous movements during the hottest times of the day), and C) how animals move through their territory or home range (e.g. changes in speed or directedness of their movements).*

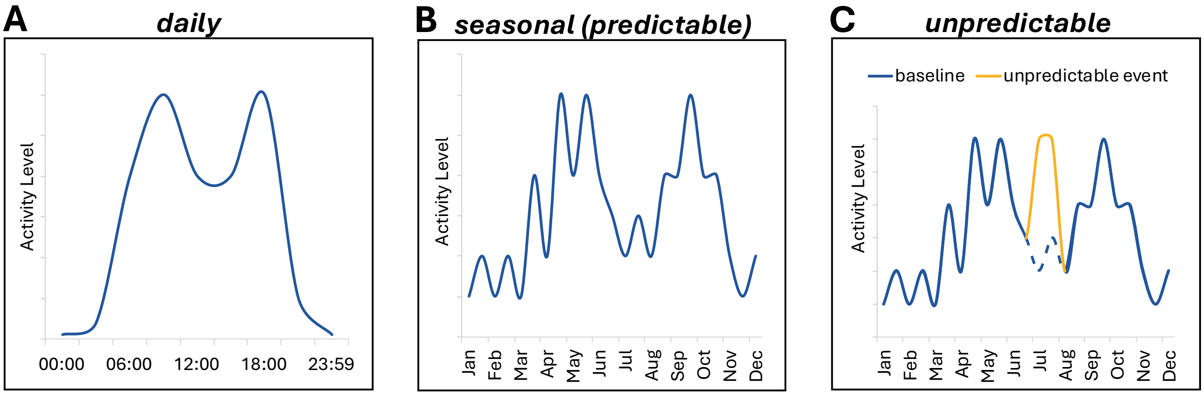


Figure 2. Changes in movement across multiple time scales. *Such changes in movement can occur A) within a day (e.g. animals that modulate their movements daily based on temperature or prey activity patterns), B) across seasons (e.g. seasonal migrants escaping unsuitable conditions), and C) in response to unexpected, unpredictable events (e.g. droughts or heatwaves that cause a sudden change in movement away from baseline expectations).*

A vast majority of animal movement studies use GPS to estimate movement patterns. Larger-scale changes in *where* and *when* animals move (e.g., range shifts between seasons, migrations) can accurately be captured using relatively coarse GPS-sampling resolutions—a few location fixes/day (20). For example, the departure dates of ibex (*Capra ibex*) migrations in spring and fall were precisely determined using as little as four GPS fixes per day, enabling the assessment of likely drivers of migration (21). The tracking of larger changes in space use and movement timing is thus readily achieved with current technologies and collaborative efforts.

With the improvement of GPS technology (both in terms of temporal and spatial resolution), we can now increasingly also obtain fine-scale data on the (micro-) habitat selection and utilisation of many species that enable them to remain in suitable conditions. For example, Cape rockjumpers (*Chaetops frenatus*) increase their use of shaded areas as air temperature increases (22). Similarly, desert lizards (*Messalina bahaldini*) prefer shade under warmer temperatures in summer (23). GPS tags with a resolution of 1,260 fixes over a 7-hour daily window (and a 4-m positional accuracy) allowed the habitat selection of grazing cattle to be determined (24). Cattle preferred open grasslands over shrubs and forests, and patch selection differed across seasons, highlighting preferential grazing under trees in summer and in a vlei (shallow wetland) in winter. The animals also more frequently used patches with higher plant species diversity and closer to water (24). Advancements in GPS technologies will increasingly facilitate the detection of fine-scale shifts in habitat use in response to environmental shifts that may not be evident from coarser-scale observations.

Animals are likely to display changes in both *where* and *when* they move as environmental conditions change. For instance, vulturine guineafowl (*Acryllium vulturinum*) move to shaded habitats when temperatures increase (detected using 5-minute GPS displacement probability windows (25)), while, at the broader scale, expanding their home range when resource availability declines (detected using 2-month windows for home ranges) (10). This highlights the importance of combining high-resolution tracking (many points per day) with long-term deployments (capturing changes in environmental conditions) to detect large and smaller-scale movement shifts.

GPS data gives us the ability to obtain a number of metrics that can be used to address the *where*, *when*, and *how* animals move (**Fig. 1**; **Fig. 3**) and how these aspects relate to the resource landscape. To assess changes in *where* animals go, studies often assess their territory or home range. For example, GPS movement data can be used to determine home ranges by fitting movement models to extract maximum likelihood Gaussian home ranges (auto-correlated kernel density estimations, **Fig. 3A**). These can then be used to assess where animals spend significant portions of their time, visualising their home range or territory (10). Movement data can also be assessed for frequent returns to specific sites (**Fig. 3B**), which may reflect site attractiveness (e.g. high resources). Similarly, residency time, the duration of time an animal spends at a particular site (26) (**Fig. 3C**), can reflect the site's attractiveness or value (27) and indicate *when* an animal moves. Measures of temporal autocorrelation (mantel correlograms; **Fig. 3D**) can further aid in distinguishing temporal movement patterns, such as periodic movements as animals move between waterholes (28). Lastly, to assess *how* animals move through their environment, GPS data are most commonly used to determine an animal's step length (**Fig. 3E**), i.e., the Euclidean distance between two consecutive points, which may then be used to estimate the speed at which an has animal travelled (29). Reduced movement speeds (shorter step lengths) may indicate foraging (30), whereas fast movement (longer step lengths) may indicate individuals are moving to or through areas to reach others. Disproportionately fast movements and, correspondingly, long step lengths can also be indicative of animals making large displacements, such as during natal dispersal (28,31), migration (32–34), or nomadic movements (35). Assessments of turning angles (changes in direction between consecutive steps; (29)) or path straightness (assessments of straightness by comparing net displacement and path length; (36)) (**Fig. 3F**) can complement step length measures and further aid interpretations of GPS data. Frequent turning is likely to indicate search behaviours (37), whereas straighter trajectories signal goal-directed movements, often recorded during dispersal (31) or nomadic movements (35), or even during commutes to foraging areas (38). These movement metrics enables us to obtain detailed insights into an animal's behaviour at a given time, which can then be compared across time to obtain an understanding of the links between the conditions that the animals experience and the movements they express.

