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Review

Environmental Predictability as a Cause and Consequence of Animal Movement

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The impacts of environmental predictability on the ecology and evolution of animal movement have been the subject of vigorous speculation for several decades. Recently, the swell of new biologging technologies has further stimulated their investigation. This advancing research frontier, however, still lacks conceptual unification and has so far focused little on converse effects. Populations of moving animals have ubiquitous effects on processes such as nutrient cycling and seed dispersal and may therefore shape patterns of environmental predictability. Here, we synthesise the main strands of the literature on the feedbacks between environmental predictability and animal movement and discuss how they may react to anthropogenic disruption, leading to unexpected threats for wildlife and the environment.

Highlights

Environmental predictability acts as a selective pressure on animal cognition and behaviour.

Together, animals' cognition, movement abilities, and environmental predictability interactively determine the emergence of movement patterns.

Conversely, animal movement can impact environmental predictability. This could create ecoevolutionary feedback loops, which are still very little studied.

Human activities can impact environmental predictability and therefore animal movement and wildlife populations' viability.

The study of the environmental predictability–animal movement interface has recently benefited from the improvement of tracking and remote sensing technologies but is lacking unification. Here we propose a unified view of this critical interface.

The Complex Link between Environmental Predictability and Animal Movement

Deciphering the cues and rules that animals use for their relocation decisions is one of the major goals of movement ecology [1,2]. Some environmental characteristics, such as seasonality, can render the environment predictable to animals with the appropriate cognitive skills or **engrained behaviour** (see Glossary). **Environmental predictability** enables animals to reduce the uncertainty of the environmental conditions they experience. It thus acts as a selective pressure favouring the evolution of engrained behaviour or cognitive skills such as spatial memory (Box 1) [3,4]. Awareness of these important evolutionary impacts, combined with the ongoing revolution in biologging and remote sensing technologies, have inspired a fast-growing literature on the movement patterns that emerge from presumed cognitive adaptations to environmental predictability (e.g., [1]). The opening of these new research frontiers is understandably inundated with diverse definitions of environmental predictability that are, as yet, only rarely quantified from data (e.g., [5,6], but see [7–9]). This sparsity of conceptual agreement and methodological tools has limited the thorough investigation of hypotheses on the **proximate** and **ultimate drivers of animal movement**.

Conversely, the potential impacts of moving animals on environmental patterns have received little attention despite their postulated consequences for many ecological processes, such as biodiversity dynamics [10], disease transmission [11], ecosystem functioning [12–14], and animal [15] or plant [16] population dynamics. In principle, a two-way link between animal movement and the environment could lead to the existence of feedback loops that either amplify the predictability of the overall system (a mechanism of **niche construction**, as suggested for some seed-dispersing primates [17]) or dissipate it.

Parallel to these considerations are concerns about rapid but little-understood anthropogenic disruptions to environmental rhythms and movement patterns. For example, supplementary feeding, which artificially increases environmental predictability, could favour the aggregation of individuals and thus facilitate disease transmission [18]. Conversely, human activities in some cases disrupt predictable environmental dynamics. For example, the spatially uneven rate of climate change across the globe could lead to different rates of warming in the breeding grounds compared with the wintering grounds of migrant birds, disrupting their **migration** [19].

To advance our knowledge of the proximate and ultimate drivers of animal movement, and to anticipate threats to the viability of animal species, we need a theory of predictability in movement ecology. Here, we synthesise the literature into a general definition, a typology, and a set of methodologies for quantifying environmental predictability, taking into account its scale dependency (Box 2). We then review the movement-related adaptations to environmental predictability and the methods

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Box 1. Engrained Behaviour or Cognition?

The environmental conditions and resources used by animals are thought to explain the evolution of movement behaviours and cognitive abilities observed in the wild [3,4]. However, the balance between engrained behaviours (i.e., behaviours genetically encoded or fixed by learning during early stages of behavioural development) and cognitively flexible responses depends on environmental predictability.

Animals generally combine different types of behaviours (engrained and cognitively flexible), but schematically we expect that genetically engrained behaviours develop as adaptations to environments or environmental features that are highly predictable over several generations (see top-right corner of Figure 1 in main text; [3]). For example, the timing and direction of migration is, in many species, at least partly engrained [42]. Other species are predisposed to follow an environmental gradient while migrating [34]. The engrained tendency of an individual to stay in its natal population (i.e., to not disperse and be philopatric) is also expected to be positively correlated with environmental predictability [82].

