

Opinion

Information Ecology: an integrative framework for studying animal behavior

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Information is simultaneously a valuable resource for animals and a tractable variable for researchers. We propose the name Information Ecology to describe research focused on how individual animals use information to enhance fitness. An explicit focus on information in animal behavior is far from novel – we simply build on these ideas and promote a unified approach to how and why animals use information. The value of information to animals favors the theoretically rich adaptive approach of field-based research. Simultaneously, our ability to manipulate information lends itself to the strong methods of laboratory-based research. Information Ecology asks three questions: What information is available? How is it used (or not)? And, why is it used (or not)?

The importance of information

Information (see [Glossary](#)) reduces uncertainty about a highly variable world. It is a fundamental element of life that, when detected and used by organisms, can improve the match between phenotype and environment. Information is particularly relevant for animal behavior; organisms can rapidly adjust their behavior in response to new information, and they can preserve and use this information at later timepoints through memory, developmental plasticity, epigenetic changes, or genetic adaptation. Almost 20 years ago, Dall and colleagues [1] set the stage for a Bayesian approach to animal decisions, with the idea that information is a valuable resource that can be studied like any ecological resource. As one of the first to focus on information in animal behavior, they highlighted the mechanics of decision theory and the specific types of information that exist. Although the publication by Dall and colleagues has been cited nearly 1400 times, we hope to extend this reach even further to those studying information in a less explicit way.

Here, we advance an approachable, information-focused, research framework ([Figure 1](#)) to unite ongoing information research taking place at different physical and temporal scales. Like the old parable of the six blind men describing an elephant (each touching only one body part), we illustrate the entire ‘information elephant’ so that researchers can identify how their particular focus connects to the complete flow of information from an animal’s environment to their decision. We propose the term Information Ecology as a discipline united by a set of theoretical goals and methodological approaches for studying how animals use information in an ecologically relevant way. This framework asks three broad questions: What information is available? How is it used (or not)? And, why is it used (or not)?

Information frameworks are not new to biology. An information theoretic approach started with Weismann’s discovery that germ cells contain information that is transmitted from parents to offspring [2], and an information framework continues to drive theory in molecular, developmental, and neurobiology [3]. However, with the notable exception of animal communication [4–8], an information framework as applied more broadly to animal behavior only gained traction in the past

Highlights

The life sciences are often divided along physical and temporal scales from molecules and milliseconds to ecosystems and millennia.

Information crosses biological scales; it is in the environment, is processed internally, and is used in decisions with broad impacts. Following the flow of information naturally bridges disciplines.

Information is increasingly an explicit focus of research in ecology and evolution; this drives laboratory research to strengthen ecological context and field research to strengthen causal mechanisms.

We propose the name Information Ecology for the emerging field of research that asks: What information is available to animals? How is it used? And, why is it used?

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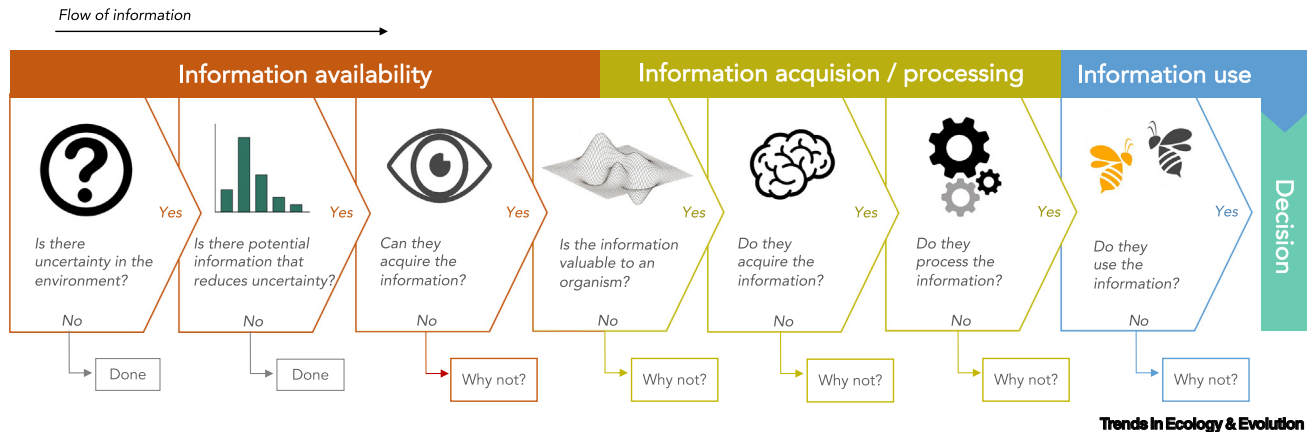


Figure 1. Flowchart for Information Ecology. Information ecology examines information availability (orange), information acquisition and processing (yellow), and information use (blue) to arrive at a particular decision (green). Information Ecology seeks to integrate the flow of inquiry across fields by pushing researchers to map the information landscape and identify the information sources available and their value, and to ask ‘why not?’ when faced with a ‘no’ answer at each stage of inquiry. Moving from left to right, the flow of information moves from the environment (orange), to the organism (yellow), and back to the environment where decisions have ecological consequences (blue/green).

two decades [1]. We build on this traction here. We do not introduce new ideas on how animal behavior research should incorporate information theory; all ideas reviewed here have been proposed by others. Rather, we seek to (i) unite under a common name all research that uses information to study animal behavior, (ii) describe how Information Ecology relates to research in other ‘animal behavior’ fields (specifically, Behavioral Neuroscience, Behavioral Ecology, and Evolutionary Ecology), and (iii) illustrate how an Information Ecology approach can be applied, specifically seeking to disrupt the traditional boundaries for each field by borrowing the theory and/or methods of the other.