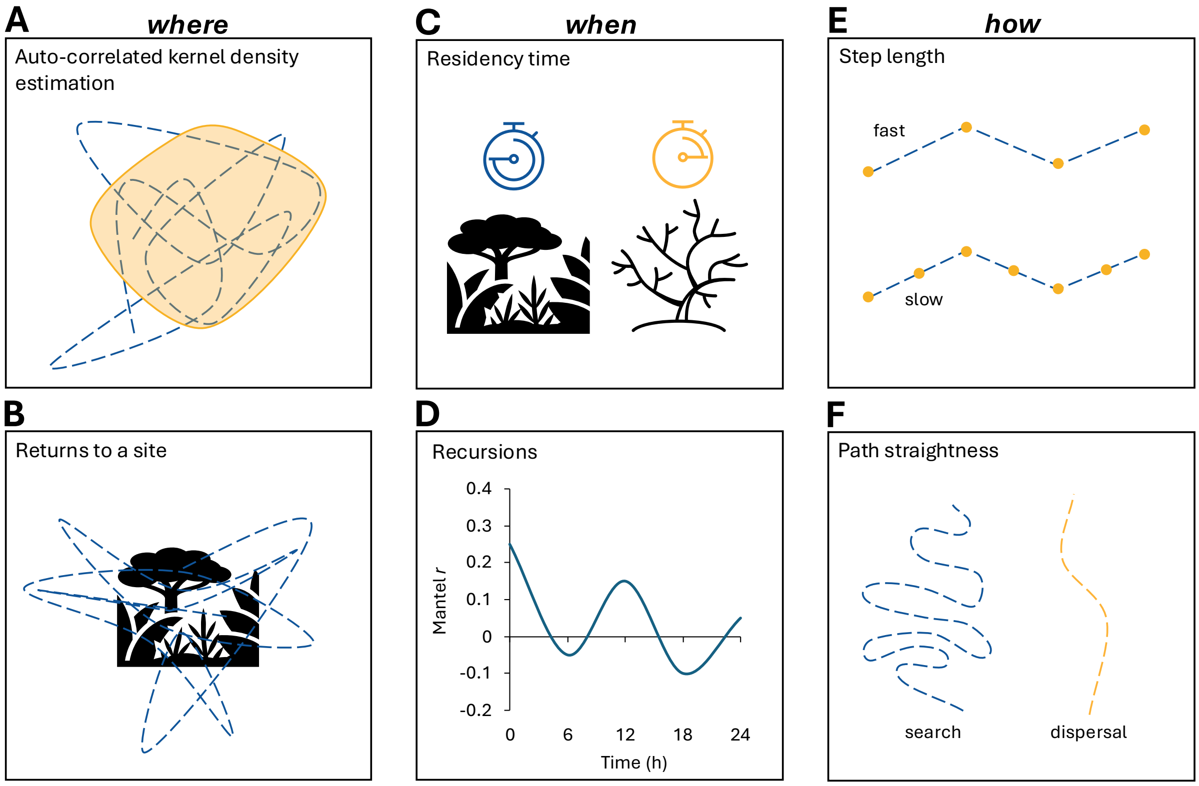


Figure 3. Examples of commonly used movement metrics split across our three movement axes—when, where and how to move. *A) GPS movement data can be used to fit movement models to extract maximum likelihood Gaussian home ranges (auto-correlated kernel density estimation). Such home ranges can then be used to determine the area an animal spends n% of its time in. B) The number of returns to a site is often used as an indicator for identifying memory-based navigation and movement and can reflect site attractiveness. C) Residency time, the time spent at a given site, can reflect its value or quality (e.g., high forage availability) and indicate when animals move between sites. D) Mantel correlograms can provide insights into temporal movement variability, allowing for the distinction between, for example, periodic (e.g., rotation between water holes) and directional (e.g., dispersal) movements. E) The distance between two consecutive GPS fixes, i.e., step length, can be used to determine the speed at which an animal travelled, with shorter steps indicating slower movement speeds. F) Path straightness or turning angle assessments can be used to distinguish between frequent turns (e.g., search behaviour) and more goal-directed movements (e.g., dispersal).*

3. Space use (where to move) in relation to environmental conditions

The recurring need for food and shelter, an animal's thermal tolerance ranges, and resource distributions across the landscape often limit daily animal movements to restricted areas. High ambient temperatures may push animals to favour shaded, cooler areas, as expressed by moose (*Alces alces*) that remain close to forests and bogs on days with elevated temperatures (39). Similarly, within a day, high temperatures drive savanna elephants (*Loxodonta africana*) to seek shade and water sources for bathing (40). Rocky Mountain elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) daily habitat use is driven by thermoregulation—such as seeking cover during midday—as well as resource availability, as evidenced by visitation of specific meadows with good-quality forage (41). Daily variation in abiotic conditions and resource dynamics can thus strongly influence where animals move.

