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Opinion

Certainty and integration of options in animal movement

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Physical energy defines the energy landscape and determines the species-specific cost of movement, thus influencing movement decisions. In unpredictable and dynamic environments, observing the locomotion of others increases individual certainty in the distribution of physical energy to increase movement efficiency. Beyond the physical energy landscape, social sampling increases certainty in all ecological landscapes that influence animal movement (including fear and resource landscapes), and individuals use energy to express each of these. We call for the development of an 'optimal movement theory' (OMT) that integrates the multidimensional reality of movement decisions by combining ecological landscapes according to a single expectation of energy cost–benefit, where social sampling provides up-to-date information under uncertain conditions. This mechanistic framework has implications for predicting individual movement patterns and for investigating the emergence of aggregations.

Highlights

Animals move in ways to exploit physical energy in the energy landscape – avoiding steep slopes or locating favourable media currents to reduce the cost of movement.

Movement decisions are probabilistic and based on prior expectation of the environment, the error of which can be reduced with up-to-date information.

Social sampling of cues in the locomotion of others can increase certainty in the expectation of physical energy availability for efficient movement.

Animals must consider and integrate a multitude of ecological landscapes in addition to physical energy when making movement decisions.

We call for the development of an optimal movement theory (OMT) that integrates this complexity and the certainty thereof according to the currency of energy – a common denominator of all ecological landscapes that influence movement simultaneously.

Moving through the physical energy landscape

Faced with a heterogeneous, dynamic, and often difficult-to-predict environment, animals must make probabilistic decisions concerning **movement** (see Glossary) to gain access to the **resources** needed for life, such as food, mates, and shelter. Although they have evolved to sense the environment to which they are exposed to directly (e.g., via mechanosensory inputs), animals often rely on their **prior expectation** of the environment (i.e., memory of spatiotemporal patterns that relate to resource distribution) to decide when and where to move to in their next movement steps. However, this prior **expectation** will be imperfect in unknown and dynamic environments [1], and therefore acquiring up-to-date information about environmental conditions can reduce uncertainty, leading to a more **efficient** movement outcome (where the gains are greater than the costs, per unit time). Such a Bayesian process is most studied in the context of foraging, where animals may sense current food availability and patch quality by observing the foraging behaviour of others within their perceptual range to improve their foraging efficiency. For example, eavesdropping on echolocation calls of fellow bats hunting for prey [2], observing seabirds dive for fish [3], or scavengers landing at a carcass [4] all provide cues about the availability, and possibly quality, of **ephemeral** food patches to other searching foragers. This process of observing **social cues** is defined as **social sampling** and extends the perceptual range of an individual by social information transfer [5,6].

However, movement decisions are not only geared towards increasing foraging efficiency as they are influenced by many spatio-temporally-varying ecological landscapes. The **physical energy landscape** (commonly defined as the 'energy landscape' [7]) is a heterogeneous landscape of fluctuating media flows, terrain profiles, and substrates that influence the energy expenditure required for movement; which is, for example, greater on uphill slopes than when moving along shallow valleys, or reduced when exploiting favourable media currents. All movement strategies are influenced by **physical energy** in some way, from the exploitation of wind by aerial species

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[8,9] and of currents by aquatic species [10,11], to the avoidance of steep slopes, dense vegetation, and costly substrate types (e.g., snow cover) for terrestrial species [12–15]. Some species have even evolved to harvest and store this energy, such as the use of thermal and slope **updrafts** by soaring birds (Box 1) [16,17] and of underwater updrafts by negatively buoyant sharks [18], where potential energy is stored in height (altitude or shallower depth) and spent (by dropping/gliding) to cover distance while minimising the use of energy-expensive types of **locomotion**. Using an optimality approach, animals must make cost-efficient movement decisions and move through their physical energy landscape in ways that maximise efficiency over all timescales [7,19] – namely exploiting physical energy while putting in the least amount of effort per unit time (comparative with intake rate in foraging efficiency). Thus, the physical energy landscape has a significant impact on space use and movement strategies for all moving beings, irrespective of the mode of locomotion or the overall motivation to move – whether this is to forage, to avoid predation, or to migrate.