Conversely, cognitive abilities allow behavioural flexibility but are costly [3]. In environments with a relatively high level of predictability, individual learning and memory can be advantageous (see Figure 1 in main text; [3]). They are widespread in the animal kingdom and their variation between species is thought to relate to environmental conditions [1,3,4,83]. For example, memory retention is expected to be favoured in more stable (i.e., more predictable) environments [83]. Even in environments where learning and memory are advantageous, some characteristics of memory can be engrained and preadapted to the highly predictable characteristics of the environments the individuals typically use. For example, the time for which captive-reared honeyeaters avoid rewarding places is adapted to the replenishment rate of the flowers they exploit in the wild [62]. However, more research is necessary to understand the specific aspects of spatial memory that are engrained or flexible depending on environmental conditions [83]. This investigation could however be complicated by the fact that recursion times finely tuned to resource renewal times can emerge from simple trial-and-error processes [55].

As environmental predictability decreases, foraging individuals are expected to increase their use of social information compared with personal memory, to improve their access to more ephemeral information (see Figure 1 in main text; [48,84]). Finally, in highly unpredictable environments, individuals are expected to use engrained behaviour because the cost of evolving the appropriate information-gathering abilities would be too high (see bottom-left corner of Figure 1 in main text; [82]).

designed to detect and characterise them, we outline recent ideas on the feedbacks between animal movement and environmental predictability, and we speculate on how human activities might alter patterns of wildlife movement by affecting environmental predictability (Box 3).

Defining Environmental Predictability for Movement Ecology

Environmental predictability, as a source of information for moving animals, is a central concept in movement ecology. However, most papers do not explicitly define or measure it (e.g., [5,6,20]) or do so as a function of the variance of an environmental variable or the degree to which it is periodic [7,8]. Most movement ecology studies thus do not refer to a common definition. However, many ecology studies (e.g., [21]) and several movement ecology papers [9,22,23] refer to Colwell's pioneering work [24] on this topic. Colwell defined two components of predictability for temporal periodic phenomena: **constancy** and **contingency** on time (i.e., regularity of temporal cycling). With this decomposition, maximum predictability is reached when the environmental variable – for example, food availability within a resource **patch** – is either constant or perfectly periodic in time (i.e., contingent on time).

However, other kinds of environmental predictability, pertaining to nonperiodic phenomena or spatial patterns, exist and can impact animal movement (see the next section). Moreover, environmental predictability depends on the spatiotemporal scale considered (Box 2), and we generally expect that different types and degrees of environmental predictability, occurring at different spatiotemporal scales, select for different cognitive abilities and in turn lead to the emergence of different movement patterns (see Boxes 1 and 2 and the next sections). In the context of movement ecology, to enable comparison of the environmental conditions experienced by different animals and the study

Glossary

Area-restricted search (ARS): the intensification of searching, through a decrease in movement speed or an increase in movement sinuosity.
Constancy: the converse of variability – an environmental variable is increasingly constant as its variability decreases.
Contingency: the degree to which an environmental variable depends (in the statistical sense of auto- or cross-correlation) on itself or another variable.
Dispersal: the movement by which an animal permanently leaves its natal or breeding area before establishing elsewhere.
Engrained behaviour: a lifelong-fixed behaviour, genetically encoded or fixed by learning during early stages of behavioural development.
Environmental predictability: the value of an environmental variable (e.g., the abundance of a resource) is increasingly predictable at a given spatiotemporal scale if it is characterised by lower variability or higher correlation with itself or another environmental variable, measured at the given spatiotemporal scale.
Home range: the stable area routinely used by an animal to meet its daily needs, typically smaller than expected from its movement capacities alone.
Information entropy: a measure of the mean degree of uncertainty in a variable Y defined as: $H(Y) = -\sum_{i=1}^{n} P(Y_i)\log[P(Y_i)]$, where $P(Y_i)$ is the relative frequency of the value Y_i out of the n values that Y can take.
Masting: the synchronous flowering or fructification of numerous plant individuals of the same or different species, which increases pollination efficiency or satiates seed predators.
Migration: the seasonal movement of an animal between spatially separated ranges.
Mutual information: a measure of the mutual dependence (in the statistical sense) between two variables. It quantifies the average amount of information that observing one variable provides about the other.
Niche construction: the process by which an animal modifies its