Seasonally, changes in the distribution and availability of resources can further affect an animal's feeding site selection and habitat use within their home ranges (42,43). When an animal's usual home range is insufficient to guarantee access to adequate resources, home range expansions (10,44) or shifts may occur (45). Optimal diet theory (4) can predict such home range shifts: when resources are scarce or unpredictably distributed, foragers may expand their movement range to find better resources. At the extreme, many species have adapted to make seasonal migrations to escape unsuitable conditions and/or track food resources. This is seen in many avian species (46) as well as ungulates that "surf the green wave" by timing their seasonal migrations with plant phenology (47–49). During these large movements, individuals may also select different habitat features, such as roads (50) or other linear features (51), to increase the energetic efficiency of movement. In contrast to migration, animals living in more unpredictable seasonal environments may make nomadic movements (52), moving through their environment and searching for suitable conditions or resources. This is frequently seen in ungulates from arid and semi-arid environments, who continuously follow the availability of food (13,53) or water (13). Similarly, many avian species exhibit nomadic movements, such as raptors that follow prey availability (54) or waterbirds in desert environments that make nomadic flights between resource patches (14,55). Yet, such environmental fluctuations are still within the ‘expected’ realm of unpredictability, and animals that live in such conditions have adapted accordingly (e.g., nomadism). Such seasonal variability in environmental factors and resources can be a major driving factor in where animals go.

Truly unpredictable shifts, such as extreme weather events—e.g. droughts, floods, and storms—can further alter animal movements. For example, Hurricane Irma displaced deer (*Odocoileus virginianus seminolus*) from their usual home ranges, pushing them to make longer movements (56). Events such as fires may lead some species to avoid affected areas, while others move towards them to exploit the new vegetation (57) or catch easy prey fleeing from the fire (58,59). Similarly, long-term, out-of-the-norm environmental alterations caused by climate change continue to reshape animal movements by altering habitat suitability and resource distributions. Unprecedented, long-lasting droughts can change animals’ space use for an extended period of time (10). Permanent environmental shifts may push animals into new areas, as seen in polar bears (*Ursus maritimus*) increasingly moving landward (60) or blue sheep (*Pseudois nayaur*) moving to lower altitudes in search for adequate forage (61). Importantly, differences in movement responses to new extremes may highlight vulnerable animal populations. For example, during a particularly harsh winter in the Gobi Desert in 2009, Asiatic wild asses (*Equus hemionus*) moved out of their usual range to avoid harsh conditions while many Przewalski's horses (*Equus ferus przewalskii*) remained in their known home ranges and did not survive (62). In line with this, more sedentary ungulate species are predicted to be especially affected by increasingly frequent and intense droughts (63). This highlights the importance of movement to cope with and survive extreme events, which are bound to become more frequent as climate change continues to affect our environment (64).

Together, these examples illustrate that both predictable and unexpected environmental shifts can drive animal space use (**Table 1**). This underscores the importance of movement as a flexible response to dynamic conditions.

4. Movement timing (when to move) in response to environmental change

The second movement axis (*when* to move) is also driven by daily and seasonal cycles and is often connected to decisions about where to go. Daily fluctuations in meteorological factors, such as temperature or rainfall, can drastically alter movement timing through direct physiological effects. For example, African wild dogs (*Lycaon pictus*) shift the timing of their hunts on days with higher maximum temperatures, reducing daytime activity (65); Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) temporarily stop moving during heavy rains (8). The ability for individuals to express changes in movement (e.g. when having to make a large displacement) over the course of the day provides insights into how the environment shapes when animals can move (66). Beyond abiotic drivers, resource availability itself can fluctuate over the course of a single day. For predators, prey detectability may follow strong diel cycles: when prey remain hidden in burrows or refuges, resource availability is effectively reduced, whereas periods of surface activity or social aggregation can produce temporary peaks in prey availability. While tigers (*Panthera tigris*) are active throughout the day, activity peaks tend to overlap with those of their primary prey species (67). Similarly, herbivores may track daily cycles of plant accessibility, such as when leaves rehydrate overnight and become more palatable, or when nectar is produced at particular times of day. Nectarivores even risk foraging at low temperatures in the early mornings, as obtaining energy-rich nectar likely outweighs associated thermoregulatory costs (68). These short-term cycles highlight how daily variation in both abiotic conditions and resource dynamics influences *when* animals move.

Seasonal changes in resources can dictate when animals should alter habitat use within their home ranges or rotate between foraging sites. For example, the movements of ungulates that "surf the green wave" are not only driven by *where* plants become available, but also by plant phenology, precisely timing their migrations with peaks in green-up (47–49). Seasonal changes in resource (prey) availability may also lead many predators to migrate as they continue to track their prey (69–71). The marginal value theorem (72) refines the predictions posed by optimal diet theory by considering *when* animals should move between food patches based on resource scarcity. Importantly, it is useful to distinguish between two forms of scarcity: patch availability (how many patches are in an animal's home range) and patch quality (the resource abundance within individual patches). When patch availability declines, suitable foraging sites become sparse, leading animals to spend more time traveling between them and, correspondingly, remain longer in each patch. By contrast, when patch quality declines, patch residence increases as animals attempt to maximize intake even in low-quality conditions, but travel time is unaffected. These distinct predictions on how animals allocate their foraging effort between searching (detectable as faster and larger movements) and feeding (typically defined as slower more tortuous movements) provide a valuable way to infer, from movement data, whether resource declines are driven primarily by reduced availability or by lower quality. Similarly, the timing of nomadic movements is frequently informed by environmental factors. Many waterbirds in arid environments often make large movements towards areas recently affected by sudden heavy rains or flooding, with some showing timing so precise that they can arrive in as little as an hour after rainfall (14,55). Thus, extreme rains and consequent flooding largely drive not only *where* these birds go but also *when* these animals move.

Though less well-studied to date, extreme climate or weather events that are outside of 'normal' unpredictable changes can further alter animal movements. An extreme heatwave in 2021 shifted bison (*Bison bison athabascae*) movements away from usual activity windows around midday to early mornings (73). Importantly, some animals may not be able to escape bad conditions in time, which can lead to drastic population declines (74), highlighting the importance of precise movement timing for coping with unsuitable conditions.

Together, these examples highlight how both predictable and unpredictable environmental changes, from temperature or precipitation to resource availability, can drive the timing of animal movements (**Table 1**), which can, in turn, give insights into when environmental conditions are changing.