Because the physical energy landscape is so important, but difficult to map, we expect animals to have evolved mechanisms to increase certainty in predicting its distribution and properties. Given

Box 1. A dynamic and invisible physical energy landscape

Obligate soaring birds have an extreme dependency on the physical energy available in airflows, a trait that has evolved alongside their scavenging ecology [62]. These soaring scavengers have high visual acuity and often share airspace with other soarers seeking the same resources [4,63] – they thus provide an ideal case-study to examine the value of social sampling in movement. Soaring birds gain height rising in updrafts and convert the height gained into distance by gliding across the landscape, at speed, to the next updraft. This is a risky game of snakes and ladders because, once the decision is made to leave one updraft, they must ensure that the glide will take them to the next before they reach the ground. Although there is some predictability in the location of updrafts according to topography [64] and in updraft intensity according to seasonal and diurnal patterns (e.g., [65]), they are a notoriously ephemeral resource. Arriving at a probable updraft location does not mean it will be present when the bird needs it [17]. Soaring birds should therefore have evolved mechanisms for detecting and utilising favourable flows, for coping with turbulent ones or avoiding those that oppose the desired movement. Thus, probabilistic movement towards likely updrafts informed by prior experience can be updated using social information to ascertain updraft availability (Figure I). Maintaining cohesion for the benefit of obtaining social cues can maximise efficiency in soaring flight, especially in marginal conditions when updrafts are sporadic and weak.

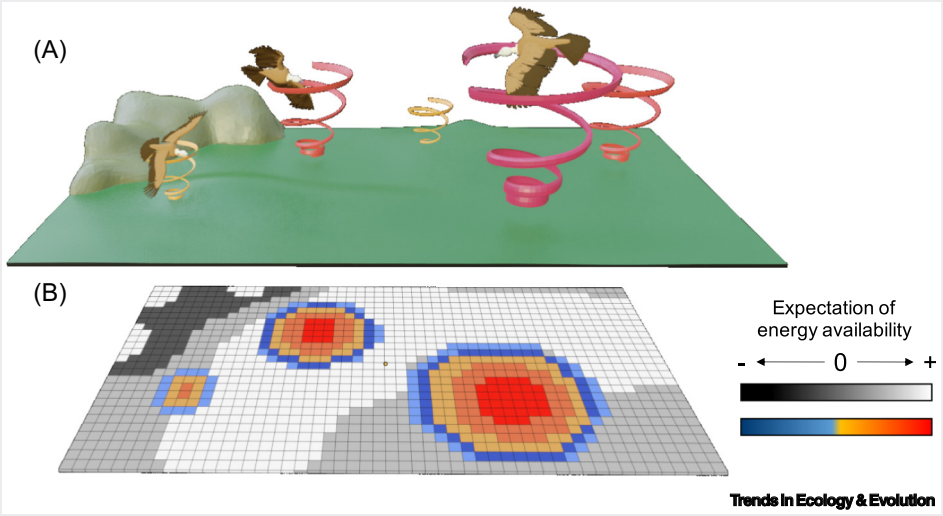

Figure I. Certainty in updraft availability in the physical energy landscape of a soaring bird. (A) Updrafts are used by obligate soaring birds. (B) Experienced flyers have a prior expectation of the availability of physical energy (i.e., updraft location and strength; grey scale), but the soaring behaviour of others that share this airspace provides up-to-date and accurate information about a specific location and properties of the updrafts they occupy (colour scale).