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Box 2. The Scale of Environmental Predictability

Most environments display multiscale organisation in space and time [85]. As a response, movement generally comprises scale-dependent processes, between which animals shift [69]. Environmental patterns at different scales can differ in terms of predictability. For example, in marine environments as exploited by seabirds, mesoscale habitat features (e.g., shelf edges) show high levels of predictability, whereas fine-scale features (e.g., fish swarms) are comparatively less predictable [26,35]. Animals thus adopt multimode movement strategies; for example, by using spatial memory to relocate predictable habitat features or patches and thereby establish a home range in a predictable landscape [7,55] and ARS to search for prey items within resource patches [69]. Many species thus display hierarchical movement behaviour [81,86–89]. Therefore, the definition of environmental predictability, in the context of movement ecology, must be scale dependent: different predictability levels at different scales lead to different behavioural adaptations and movement patterns. The scale dependency of environmental predictability has been highlighted in other ecology subfields (e.g., anticipatory parental effects [36]).

of environmental predictability as a driver of animal movement, environmental predictability must therefore be defined for a given environmental variable and for a given spatiotemporal scale. This definition may be expressed in terms of spatiotemporal variability (i.e., constancy) and auto- or cross-correlation (i.e., contingency):

the value of an environmental variable (e.g., the abundance of a resource) is increasingly predictable at a given spatiotemporal scale if it is characterised by lower variability or higher correlation with itself or another environmental variable, measured at the given spatiotemporal scale.

The spatiotemporal scale should be chosen depending on the type of animal and movement considered. For example, when comparing the environmental predictability experienced by individuals over their **home range**, the spatial distance considered should approximate the diameter of their home range, whereas the temporal interval considered should approximate the average usage duration of a home range (i.e., the lifespan of the individual for a lifelong home range or a season for a seasonal home range).

Characterising and Quantifying Environmental Predictability for Moving Animals

We adapt Colwell's [24] typology of predictability to movement ecology by also considering predictability in space and by distinguishing different kinds of contingencies (i.e., on absolute spatiotemporal position, on relative time position, and on other environmental variables). We build on the existing literature to give, for each of the predictability types we describe, operational definitions and methods, along with examples of environmental features known or suspected to be used as information sources by moving animals. As Colwell did for temporally periodic phenomena [24], we suggest that **information entropy**, created by Shannon [25] to measure the mean degree of uncertainty in a variable, could be a central concept for the study of environmental predictability in movement ecology. In Figure 1, we provide a representation of the two orthogonal axes of predictability and the corresponding presumed behavioural adaptations (detailed in Box 1) in the different regions of the constancy–contingency plane. In Table 1, we provide examples of environmental features for each of the predictability types, and we relate them to the movement patterns that can emerge from their use by animals.

Constancy

For moving organisms, constancy in time concerns fixed, nondepletable (or immediately renewable), and nonmoving resources like permanent water holes, but also resources concentrated into patches that deplete little (e.g., mesoscale marine features concentrating a higher density of fish [26], grass in forest meadows [27]). Similarly, perfect spatial constancy corresponds to a spatially homogeneous environment, which is likely to be rare at the scale of real animals' lifetime movements because movement is an adaptation to spatiotemporal environmental heterogeneity [6,28].

environment in a way that is beneficial to itself.
Nomadism: the movement type by which the individual irregularly moves and does not stabilise inside a restricted area.
Patch: a traversable area over which resource density is higher than in the surrounding matrix.
Proximate driver of movement: an immediate driver of movement; for example, a physiological constraint or the specific environmental conditions an animal encounters while moving.
Recursion: the return of an individual to a previously visited area.
Routine movement behaviour: the repetition of movement sequences between different recursion sites.
Temporal periodicity: the regular cycling across time of an environmental variable.
Time–place learning: the capacity to relate the presence of food at a location with a precise time of day.
Traplining: the repeated use of a single movement circuit, typically starting and ending at a central location.