5. Movement characteristics (how to move) in response to environmental change

Environmental fluctuations can also alter *how* animals move owing to effects on their physiology and the resource landscape. Daily fluctuations in environmental factors and resource availability can influence how animals move. For example, animals can express faster, more directed movements when moving towards time-limited resources (75), and adopt slower movements during the hottest part of the day to avoid overheating (65). Predators hunting mobile prey may also switch how they move based on prey availability (76). When prey are hidden or inactive, predators may remain more inactive themselves, while switching to faster, more directed movements when prey is accessible. Fine-scale adjustments in movement behaviour across the day capture changing priorities of individuals and these capture the dynamic environmental conditions that individuals experience.

Seasonal cycles can be a major driver of movement characteristics. In equatorial climates, shifts between dry and wet seasons alter both movement speed and extent, with animals typically moving faster and over larger areas during cooler wet seasons, and moving more slowly and in restricted ranges during hotter dry seasons (89). Similar seasonal contrasts emerge in temperate regions. GPS-tracked muskoxen (*Ovibos moschatus*) increased movement speed as temperatures dropped in winter and autumn, but moved slower in summer at higher temperatures, likely to avoid thermal stress. However, tighter turning angles during summer months also indicated increased foraging, especially in high summer, when days are longest and resources are readily available (77). These examples highlight how seasonal environmental shifts can change *how* animals move through their habitats, owing to both thermoregulatory and foraging needs.

In addition to predictable cycles, sudden or unpredictable fluctuations in environmental conditions outside of baselines can also alter movement strategies. While few studies have looked at changes in *how* animals move in response to such events, presenting a large gap in movement ecology studies, some examples exist. Vulturine guineafowl exhibit straighter and faster movements during prolonged droughts that induce them to shift their ranges (35). Groups also move faster (and leave their roost earlier, showing a change in *when to move*) as they leave their roost when high quality resources are available (75). Such changes in *how* animals move can allow them to cope with unpredictable environmental shifts, such as fluctuations in resource availability.

Together, these examples suggest that animals adjust how they move in response to environmental variability (**Table 1**). Because such adjustments in *when*, *where* and *how* animals move mirror underlying conditions, movement can serve not only as a response to change but also as a sensitive indicator of environmental shifts.

Table 1. Summary of examples that highlight how environmental conditions can alter animal space use (*where* to move to), movement timing (*when* to move), and movement characteristics (*how* to move).

Species	Environmental Factor	Movement Response	Drivers	Movement Axis	Reference
African wild dog (*Lycaon pictus*)	Higher temperatures	Decreased daytime activity but more nocturnal activity	Thermoregulation	when	(65,143)
	Brighter moon light	Larger travel distances at night	Weather → vision	how	(143)
African forest elephants (*Loxodonta cyclotis*)	Higher rainfall and fruit availability	More straight, long-distance, goal-directed movements	Resources; weather → energy expenditure during movement	how	(9)
Asiatic wild asses (*Equus hemionus*)	Harsh winter	Movement outside of home ranges	Extreme weather event	where	(62)
Atlantic bluefin tuna (*Thunnus thynnus*)	Ambient temperature	Migration between foraging and breeding grounds	Temperature / reproduction	where	(144)
Banded stilts (*Cladorhynchus leucocephalus*)	Precipitation	Timing of nomadic movements	Precipitation → resources	when	(14)
Bighorn sheep (*Ovis canadensis nelsoni*)	Moonlight availability	Farther travel distances on nights when the moon is brightest	Weather → vision	where	(145)
Blue sheep (*Pseduois nayaur*); snow leopards (*Panthera uncia*)	Shifting tree lines → changes in grass availability → blue sheep distributions → snow leopard distributions	Blue sheep move to lower elevations, snow leopards follow their prey	Climate change → resources / prey	where	(61)
Blue whales (*Balaenoptera musculus*)	Phytoplankton phenology	Migration	Resources	when, where	(69)
Bumblebee (*Bombus vosnesenskii*)	Low landscape-level resource availability	Preference for patches with high floral cover and forage; increasing proportion of long-distance movements	Season → resources	where, how	(146)
Brown howler monkeys (*Alouatta guariba clamitans*)	Fruit availability	Changes in habitat use	Resources	where	(42)
Caiman (*Crocodilus crocodilus*)	Receding water levels during dry periods	Migration between swamps and permanent water bodies	Weather → water levels	when, where	(147)

Feral cats (*Felis catus*)	Fire	Attraction to affected areas	Extreme weather event → resources	where	(59)
Grey teals (*Anas gracilis*)	Precipitation	Timing of nomadic movements	Precipitation → resources	when	(55)
Iberian ibex (*Capra pyrenaica*)	Year-round fluctuating resource availability along an altitudinal gradient	Larger home ranges than conspecifics living at lower altitudes	Altitude → resources	how	(148)
Japanese macaques (*Macaca fuscata*)	Fruit availability and distribution	Changes in habitat use and feeding site selection	Season → resources	how, where	(43)
Lions (*Panthera leo*); ungulate spp.	Fire	Lions avoid fire-affected areas; ungulates exploit new growth	Extreme weather event (→ resources)	where	(57)
Montagu's harrier (*Circus pygargus*)	Prey availability	Migration	Season / precipitation → resources	when	(70)
Mesoamerican spider monkey (*Ateles geoffroyi*)	More rainfall; higher temperatures	Less time spent traveling	Weather	how	(149)
Moose (*Alces alces*)	Higher temperatures	Preference for shade, bogs and mixed forests; decreased movements	Thermoregulation	where, how	(39)
Neotropical lesser bulldog bats (*Noctilio albiventris*)	Insect availability	Double travel distance and longer travel duration when insect availability is low; less time in each forage patch, longer searches for subsequent patches	Season → resource availability	how	(45)
Polar bears (*Ursus maritimus*)	High winds, melting sea ice	Landward movements	Climate change	where	(60)
Saiga antelope (*Saiga tatarica tatarica*)	Plant productivity, precipitation	Migration	Season / precipitation → resources	when	(48)
Snail kites (*Rostrhamus sociabilis*)	Resource availability	Nomadic (exploratory) behaviour when food abundance is high	Resources	how	(54)
Swainson's hawks (*Buteo swainsoni*) and other raptor spp.	Fire	Attraction to affected areas	Extreme weather event → resources	where	(58)
Thomson's gazelles (*Gazella thomsoni thomsoni* Günter)	Changes in short grass distribution	Nomadic movement	Resources	where	(53)
Wild horses (*Equus caballus*)	Changing distribution of herbaceous vegetation	Home ranges and core areas during the breeding season are larger than in winter	Season → resources	where	(44)
Vulturine guineafowl (*Acryllium vulturinum*)	Lower resource availability during dry periods	More frequent movements to new places; use of larger areas and longer travel distances	Season → resources	where, how	(10)