Glossary

Efficiency: the ratio of energy gain to energy expenditure across ecological landscapes, including the rate of food intake or the ratio of potential energy gain to the mechanical energy input in movement; efficiency is high where gain is greater than cost per unit time.
Energy wave: a naturally generated gradient in energy availability across space that is the combined product of energy distributed in all ecological landscape layers. At its peak, there is overlap in good environmental conditions (for physiological processes, movement, and foraging, etc.).
Enhancement: where a demonstrator provides a cue or stimulus that invokes a response in an observer, either by changing location or behaviour.
Emergent sensing: a mechanism for collective movement where no one individual determines the current direction of motion and the group moves as a whole [6].
Ephemerality: a relative measure of the dynamism of an ecological landscape along a scale from temporal stability to highly fluctuating.
Expectation: the predicated value of an environmental characteristic at a given time and space as a function of probability of occurrence.
Landscape of fear: based on predators eliciting a fear of being killed, high risk of predation at a specific space and time invokes a high fear response in prey [44], for example, vigilance behaviour.
Locomotion: the mechanical motion of an animal.
Movement: the displacement of an animal from place to place through time.
Motion capacity: the set of biomechanical or morphological traits that facilitate movement [20].
Optimal movement theory (OMT): a concept that unifies ecological landscapes (i.e., food, physical energy, and fear) into a single expectation of energy cost–benefit. Certainty in the expectation of energy distribution is increased by up-to-date information on energy availability/requirements across landscapes.
Performance: optimal locomotion efficiency according to biomechanics and species motion capacity.
Physical energy: a form of energy that exists in the static and dynamic features of the physical energy landscape. Where energy is available and of high quality,

conspecifics are equally limited in their **motion capacity** (i.e., locomotor abilities) [20], and are under equal pressure to maximise efficiency while sharing the same physical energy landscape, we are of the opinion that animals must recognise social cues as a reliable and invaluable source of information. Therefore, if we are to predict animal movement, it is clear that the concept of the physical energy landscape needs to extend its dimension of certainty by the inclusion of social information.

Social sampling of physical energy

In its simplest form, the presence of a moving individual indicates that there are suitable levels of physical energy available for movement, and provides this information inadvertently to others via **enhancement** – in other words by social copying [21]. This process requires minimal interpretation of a social cue, but nonetheless has the potential to reduce movement costs significantly. For example, in the case of obligate soaring birds, daily fluctuation in wind and insolation means birds must wait for updrafts to gain enough strength before they can support sustained soaring flight. Soaring attempts too early could mean that an individual may be forced to land and invest in additional take-offs, and thus pay the costly consequences of incorrect timing. Although this risk may be low for individuals that have built up a more accurate prior expectation through experience [22], for naïve individuals it would be beneficial to wait for others to soar successfully because their predictions of physical energy availability are likely to be more inaccurate. A producer–scrounger dynamic emerges wherein the benefits of early take-off and arrival at food sources with lower competition levels are forgone for reliable social cues of suitable flight conditions and reduced need of multiple take-offs [17]. Enhancement will aid individual decision making in any system where and whenever individuals share space (such as that demonstrated in olive baboons, *Papio anubis* [13]) or evidence of their movement persists in the landscape in cues that decay gradually. At river-crossings for terrestrial species, for example, the movement of animals on the opposite riverbank, or the footprints and trails left behind, undoubtedly indicate a suitable path for crossing.

Social sampling can also provide information on the quality of physical energy patches that facilitate movement, including the degree of the slope or the strength of a current. Locomotion provides an honest cue for the amount of environmental assistance or obstruction to movement as (i) patterns in locomotion behaviour unavoidably reflect energy investment, and (ii) there is no expectation that physical energy is depleted by its use (unlike food patches when foraging, although physical energy may be modified at a fine scale when moving in the wake of another individual). By recognising a combination of low limb-beat frequency or amplitude with high speed, an observer can assume that the animal is assisted in its movement by a significant amount of physical energy (or is not obstructed), and thus is made aware of a high-quality energy source. This may be the case across taxa and environments where gait or limb-beat frequencies, indicative of the effort invested in motion, may be perceived by others through various sensory modalities to indicate expensive or cheap **routes** for terrestrial, aquatic, or aerial movement (e.g., olive baboons [23], or Pacific salmon, *Oncorhynchus* spp. [24]). Even in passive movement there is quantitative information [25]. For a soaring bird to exploit an updraft it must adopt a specific bank angle and turning radius which, along with the bird's own vertical speed and according to the laws of physics, reflect the strength (vertical velocity) of the underlying updraft [26,27]. Importantly, these active and passive behaviours cannot be false or dishonest because movement can only ever be the combined result of locomotion and the environment – for instance, 'soaring' animals (birds or aquatic species exploiting underwater updrafts) would otherwise drop in altitude or depth if they displayed soaring behaviour but without the support of an updraft [18,28].