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Box 3. The Human Impacts on Environmental Predictability and Their Animal Movement Consequences

The very rapid and heavy anthropogenic changes that ecosystems are currently undergoing have consequences for animal movement [90]. Human-induced increases in environmental predictability could constitute an ecological trap if, for example, animals are more attracted to predictable resources and thus use suboptimal habitats [91]. Many seabirds alter their movements to exploit fishery discards [92] and landfills [93]. The year-round availability of food in landfills has led to the loss of migratory behaviour in some species [94]. The availability of human-derived foods in cities has also led to the modification of the movement behaviour of many animals, such as chacma baboons (*Papio ursinus*) [95] and black bears (*Ursus americanus*) [96]. Agriculture also provides highly abundant and predictable food resources, thus modifying the foraging behaviour of many animals and leading to human–wildlife conflicts [97]. Finally, several studies have revealed weekly periodic patterns in wild animals' movements, suggesting an impact of human activities [30,66].

Some human alterations to environmental predictability are initially intended to help wildlife. Supplementary feeding, a common management measure targeting animals thought to be limited by food, increases environmental predictability but could create dependency on humans [5]. This can percolate to nontarget species; for example, supplementary feeding of wild ungulates impacts the movements of brown bears (*Ursus arctos*) [98]. Beyond the possible detrimental effects of an increase in environmental predictability due to human activities, the fact that it leads to more predictable movement could be used to inform management measures. For example, supplementary feeding can divert avian scavengers from the consumption of poisoned carcasses [18] and could be used to reduce traffic collisions with wild ungulates by leading them away from roads [99].

In some cases, human activities disrupt a predictable environmental pattern or dynamic. Our knowledge of how this impacts animal movement, however, remains limited. For example, the spatially uneven rate of climate warming across the globe is thought to disrupt bird migrations if they experience a greater rate of warming in their breeding than their wintering grounds [19]. **Masting** is being impacted by climate change in a way that is still little understood [41]. As synchronous fruiting is used by some animals to better time their recursions to specific plants [67], this could deprive individuals of a valuable information source. Finally, light pollution alters diurnal cycles in many places in the world [21], thereby disrupting the movements of many species [100,101].

For a discrete random variable Y, constancy can be quantified as [24]: $C = 1 - H(Y)/\log(s)$, where s is the number of observed values of the variable and $H(Y)$ is its information entropy [25]. Y can represent any kind of temporally or spatially varying environmental variable, broken down into classes. This measure of constancy has already been used in several movement ecology studies to quantify interannual variability of normalised difference vegetation index (NDVI) [9,23]. In landscape ecology, researchers use the information entropy of land-cover type over a landscape, which they call compositional entropy, as a measure of its compositional complexity [29]. Despite its different name, this is the same measure of constancy in space. Alternatively, the inverse of the standard deviation of the environmental variable could be used as a measure of its constancy.

Contingency

Here, contingency represents the degree to which an environmental variable is determined (in the statistical sense of auto- or cross-correlation) by itself or another variable. For example, fruit availability on a tree is autocorrelated across years because it depends on the tree's intrinsic productivity and is also contingent on the time of year (i.e., the season) and on temperature, solar radiation, and rainfall. As an extension of Colwell's definition [24], contingency can thus generally be measured by the **mutual information** of the environmental variable and absolute spatiotemporal position, relative temporal position, or another environmental variable.

Contingency on Absolute Spatiotemporal Position

Temporal periodicity is a central characteristic of ecosystems worldwide [21]. The best-known example of environmental cycling is seasonality, but periodic environmental variations can also be daily or follow the lunar cycle [30]. A classic tool to characterise periodic temporal dynamics is autocorrelation [31]. However, as mentioned above, contingency can also be measured as the mutual