Various ungulate spp.	Resource availability	Nomadic movement; forage-driven nomadism in resource-rich areas, water-driven nomadism in resource-poor deserts	Resources	where	(13)
White-tailed deer (*Odocoileus virginianus seminolus*)	Hurricane	Increased movements; selection for higher elevation pine and hardwood forests, avoidance of marshes; movements outside of home ranges	Extreme weather event	how, where	(56)
Wolves (*Canis lupus*)	Prey availability and distribution	Migration timing and destination	Season → resources	when, where	(147)
Yunnan snub-nosed monkeys (*Rhinopithecus bieti*)	Day length, temperature	Changes in daily travel distance	Temperature, light	how	(8)

6. A framework for predicting responses to environmental change through animal movement: integrating *how*, *when*, and *where*

Studying animal movements can capture responses to changing environmental conditions. Here, we propose that by focussing on the three axes outlined above—i.e., *where*, *when*, and *how* to move—the different types and combinations of changes in movement can give insights into what environmental shifts are taking place, and therefore, substantially improving our understanding animals' responses to environmental changes. When applied over longer time frames (e.g., multiple seasons or years), this can ultimately provide us with the means of predicting future changes (or bottlenecks) involving movements (this section) and of detecting environmental changes (*Section 7*).

To enable movement ecology to become a predictive science, we first need to establish a baseline knowledge of responses to daily and seasonal changes in environmental conditions (**Fig. 4A**). Diel profiles of speed, step length, turning angle, residence time, and activity state often track fluctuations in temperature, humidity, wind, light, and short-lived resource availability (e.g., prey emergence, nectar production, water accessibility). Estimating these signatures under ‘typical’ conditions can allow us to identify what movement features are linked to what environmental factors (which can either promote certain movement features or restrict them). These links can be obtained through correlations (e.g. tracking how day-to-day changes in *where*, *when* and *how* animals move) and by leveraging existing theoretical models, such as optimal foraging theory.

Seasonal patterns in temperature, rainfall, and resource availability should shape space use, activity budgets and movement characteristics in repeatable ways. By monitoring animals across multiple seasonal cycles, researchers can identify typical changes in movement signatures—such as recurring expansions of home ranges during dry seasons or shifts in movement speed and direction during migration periods. These signatures can be quantified using metrics like home range size, step length distributions, turning angles, recurrence rates, and timing of migrations. Ideally, we should aim to capture multiple years of data to separate typical seasonal variation from anomalous changes (while we emphasize that this is ideal, even shorter-term measurements of typical movement characteristics provide valuable information as we outline above). In the absence of long-term data on a certain species, we can increasingly draw from long-term data repositories on other, related species to develop a basic expectation. For example, several studies have identified shared movement metrics that enable the identification of common movement responses seen across taxa (see (78,79)). These baselines then provide us with the ability to detect deviations from expected patterns, thereby signalling unusual or extreme environmental conditions.

Once baselines are established, movement data can be used compare across conditions to predict movement behaviours under novel conditions or detect atypical deviations that might reflect a sudden environmental event (**Fig. 4B**, *Section 7*), such as extreme weather events, habitat fragmentation, or altered prey dynamics. Crucially, because movement adjustments mirror underlying conditions (whether patch availability, resource quality, or climatic extremes) they can be used to infer environmental change even when direct measurements of conditions are unavailable. Climate change, for example, is expected to alter species distribution and ranges by reshaping habitat suitability (e.g. changes in thermal conditions) and food availability (61,63,80–82). Using baselines, day-to-day and seasonal shifts in movement behaviours (e.g. seasonal increases in home range sizes under resource scarcity, later departure from dens during colder conditions, increased movement speeds when resources are more predictable), we can make predictions on how animals might respond to novel conditions and where conditions might limit their persistence under different climate change scenarios.

Movement offers the key to predicting the ability for future landscapes to continue to support survival. For example, evaluating the likely persistence of an endangered species in a protected area can be informed by predicted changes in movement. If conditions expected under future climate change alter the area used by individuals, this could increase chances that they move outside the protected area and increase threats (e.g. as experienced when elephants move into human areas (83)). Conditions might also create worse trade-offs in terms of when individuals can move, such as if resource scarcity coincides with hotter weather (84), meaning that individuals must forage more while also having less suitable time to forage in. Finally, habitat modifications (e.g. increased fragmentation, loss of movement corridors) due to human or climate changes might affect the ability for individuals to express important movement features, such as the ability to increase efficiency when making large displacements. Developing such a mechanistic understanding is critical given that climate change is predicted to cause even protected areas to become unsuitable habitats for some endangered species (85).