Quantitative information is available only through comparisons either to one's own movement (or internalised understanding of it) or to another observed individual, and hence is likely to require a

movement costs are reduced, for example, in updrafts for aerial species and on open and level ground for terrestrial species.
Physical energy landscape: environmentally dependent spatiotemporal variation in the cost of movement, determined by the energy required to locomote given the characteristics of physical energy available at a point in space and time [7].
Prior expectation: the expectation of an animal about energy distribution and quality acquired from previous experience [5].
Resource: provides energy in some form, which animals can store and use.
Resource landscape: the spatial and temporal distribution and availability of resources [41].
Resource wave: an ordered gradient in resource availability across space that is generated by natural gradients in physical features [41], for example, elevation and abiotic parameters such as solar heating.
Route: a spatially defined movement path that emerges out of decisions to move to specific locations in consecutive timesteps.
Social cue: a type of inadvertent social information that reflects the availability of a resource [5].
Social sampling: the process of gaining social information to update a prior expectation based on experience.
Updraft: a patch of air or water that rises due to thermal convection, wind, or fluid dynamics.

relatively high level of cognitive ability. However, it is hypothesised that animals make movement decisions in response to a projected future state of the world, which could be achieved with simple behavioural rules, comparable with trajectory tracking of a prey item by a predator (e.g., [29,30]). Thus, we expect the potential for social information to reduce movement costs to outweigh the cognitive demand of the physical intelligence, and therefore will be of adaptive value for the species most dependant on physical energy for cost-efficient movement.

Consequences of social sampling of physical energy

Maintaining sensory contact with multiple individuals augments the information available for individuals to increase certainty of their environment over a greater number of possible movement steps [31] and allow for comparisons of quality (as earlier). Consequently, provided that there is a positive effect on individual movement efficiency, cohesion should be maintained within aggregations [32]. In this respect, the strength, persistence, and stability of cohesion are determined by the value of information gained from social sampling, which should depend on (i) variations in the distribution and ephemerality of physical energy, and (ii) the individual-dependence on this energy (according to their motion capacity). By adjusting cohesion with others, individuals secure access to the most relevant information for optimal decision making (Box 2). This means that dense aggregations should be better able to operate under marginal conditions where the physical energy landscape is difficult to predict. Thus, under deteriorating environmental conditions, for example, through anthropogenic change, population declines may be accelerated by increasing loss of information, and the movement of sparse aggregations will become restricted to regions of highest quality that have stable physical energy landscapes. This also influences the assembly of aggregations as conspecifics provide the most valuable information, but heterospecifics that share similar motion capacities may also provide relevant information about the availability of physical energy.

Synchrony in movement will emerge as a property of shared resource use because energy efficiency at the individual level is linked to the efficiency of an aggregation. Social sampling thus provides a mechanism for optimal route finding via collective **emergent sensing** [6,33,34]. The wisdom of the crowd [35,36] should allow tracks to funnel trailing individuals towards the most energetically optimal path (Figure 1), possibly facilitated by information in the tracks themselves – for example, footprints that reveal gait patterns, stride length, or stepping force (in imprint depth) may reflect variation in the cost of movement. However, the quality of tracks will degrade and become less relevant with time, meaning that there is value in synchrony and temporal proximity irrespective of how the cue is sensed.