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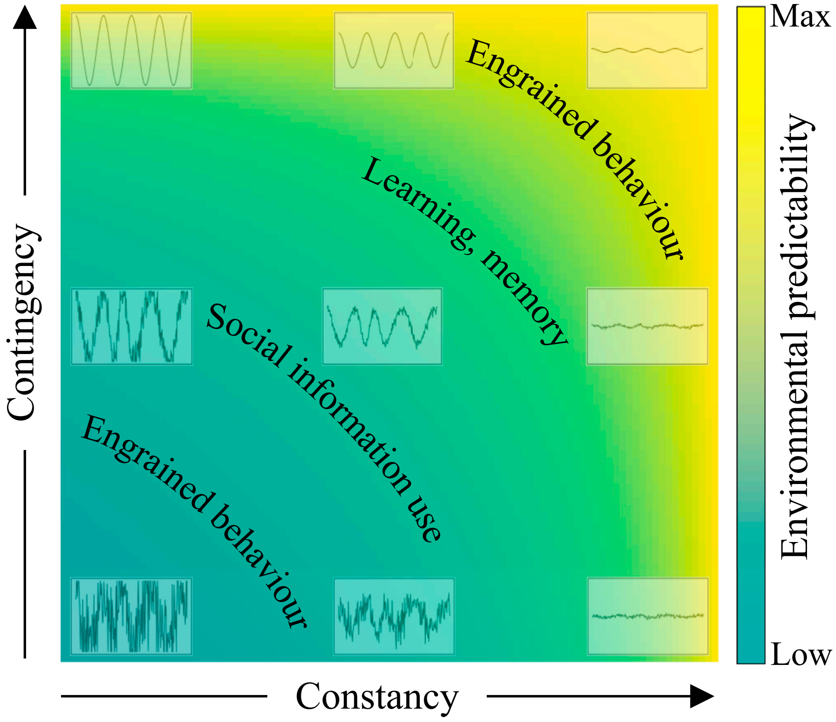

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Figure 1. The Behavioural Adaptations to the Two Orthogonal Axes of Environmental Predictability
Environmental predictability can be decomposed into two elementary components: constancy [i.e., the converse of variability (in space or time)] and contingency (i.e., the degree of dependency of the environmental variable on the absolute spatiotemporal position, the relative temporal position, or another environmental variable). Maximum predictability is reached with perfect constancy or contingency. The subplots represent examples, for a variable varying in time or 1D space (x-axes of the subplots), of different levels of constancy and contingency. For very high degrees of environmental predictability at a given scale, engrained behaviour is favoured at that scale. For still relatively high levels of environmental predictability, individual learning and memory are favoured. As environmental predictability diminishes, individuals are expected to rely more on social information use. For very low levels of environmental predictability, it is not physically possible to develop the cognitive capacities that could extract relevant information from the environmental pattern, and engrained behaviour is, once again, favoured. Examples of environmental features with high constancy and contingency include permanent water sources (constancy in time) whose small variations are highly seasonal (contingency on time). High constancy and low contingency occurs, for example, in quasihomogeneous resource patches (constancy in space) whose small spatial heterogeneities are randomly spaced (low contingency on absolute space). Seasonal fructification exemplifies low constancy and high contingency, whereas extreme climatic events (e.g., hurricanes) demonstrate low constancy and contingency.

information of the environmental variable and the explanatory variable (e.g., here, time) [24]. Some recent movement ecology studies have used this method to measure the contingency of NDVI on time and thus seasonality [9,22,23]. Alternatively, spectral analysis enables the determination of multiple frequencies that together best explain a time series [31,32], while wavelet analysis specifies whether the contributions of these periodicities change with time [21]. Finally, normalised spectral entropy quantifies the strength of periodicity of a time series by applying the entropy measure to the spectral density distribution [33]. It has been extensively used in landscape ecology [33] but not, as yet, in movement ecology.

The spatial organisation of environmental heterogeneity (i.e., its spatial contingency) can also constitute an important source of information for moving animals. In some cases, spatial heterogeneity is

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Elementary dimension of environmental predictability	Subdimension of environmental predictability		Expected emergent movement patterns
	Type	Examples	
Constancy	In time	Permanent water hole, nest location, patch that depletes little (e.g., marine mesoscale habitat feature)	Recursions
	In space (converse of spatial heterogeneity)	Quasihomogeneous environment (over a given area; e.g., a forest meadow from an ungulate's perspective)	Random movement in this area (if there is no resource depletion) or self-avoiding movement (if there is resource depletion)
Contingency	On absolute spatiotemporal position	Seasonal flowering or budding	Migration
		Day/night predation risk cycles	Periodic movement recursions
		Gradient of plant phenology	Gradient-following migration
		Environmental patchiness	ARS, aggregation of within-home-range space use
	On relative temporal position	Grass regrowth, nectar replenishment, environmental parasite life duration, prey vigilance decrease, etc.	Timing of recursions matches the delay of resource replenishment or risk decay
	On another environmental variable	Synchronised fructification	Matching timing of recursions
		Link between rainfall and parasite life duration	Recursions triggered by secondary environmental variable