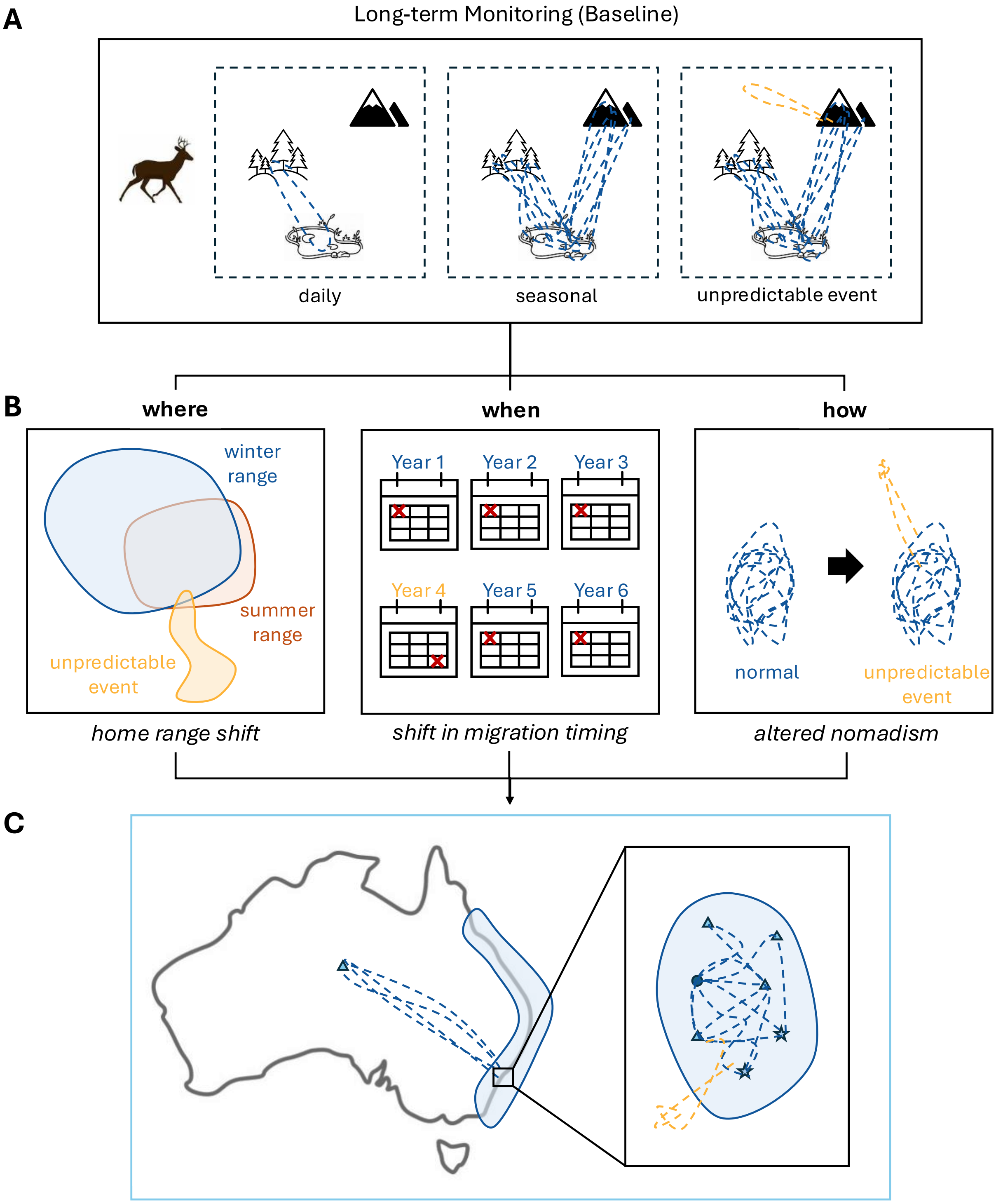


Figure 4: A framework for studying animal movement to infer environmental shifts from movement data. *(A) Step 1: long-term monitoring of animal movement that integrates when, where and how an animal moves daily and across seasons (in blue), as well as during unpredictable, out-of-the-norm events such as droughts or storms (in yellow). (B) Step 2:*

obtaining a detailed understanding of the different aspects of movement (where, when, how) and how they may change in response to unpredictable shifts in environmental conditions. (C) Step 3: long-term movement studies of suitable species can enable us to infer key environments and elements within their ranges (i.e., food, shelter, roosts etc.; star and circle symbols in zoomed in panel, triangle symbols in zoomed out panel, blue lines). Changes away from established baseline movements (yellow line in right panel) may be used to infer environmental fluctuations from movement data (contingent on GPS temporal resolution; see Section 8.2). This may also enable us to use animals as sentinels for environmental change.

7. Real-time monitoring of environmental conditions through animal movements

One emerging idea is that tracking the dynamic changes in animal movements could allow us to detect sudden changes in environmental conditions (86). Already, some species and a variety of factors (e.g., population numbers, distributions, diet, breeding success) are used as indicators for ecosystem health (87–90) and can even aid with waste management (91). Farm animals equipped with acceleration loggers can be useful short-term predictors for earthquakes, showing unusually high activity prior to both high and low seismic activity (92). Movement may be a particularly powerful indicator because we can develop baseline knowledge and use existing theory (e.g. on foraging) to develop an ‘expectation envelope’ and quickly detect when animals move outside these expectations. Movement is particularly ideal because environmental changes affect it immediately, as movement is central to day-to-day survival, whereas demographic consequences often take longer to manifest (93).

A key to implementing this vision is to establish baseline knowledge about how different axes of movement behaviour are impacted by within-the-norm environmental fluctuations to develop an expectation envelope (our framework). This then needs to be combined with continuous movement tracking studies that can serve as early detectors for if and when ecologically meaningful environmental changes take place. For example, tropical birds in

Kenya showed distinct movement patterns depending on whether they were in landscape fragments or the surrounding areas: birds in fragments had short step lengths and small displacements, while those in the surrounding areas had long step lengths and large displacements (94). Continued tracking could detect changes to habitat geometry experienced by individuals through the properties of their step lengths. The space use of predators allows for inference of the diversity and abundance of their prey animals (95), such as the use of basking shark (*Cetorhinus maximus*) movements to determine prey-rich areas (96). Tracking where sharks go can provide insights into where resources are currently most abundant. These examples highlight how movement can reflect environmental conditions and, ultimately, allow inference of the status of an ecosystem. The obtained baseline knowledge on how movement changes in response to shifts between normal and unpredictable conditions will then enable us to use movement to identify key environmental elements or habitat features that are critical for survival (e.g., food, shelter, roosts, etc.). In turn, this knowledge will enable us to predict where and how populations may persist under our changing climate.