Maintaining cohesion in a social group structure will ensure that individuals have access to relevant cues when they are most valuable, and therefore create a social barrier to movement away from the aggregation [37] (and most definitely for optimal movement), and ultimately may promote colonial living [38]. For example, seabirds and marine animals likely maintain cohesion for foraging efficiency and for safety in numbers at nest sites, but the idea that colonial living may have evolved, at least in part, to facilitate movement efficiency is rarely considered. Landing and departure of colonial animals at the rest site [from air or sea, such as albatross (Diomedeidae), penguins (Spheniscidae), seals (Pinnipedia), or marine iguanas (*Amblyrhynchus cristatus*)] involves critical decision-making to negotiate highly powerful and turbulent flows that vary in space and time at a fine scale [39]. Should individuals attempt the landing at a site with unfavourable physical energy dynamics, or in a manner not appropriate to the conditions (e.g., speed and heading), then the result ranges from excessive energy cost of an additional required landing attempt to fatality (by the elements or predation; e.g., [40]). By observing cues in the landing attempts of others, individuals may be able to land more cheaply and safely.

Box 2. Projection of energy availability in a dynamic environment

Moving in moving media (air or water) means that, once a decision is made to leave one physical energy patch for another, the media flow can change the energy characteristics of this second patch while *en route*. The relationship between the temporal and spatial dynamism of the landscape determines optimal distance between individuals for valuable information gain. In the scenario illustrated (Figure I), the focal individual (marked black) in physical energy patch A has a perceptual range (grey) that allows it to observe the behaviour of individuals in two additional and separate patches, B and C. In a static physical energy landscape, the behaviour of all individuals within perceptual range is of equal value to our focal in deciding where and when to move to in its next movement step. By contrast, if the same landscape has relatively high temporal-dynamism in energy patch availability, the distance between our focal individual and those in the farthest patch C decreases the value of this information compared with those in the near patch B. Likewise, under extreme conditions with high temporal dynamism, only within-patch social sampling may be of value (i.e., those also in patch A). In this scenario, the information related to patch D is not perceived by the focal. Maintaining an optimal interindividual distance that aligns with the scale of dynamism will influence the degree of behavioural synchronisation [66] for moving aggregations.

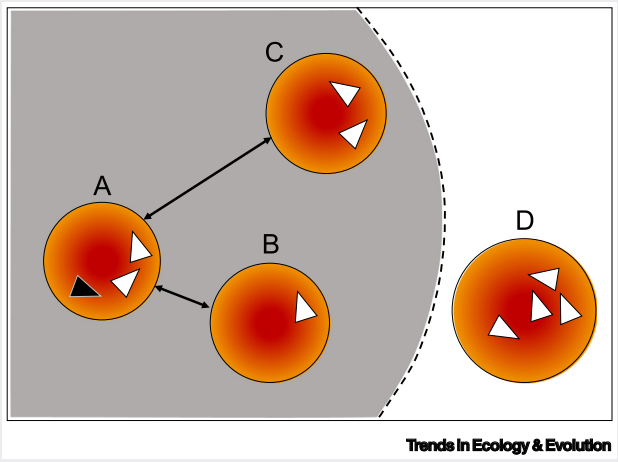

Figure I. The optimal spatio-temporal distance between individuals depends on the dynamism of the physical energy landscape, the inter-patch distance, and the perceptual range of individuals. Different species may have adapted different social sampling optima accordingly.

Certainty across ecological landscapes

Social sampling can increase an individual's certainty in expectation not only in relation to its physical energy landscape but also across all ecological landscapes. One approach to describing decision making has been to partition environmental variation into discrete ecological landscape layers; the most prominent representatives being the energy landscape (physical energy [7]), the **resource landscape** (food [41,42]), and the **landscape of fear** (predation risk [43,44]). In each of these layers there is error associated in predicting the environment because of their inherent dynamism, as well as the necessity to be as accurate as possible for efficiency. With the presence of other individuals, animals gain information about resource availability and safety. There is a large body of literature on the importance of social information to increase energy gain from food resource distribution landscapes [34], showing how social information affects access to food resources including, for example, the information centre hypothesis [45] and resource tracking [41,46]). From the perspective of the landscape of fear, social sampling to avoid high-risk situations can reduce energy expenditure invested in vigilance or predator escape (reviewed in [47]). Furthermore, in addition to the benefits of readily available (and relevant) social information, there are direct benefits within aggregations. For example, predation risk is diluted [48–50] and cohesive movement can decrease individual movement costs directly by altering the physical energy landscape, such as the reduced cost of flight in the wake of others in V-flock formation [51] or when walking in the footsteps of another (where well-trodden trails reinforce reduced movement costs alongside information gain [52]). These direct benefits are, however, balanced by their various well-known costs