Table 1. Examples of Environmental Features Corresponding to the Different Kinds of Environmental Predictability, Along with the Movement Patterns That Are Expected to Emerge from Their Use

manifested along a gradient (e.g., of plant phenology [34]). Moreover, many natural environments are patchy. The scale and regularity of patchiness can be determined by plotting spatial autocorrelograms (which represent the spatial correlation coefficients for each distance class): the distance at which the autocorrelation is no longer significant corresponds to the spatial scale of patchiness [35,36].

Contingency on Relative Temporal Position

Many resources renew after depletion: nectar replenishes, grass and leaves regrow, new prey arrive in the area, or prey vigilance decreases (implying a renewal process for prey catchability, beyond prey abundance [37]). Likewise, many risk factors decrease after having reached a maximum: parasite larvae in the environment die or predators leave the area. If the rates of resource renewal and of risk decay vary little, both resources and risks can be predictable to a focal animal [37]. These rates – for example, the growth rates of vegetation and the survival time of parasite larvae – may be amenable to direct observation. However, to our knowledge, resource renewal rates are very rarely directly measured in movement ecology studies, except in experimental setups where they are usually artificially fixed [38] (but see [39]).

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Contingency on Another Environmental Variable (Cross-Correlation)

Some environmental variables are cross-correlated. For example, some trees fructify synchronously [40]. This synchronisation can even occur between trees of multiple species [41]. Spring onset timings can be correlated between consecutive stopovers along migration routes [42]. In some cases, causal relationships between different environmental variables, such as between temperature and solar radiation and tree fructification [43] and between rainfall and environmental parasitic load [44], could be used by animals to inform their movement decisions.

The Movement Patterns Emerging from the Use of Environmental Predictability

Cognitive abilities are not directly observable in the wild [3,4], but the use of environmental predictability by animals may be inferred from emergent movement patterns [1,45]. **Nomadism** is expected to emerge in response to unpredictable resources [20,46]. By contrast, below, we review the main types of movement that are likely to rely on environmental predictability. We outline how each of these movement types is expected to emerge from the use of different types of environmental predictability (Table 1) and we discuss the behavioural mechanisms likely to underly them (Box 1).

At large spatiotemporal scales, as a response to spatially heterogeneous and seasonal resource availability (i.e., contingency of food availability on absolute spatiotemporal position), many species migrate [8,34,47]. Migration may be genetically engrained but may also rely on a combination of individual memory or social information use [34,42,48–50]. In some cases, animals use the correlation of the spring onset timings between places to better time their migration [42] (i.e., contingency of spring onset timing in one place on spring onset timing in another). Migration is thus a major movement adaptation to large-scale environmental predictable (periodic) variations and as such has received theoretical, empirical, and methodological attention [48,51,52].

At a within-resource-patch scale, as a response to environmental patchiness (i.e., the contingency of resource availability on absolute spatial position), many animals use **area-restricted search (ARS)** (also called 'intensive search') by adopting a more tortuous path or reducing speed when entering a profitable area [53]. One can compare the size of resource patches and the size of ARS zones [54]. However, this has as yet very rarely been done.

At a between-resource-patch scale, many animals use spatial memory and display recursive movement patterns [1,37] (Box 1). **Recursions** are a behavioural response to environmental patchiness (i.e., the contingency of resource availability on absolute spatial position) combined with high degrees of temporal predictability of within-patch resource availability [45]. At a larger spatial scale, memory use can lead animals to display **routine movement behaviour** [45,55] or **traplining** in its most stereotyped form [56]. We might expect that the degree of routine movement should be correlated with the degree of environmental predictability, but this has not yet been investigated [45]. In addition, the use of inadvertently shared social information in conjunction with memory can lead to the sharing of movement routines between several individuals [57].