Notably, it is important to carefully evaluate our assumptions about how an indicator or sentinel species is expected to change their movement behaviours in response to changing resource availability. For example, recent studies have shown that higher foraging effort (e.g., as indicated by area-restricted search behaviour, i.e., less-direct movements, higher turning rates, and lower travel speeds; see **Fig. 3**) does not necessarily reflect higher prey abundance, as frequently assumed, but can also be indicative of lower prey abundance and biomass and the consequently higher effort animals must make to meet energy needs (e.g., seals (97), bats (45)). Animals may also be prioritising different aspects of food resources when selecting where to move (e.g., quality or accessibility over quantity *per se*). For instance, red deer (*Cervus elaphus*) selected areas with higher vegetation biomass over areas with higher vegetation nutrition (98) and diving marine predators selected areas where prey species were predictably available at shallower depths, rather than where prey was predictably abundant (99). Finally, high-quality food patches may be ignored if they fall short in other important dimensions (e.g., proximity to water or shelter). For example, semi-free ranging cattle did not utilise high quality patches of grass if these were too far removed from water sources (24). These examples illustrate why a strong knowledge of the natural history and baseline tracking data of the study system and their environment are important before using species as a sentinel.

Another important consideration is that species will show different levels of sensitivity to environmental change. We might expect that specialist foragers and those with narrower physiological thermal ranges will show alterations along the *where* and *when* movement axes, as they will leave areas as soon as they become unsuitable. In contrast, more generalist species with wider thermal tolerances may not be immediately displaced but still show signs of modified habitat use (the *how* axis). For instance, sympatric hawksbill sea turtles (*Eretmochelys imbricata*) and southern stingrays (*Hypanus americanus*) responded differently to catastrophic hurricane events. While the stingrays left the bay following the hurricanes, the turtles remained but altered their dive depth and increased their overall space use to compensate for the habitat/forage loss after the hurricanes (100). It has been suggested that generalist species may be less valuable as sentinels as they can behaviourally buffer environmental change (e.g., through prey switching) (101). However, we would argue that these taxa could serve as valuable sentinels if we consider the *how* axis (e.g., animals remain in place but indicate environmental fluctuations through other movement metrics). Moreover, ‘resilience’ in this context might not be categorical but rather manifest along a spectrum: species might remain in a given area experiencing environmental change (showing initial shifts along the *how* axis), before leaving the area entirely (showing signals along the *when* and *where* axes later).

Finally, we must consider that not all movement responses are adaptive in the Anthropocene (102). As seen after the harsh 2009 winter in the Gobi Desert where Przewalski’s horses did not leave and suffered high mortality (62), some species may fail altogether to adjust their movements in response to sudden environmental disturbances. Thus, determining what resource characteristic is of interest (e.g. quality, quantity, accessibility) and how the indicator species is expected to respond is important to consider when making inferences about the underlying environmental processes. These caveats notwithstanding, animals could be used as sentinels for both predictable, within-the-norm shifts, and as early warning systems for unpredictable events (i.e. when movements characteristics move outside of the normal expected range for a given season, location, or time).

With the right baseline knowledge, animals can function as sentinels that reflect current ecological and environmental conditions through their movement (**Fig. 4C**). This includes the detection of novel or otherwise unpredictable conditions (i.e. events with a longer duration, such as droughts) and transient events, offering sensitive indicators in an era of rapid global change. Such indicators may, in turn, be valuable tools for predicting population persistence. Achieving this aim effectively requires us to be explicit about the *how*, *when* and *where* axes of movement. Doing so opens the door for future studies to develop accurate, mechanistic predictions of how environmental processes will affect species and ecosystems. Additionally, the high-resolution data obtained from such movement studies may also improve current classifications of species into movement syndromes (26), advancing a bottom-up framework for predicting how groups of species will respond to environmental change.

8. Future challenges and some potential emerging solutions

8.1. Obtaining high-resolution resource availability data

Many studies link resources to the movements of animals. One common approach is to use satellite imagery that estimates resources, such as plant phenology via the Normalized Difference Vegetation Index (NDVI; (103)) or water availability via the Normalized Difference Water Index (NDWI; (104) CITE), and combine these with GPS telemetry (105) or camera trap data (106) to estimate the effect of resources on animal movements (107). However, such studies highlight the significant challenge of getting a detailed estimate of resource conditions. While satellite-borne measurements are relatively widely accessible and easy to calculate, their temporal resolution often does not match that of fine-scale GPS movement data (108). The temporal resolution of GPS data needs to be adjusted both to the study system and environmental conditions in which foraging is being inferred (Christensen & Klarevas-Irby et al., *in prep*). For instance, animals that forage on clustered resources (many marine predators and frugivores) may show clearer reductions in step length and path straightness compared to animals intermittently foraging on more homogeneously dispersed resources (e.g., many grazing herbivores). Comparative movement studies (e.g. (109)) will play an important role in developing general predictions across different species groupings.