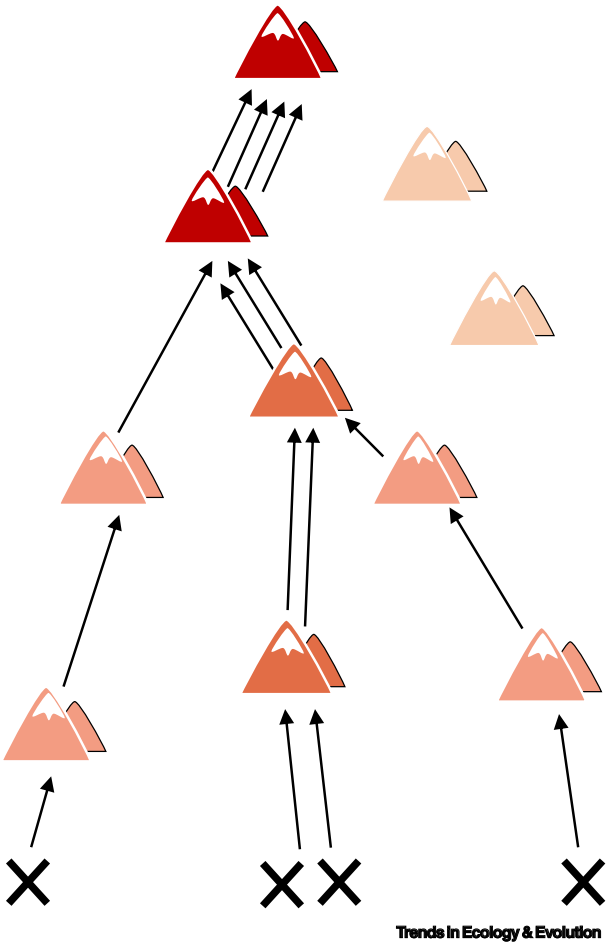

Figure 1. Optimal routes emerge through synchrony and social sampling of movement. Individuals converge on common and efficient routes given that social cues increase certainty in the expectation of physical energy availability (darker red represents increased certainty from shared use).

(competition for access to resources, disease transmission, etc.), including the possibility that predators may be able to recognise the locomotion cues that lead to their prey converging on shared routes (see Outstanding questions). Ultimately, however, wherever there is a net benefit of the presence of others, some form of sociality will be selected for (from multispecies aggregations to fission–fusion societies and stable social groups).

Integration of landscapes

Movement is the outcome of a series of complex decisions as animals must consider a multitude of factors to integrate the various ecological landscapes and the certainty therein. Separating these landscapes and introducing different currencies somewhat oversimplifies how we understand and model decision processes in movement. These landscapes are not independent static entities, instead they act simultaneously on decision making, and all include varying amounts of error in expectation. In addition, they change their form through time, and their absolute and relative values depend on the changing physiological needs (demographic differences, reproductive state, etc.) of the animal (e.g., [53]). This complexity asks for unification into some type of overall decision-based landscape, measured in a single currency, which we argue could be energy.