When resource availability within patches varies in time, animals should benefit from timing their recursions in accordance with the resources' dynamics. **Time–place learning** has been observed in many animals (as a response to contingency on absolute temporal position [58–60]). Moreover, many animals avoid locations where they have depleted the resources and adapt the timing of their recursions to the renewal dynamics of the resources (i.e., as a response to contingency on relative temporal position [61–63]). In other species, the recursion delay is sufficiently long for parasite larvae deposited in the environment to die, but the empirical tests of this are still scarce [44,64]. Fourier and wavelet analyses are increasingly used in movement ecology, especially to relate the observed significant periods of recursion to those of environmental drivers, such as day/night and lunar cycles [30,64–66]. We suggest that the strength of periodicity in movement recursions could also be quantified using spectral entropy [33] and quantitatively compared with the strength of periodicity in environmental variables. Finally, some animals also use correlations between variables to time their movement recursions, but this has been only marginally studied so far. For example, grey-cheeked mangabeys

(*Lophocebus albigena johnstonii*) take into account weather [43] and the synchronisation of fruiting between trees [67] to infer the likely fruiting timing of some tree species.

Many vertebrates develop a home range [68]. Animals are expected to develop one in environments that vary little at a large spatial scale (i.e., with relatively high constancy: large-scale spatial variability is expected to lead to nomadism or migration [7,46]) and whose spatially local temporal variations are predictable (i.e., contingent on absolute or relative time or on another environmental variable [7,55]). It was recently shown that home ranges can emerge from simple memory-based movement in such an environment, even in competitive situations that could be expected to disrupt the intrinsic predictability of the environment [55]. The literature on home ranges is extensive and a comprehensive review of it is beyond the scope of the present paper. For recent discussions and reviews of the determinants of home ranging behaviour and of the methodologies to characterise it see e.g. [68,69]. An empirical study confirmed on four species of ungulates that individuals living in the most predictable environments display home ranges, whereas those living in the most unpredictable environments are nomadic [7]. This type of study could be expanded in the future on more species, using our typology of environmental predictability (see Outstanding Questions).

We can generally expect that the spatial organisation of environmental heterogeneity (i.e., contingency on space) drives an individual's space use. The scale of environmental patchiness can be directly compared with that of individuals' space use by calculating the spatial autocorrelation of space use measures, such as the residence time mapped over the individual's home range [70] (i.e., the Intensity Distribution [71]). For example, Fauchald *et al.* [35] performed cross-correlation analyses between the spatial distribution of murres (*Uria* spp.) and their prey and showed that they overlap at large and medium scales.

Therefore, theoretical and empirical studies have proved useful for testing hypotheses on how environmental predictability drives animal movement patterns. However, we still lack a full characterisation of the empirical correlations between environmental predictability and animal movement patterns at various scales and a full theoretical knowledge of the mechanistic links that are likely to exist between environmental predictability, cognition, and animal movement.

The Effects of Animal Movement on Environmental Predictability

Intuitively, we might expect that the use of resources by an animal could interfere with underlying environmental patterns and dynamics and hence decrease environmental predictability for all animals using these resources. For example, the presence of competitors in the environment could reduce the predictability of patch renewal dynamics (i.e., its contingency on time since last visit) [55]. However, emergent properties of memory-based movement can overturn this intuition; for example, by leading to spontaneous segregation between individuals [15,55]. This emphasises the need to consider the two-way interactions between entire populations of moving animals and environmental predictability.

Conversely, in many cases, moving animals increase environmental predictability in a way that can be perceived not only by themselves but also by other animals. Depending on the temporal scale at which the environmental predictability increases, it can impact directly the moving individuals during their lifetime or conspecifics later. For example, seed dispersal by animals performing recursive movement can lead to the spatial structuring of plant populations and increase their contingency on space [72,73]. Depending on the relative durations of the animals' lifetime and the plants' life cycle, it will be directly experienced by these animals during their lifetime or by others later. In both cases, this can lead to niche construction whereby this further increases the individuals' foraging efficiency [17]. Routine movement can also generate, via trampling, physical trail networks that structure the landscape, increasing its spatial predictability, and that can then be used by other animals and limit their cognitive load of decision making [74]. Mammalian grazers promote nutrient cycling and create areas of higher vegetation productivity and of high spatiotemporal constancy that benefit all grazers [75]. Overall, we can thus expect these feedbacks to amplify predictability in the whole