Obtaining detailed data on resource availability through on-the-ground sampling, such as transect surveys or fruit tree / prey species counts (e.g., (42,110)), is labour-intensive and costly. Furthermore, these methods often only yield accurate results under specific assumptions (111,112). For example, strip-transect surveys assume that all prey animals within a strip are counted, which is rare under field conditions (111); choosing suitable plant sampling methods relies on a specialised understanding of plant distributions and plant community organisation (112). These challenges typically restrict assessments to smaller geographical areas and shorter durations. Thus, linking on-the-ground measures of food availability (or other environmental indicators) to movement metrics may be a challenging but necessary first step, before we can scale up the use of animal movement as a monitoring tool. Movement ecologists will substantially increase the predictive power of their work through collaborations outside the animal ecology community. Climatologists, plant ecologists and agricultural scientist have developed targeted environmental monitoring solutions that can aide with detecting and predicting key tipping points for ecological functions (e.g., carbon capture, food production). Indeed, some detailed data on environmental indices (e.g., plant productivity (113), water availability (114), biodiversity (115)) may already be available for areas of high conservation interest and could be leveraged if cross-disciplinary research was encouraged.

Resources or weather patterns themselves may also fall along *where*, *when*, and *how* axes, which can be used to generate predictions on how animal movement is likely to be altered in response. For instance, if plant phenology is shifted earlier in the year due to warming climates (116), this is likely to generate a *when* change in any plant-(sentinel) animal interactions (e.g., (117). If nutritional value of grasses decreases in periods of drought (118), this is likely to generate a *how* change in the movement axes, as animals may need to spend more time exploiting the same resource to meet nutritional demands or broaden their diet to include more food items (e.g., exploiting underground foods (119). Heat-sensitive migration of prey species (e.g., fish moving upstream (120)), will affect the *where* movement axes of their predators. Asking tailored questions about the environmental change of interest (resource timing (*when*); resource quality/accessibility (*how*); resource absence/presence (*where*)) will significantly streamline the daunting challenge of measuring the environmental change on-the-ground.

8.2. Financial and logistical challenges of long-term baseline monitoring

Long-term tracking of animal populations across all three movement axes to give us the best chance of detecting deviations from the norm. Indeed, long-term field studies have repeatedly proven themselves to be important in understanding ecological changes that play out over long periods, providing a platform for scientific collaboration, informing policy, and predicting/preparing for climate change impacts (121,122) in a cost-effective way (123). However, many studies face financial and/or logistical uncertainty (e.g., relying on year-to-year grants or being conducted in areas where political support for science and conservation is not consistent). Tracking devices can constitute a large part of the research budget. While the price of tags is dropping as they become more widespread (124), this technology is still prohibitively expensive when it comes to tracking a representative sample of the population or when tracking social groups (see *Section 8.3*). Additionally, ethical concerns regarding tagging animals need to be balanced against expected conservation/scientific outcomes (125). Continuous tracking is also logistically challenging (e.g., requiring frequent downloading and storing of data and sometimes losing data if tags fail, drop, or animals leave areas where their data can be downloaded (126–128)). Newer and cheaper technologies with lower download costs (e.g. LoRaWAN, BLE tags; (129)) can help mitigate some of these challenges.

While there are challenges associated with long-term tracking, expanding movement ecology from an observational to a predictive science will also open novel funding opportunities. This includes collaborative projects with fields where funding rates (or amounts) are often much higher (e.g. climate sciences) as well as access to new funding bodies. However, making these collaborations work will require clear data on how animal movements reflect underlying environmental changes, a task that can be facilitated by adopting the three axes of our framework (when, where, and how).

8.3. Social factors that can influence movement

Animal movement is not only shaped by environmental drivers but also by the social context in which individuals live (130). In many taxa, movements are coordinated, negotiated, or constrained by group members. For example, in social ungulates, primates and birds, collective decisions determine when and where to travel, meaning that an individual’s movement may reflect consensus outcomes rather than only environmental conditions (131–133). Dominance hierarchies often influence which individuals gain preferential access to resources (134) , and integrating these dynamics into optimal foraging theory has revealed that they then affect who initiates movements (135,136). Mating systems and sex-based life-history differences can also generate consistent variation in movement strategies between males and females (137,138). Social networks also create indirect effects: for instance, if key individuals (139,140) with knowledge of resources are lost due to mortality or poaching, then group-level movement strategies may shift. Finally, individuals can express different movement characteristics in different social conditions. For example, if they are in a group of intermediate size, they might have a larger home range than if they were in a smaller or larger group (141), and they likely travel slower when moving in a group than they can when moving alone (35).

These dynamics pose challenges for interpreting movement data in relation to environmental conditions, since shifts may reflect changes in group composition or social organisation rather than external ecological drivers. To address this, combining movement tracking with detailed behavioural and demographic monitoring, or combined tracking of multiple individuals in each group (142), can help disentangle environmental versus social contributions to movement. This is particularly important for sentinel applications, since social buffering or group cohesion may mask early-warning signals that would be evident in solitary species.

9. Conclusions

Animals are increasingly confronted with novel and unpredictable environmental changes. Understanding movements in response to such shifts—both seasonal and atypical—is critical for predicting how animals will be impacted by future conditions. This also opens the door to novel approaches, notably using animals as ‘sentinels’ for change. Doing so requires integrating the multiple axes of movements, notably *when*, *where*, and *how* animals move. Our review of the existing literature shows that much is known about these, but that few studies integrate all three axes explicitly. This is important because our ability to understand (and thus predict) the impacts of different forms of environmental changes will require capturing relative changes across different combinations of these axes.

Our framework is simple, but comprehensive in its ability to identify shifts in environmental conditions using animal movement data. There are limitations, for example it requires building a strong baseline understanding of animal movement responses to environmental changes that have already begun. There are also challenges involved with scaling up tracking across longer time periods and/or a larger sample of the population. However, broadening movement studies to capture key movement axes—*when*, *where*, and *how* to move—in conjunction with continued technological advancements to address these challenges opens the door to new inter-disciplinary collaborations. These can facilitate turning movement ecology into a stronger predictive science, strengthening our ability to estimate population responses to novel conditions and enabling the use of animals as sentinels for ecological change.

Declarations:

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