Animals (and in fact all living organisms) exist in an energy balance and by occupying space they gain, store, and use energy from their environment through time. Consequently, decisions should be evolutionarily selected to optimise this energy balance, as demonstrated by recent studies investigating the elevation migration of Galápagos giant tortoises (*Chelonoidis* spp.), for example [53,54]. Thus, we propose an **optimal movement theory (OMT)** that integrates all ecological landscapes that determine movement decisions. This can be quantified energetically because individuals use energy to express all landscapes, the result being (i) the direct energy cost or benefit of the movement outcome, including the energy gained (from food, heat, or as potential energy) and the energy cost to the animal's physiology, the cost of locomotion, and the use of energy in vigilance or predator avoidance (where risky areas require greater energy investment and predation is the ultimate price paid), and (ii) the energy savings and future returns incurred by the movement (comparable with 'projected payoffs' within economics). At any decision point the probability of moving to a specific location will be greatest where the net energy gain and future return is highest, but will be influenced by the certainty and accuracy of expectation (Figure 2). This thinking can

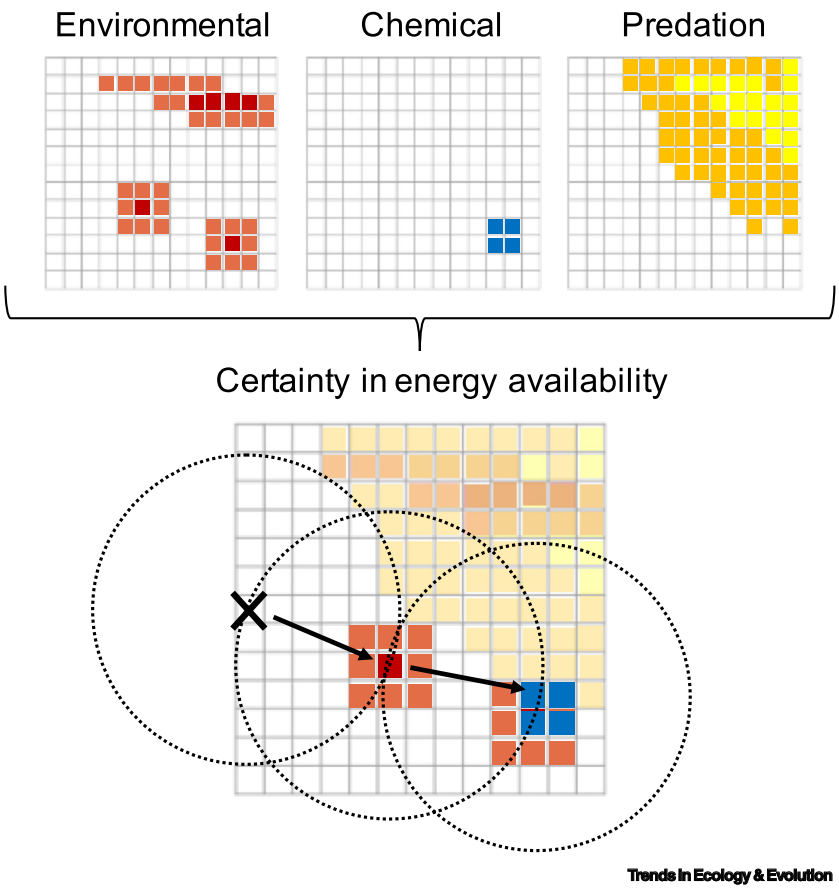

Figure 2. Optimal movement theory (OMT) combines certainty in energy availability in the different landscape layers. In all defined ecological landscapes, energy can be gained or conserved (darker colours indicate greater positive energy value; e.g., reduced expenditure devoted to vigilance in low-predation risk areas in the landscape of fear and in the cost of movement in the physical energy landscape). These landscapes can be combined into a single energy value of direct benefit and future returns. An animal (X) should move in a way that optimises energy efficiency, but decisions are influenced by certainty in expectation. Social sampling of conspecifics within perceptual range (broken line circles) increases certainty (indicated by greater opacity) in movement decisions towards an energy-efficient outcome at each step.

provide the empirical basis to better predict how individuals respond to their multifaceted environments (with a more holistic approach than the focused optimal foraging theory [55–57]). The spatiotemporal variation in the availability and depletion of energy has consequences resulting in, for example, the mass-movement tracking of resources [41,58,59] and thus animal migration (i.e., following a **resource wave**). As we begin to understand the value of energy as a single currency and its variation, social sampling should facilitate gradient-tracking across landscapes, including regional and seasonal gradient-tracking, that gives rise to a concerted **energy wave** – namely balancing and synchronising the tracking of good conditions for movement (such as winds, currents or substrates) with good conditions for foraging (such as green-up [60] or snow melt [61]) and safe conditions of refuge (away from predator activity), simultaneously.