Outstanding Questions

On the impacts of environmental predictability on animal movement:

- To what extent is the hypothesis of a positive correlation between environmental predictability and the degree of routine movement met in real systems?
- What kind of environmental predictability (constancy or contingency on absolute spatiotemporal position, relative temporal position, or another environmental variable) is most influential on movement routines and the use of spatial memory?
- Can we develop more empirical studies that compare the environmental predictability and movement patterns of animals in different environments or of the same population before and after an environmental change?
- Can we design mechanistic theoretical studies to compare the movement patterns emerging from different environmental conditions and cognitive abilities?

On the impacts of animal movement on environmental predictability:

- Can we design mechanistic theoretical studies to explicitly investigate the effects that animal movement can have on the environment?
- Could experimental studies be performed to test the effects of animal movement on environmental predictability in controlled settings?
- For the understanding of which environmental dynamics and patterns is the explicit modelling of individuals' information usage necessary?

On the feedback loop between animal movement and environmental predictability:

- Are the feedbacks between environmental predictability

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system. Competition between animals for resources could impede this amplification, but we still lack knowledge of the relative strengths of these effects. We can also expect that the modification of environmental predictability by moving animals could consequently modify the selective pressures acting on their own movement behaviour. This would create ecoevolutionary feedback loops [76] involving animal movement, but the operation of such mechanisms has rarely been investigated outside the setting of **dispersive** movements [77].

In all of the above examples, animals increase the predictability of their own environment and consequently that of their conspecifics. In many other cases, a moving animal increases the predictability of the environment of other species. For example, migrations lead to periodic environmental dynamics (i.e., contingent on time) that are beneficial to many resident species [13]: the yearly Serengeti migration leads to a periodic influx of nutrients in the Mara river [14], as do fish spawning migrations in many riverine ecosystems [78]. Some ungulates, when feeding on aquatic plants, release pulses of nutrients by bioturbation [79]. If these individuals use space periodically, we can expect these pulses to be themselves predictable (highly contingent on time), but to our knowledge this has not yet been investigated.

Concluding Remarks and Future Directions

Here, we posit that environmental predictability is a major ecological and evolutionary driver of animal cognition and movement: different levels and types of environmental predictability acting at different scales drive the evolution of different cognitive abilities and the emergence of different movement patterns. In return, animal movement has non-negligible impacts on environmental predictability. Our review also maps the hypotheses that still need to be theoretically and empirically tested (see Outstanding Questions). The thorough investigation of these two-way interactions is hindered by a lack of a shared definition and typology of the concept of environmental predictability. Here, we have attempted a more formal framing of environmental predictability in the context of movement ecology. Moreover, we suggest that the study of the interface between environmental predictability and animal movement has a bearing not only on fundamental research questions, such as the evolution of spatial memory and the ecoevolutionary feedbacks between animal movement and environmental predictability, but also on the practicalities of wildlife management and conservation (Box 3).

Movement ecology is seeing ever-more-detailed movement data, but these are rarely combined with time series of detailed environmental data [80]. We suggest that advancing our knowledge of the feedbacks between environmental predictability and animal movement now necessitates the concurrent analysis of environmental and movement data [9,80,81]. Remotely sensed data should be especially useful in that regard [80], but we also need more field-based measurements of environmental data, in particular of resource renewal rates. To disentangle the direction of the feedbacks between animal movement and environmental predictability, we also need to develop three complementary lines of research: theoretical, empirical, and experimental.

and animal movement strong in both directions?

- What are the effects of population size on the interactions between environmental predictability and animals' movements?
- Under what conditions do the feedbacks between environmental predictability and animal movement lead to the stabilisation (or destabilisation) of the overall predictability of the system?
- What insights would theoretical studies provide on the ecoevolutionary feedback loops between environmental predictability and animal movement?
- In which contexts are the two-way feedbacks between environmental predictability and animal movement non-negligible for our understanding of the overall system?
- Could mechanistic models of the interactions of animal movement and environment predictability help to better predict the impacts of anthropogenic disruptions? How can we statistically fit such models to real data?

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