Concluding remarks

We extend here the physical energy landscape by its dimension of certainty, and we introduce a mechanistic framework to integrate the multidimensional reality of movement decisions, where social sampling provides up-to-date information under uncertain conditions. In the OMT framework we recognise that movement is a multilayered process that does not need to consider single ecological landscapes independently in predicting movement decisions. Ultimately, this holistic view has consequences for the emergence of animal aggregations and movement patterns across scales. Aggregations may be temporary or fixed, and will occur along a spectrum of exclusivity – from demographically segregated social groups (where intra-specific niche segregation may result from the different motion capacities and limitations of age-classes or morphologies) to multi-species assemblages that move together temporarily (i.e., heterospecific aggregations with similar motion capacity and overlap in ecological landscapes). We argue that OMT could provide a fruitful and versatile framework for understanding the benefits accrued from social sampling more completely, as well as for investigating the ecological causes and consequences of movement. Perhaps the greatest challenge will be to adjust our analyses to this way of thinking (Box 3). This will require data collection that captures variation in energy availability, analytical assessment of options available to animals at decision points (as some studies are beginning to explore, e.g., [15,53,54,74]), and the mathematical development of OMT within movement ecology [20].

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Box 3. Recording the social sampling of physical energy and efficiency in movement

Researchers can examine the consequence of social information for movement efficiency by monitoring the movements and **performance** of individuals that occupy the same space simultaneously, and/or by presenting cues to individuals in experimental set-ups. Analogous to the well-established playback experiments for the study of auditory signalling, unmanned autonomous vehicles, robots, or virtual reality can be used to create cues for high-quality physical energy patches where there are none (e.g., [67,68]). This can be paired with monitoring techniques that record an animal's perception of their environment (e.g., gaze direction [69,70] or exposure to sound cues [71]) as well as their movement outputs. Should studies find that social sampling allows animals to make more efficient movement decisions than uninformed individuals, we can quantify the adaptive value of social sampling of the physical energy landscape at an individual level. For example, in soaring flight, the speed at which birds glide from one updraft to another is a measure of efficiency, and individuals should only increase their speed when they are certain about the availability of the next updraft [72]. Monitoring glide speeds when presented with these false cues may reveal the energy benefit of social sampling [25,73].

Outstanding questions

Do individuals consider the motion capacity of a demonstrator in social sampling of physical energy? Skill or motion capacity may be reflected in the movement itself (e.g., erratic locomotion or caution in movement), and will differ depending on the experience and morphology of the demonstrator, respectively. This may result in intra-specific niche segregation and mean that heterospecifics can also provide relevant information about the physical energy landscape.

Does inter-individual distance in cohesively moving aggregations reflect the ephemerality of physical energy?

How do social information and movement energetics factor into the ability of a species to respond to environmental change?

In the OMT framework, does the expectation in the distribution of energy manifest in a spatial map?

What is the relative importance of social cues for energy availability over the prior expectation of an individual where there may be conflict between information types?

Do animals in highly fluctuating environments have greater cognitive ability to recognise cues in locomotion?

Can social sampling of physical energy provide a mechanism for the development of movement performance in naïve individuals?

What traits evolve to facilitate and enhance social sampling? This would likely be towards increased information broadcasting, such as the evolution of distinct physical features (e.g., plumage countershading) or increased sensory acuity to recognise detail in locomotion.

Is information broadcasting also be available to predators? Cues in locomotion that highlight where the movement of prey is obstructed or aided by physical energy are likely to increase or decrease the chances of successful predation, respectively.

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Declaration of interests

The authors declare no conflicts of interest.

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