Why focus on information?

Anything that reduces uncertainty (i.e., improves predictions) contains information. Information is created and stored in the ecosystem, in physiological systems, in the brain, and in the genome. That such disparate but fundamental biological systems are united by information underscores the importance of acquiring, processing, and using information for living systems [9,10]. Information shares many features with traditional resources (such as food [11] and mating partners [12]) in that it can be costly to obtain, and once obtained it can be hoarded [13] or shared [14]. However, information also has a number of unique features that make it unlike traditional resources; it can be invented [15], replicated [16], manipulated [17], and eavesdropped upon [18–20]. These features make information an extremely dynamic resource that can be difficult, but not impossible, to track. Critically, by using information to anticipate the likely environment they will face, animals can produce a more-effective response (i.e., an informed phenotype). Thus, information – as a resource – is valuable, and this opens it up to the rich theory that applies to other valuable resources.

Simultaneously, information – as a variable – is tractable. Similar to other abstract variables in Behavioral Ecology (e.g., ‘resource holding potential’, ‘cognition’, or ‘attractiveness to mates’), information can be measured and compared (increasingly facilitated by emerging technology [21,22]). Furthermore, we can experimentally add or alter information sources, allowing us to manipulate this variable more easily than many others and facilitating our ability to establish causation. The dual nature of information as valuable (to animals) and tractable (to researchers) makes it an effective research focus for understanding animal behavior. It has recently been argued that the marriage of theory and measurement is critical for successful science [23]. As both a resource and a variable, information

is situated at a scientific ‘sweet spot’ that links the strong theory of Behavioral Ecology (see Theory) with the strong methods of Behavioral Neuroscience (see Approach).

Information flows through each step of the framework, naturally connecting mechanistic studies from the laboratory with adaptive studies from the field (Figure 2). By focusing on information explicitly, the traditional boundaries of fields like Behavioral Ecology and Behavioral Neuroscience are relaxed, pushing researchers in new theoretical, methodological, and taxonomic directions. Insight at one stage guides research at another. Thus, Information Ecology provides a roadmap to the mechanism-function nexus that others have recently highlighted [24,25].

Some researchers are already using (what we see as) an Information Ecology approach with exciting results. In one example from primates, a well-developed understanding of information processing (in this case, color vision) helped researchers test adaptive hypotheses about information use [26,27]. Color vision in capuchin monkeys (*Cebus imitator*) is dimorphic; females have mostly trichromatic vision (like humans) while males are dichromats. As predicted, females are better at detecting ripe fruits based on color information [26]. Males, by contrast, are better at detecting another food source, cryptic insects, suggesting a tradeoff in processing color versus patterns [27]. In another example, a rich ecological understanding of pinyon jays (*Gymnorhinus cyanocephalus*) and scrub jays (*Aphelocoma californica*) helped researchers develop and test hypotheses about information processing. Pinyon jays live in groups with dominance hierarchies; scrub jays do not. Therefore, pinyon jays (and not scrub jays) should be adept at processing social information, specifically by using transitive inference [28]. Testing in the laboratory demonstrated that pinyon jays were better than scrub jays at using transitive inference to learn artificial sequences; moreover, they transferred this processing ability to staged dominance interactions with other birds [29].

In addition to generating new hypotheses, an information perspective encourages methodological integration. For example, in our own research on cognition in wild primates, we have benefited from adopting experimental approaches used in the laboratory. Specifically, we use playback experiments to manipulate the presence or coherence of information, allowing us to ask questions about information use and information processing (e.g., [30,31]). Conversely, mechanistic studies can benefit from the comparative approaches more typical of adaptive research. An example of this can be found in the neurobiology of birdsong learning. In contrast to many model organism approaches that seek to identify the commonalities in brain structures (e.g., across rodents and humans), birdsong work started by focusing on the variation – specifically, variation in the use of auditory information in producing an adult song. There are differences across species, sexes, ages, and seasons in how ‘open’ birds are to auditory information in shaping their own song. This natural variation was crucial for guiding initial investigations of the neurobiology of song-learning as gross differences in brain morphology associated with song-learning helped identify key regions for further exploration [32,33]. Looking ahead, we see many opportunities for using information to connect disparate researchers, approaches, and study systems. We highlight two simple examples in Box 1.

Information can be studied at multiple scales – from neurons to ecosystems (Figure 3). However, Information Ecology is centered around the organism; how organisms acquire, process, and use information to enhance their fitness (i.e., survival, reproductive success) in what falls squarely within the field of Behavioral Ecology. As such, Information Ecology largely subsumes the sub-fields of Sensory Ecology [34,35], Cognitive Ecology [36,37], and Movement Ecology [38,39] offering a larger umbrella term because it considers outcomes beyond ‘movement’ and includes processing beyond ‘cognition’. Although Sensory Ecology focuses on every type of information, it has struggled to incorporate evolutionary outcomes (but see [40]). Although these other

Glossary

Fitness gain: the gain in fitness for making an informed (‘correct’) decision (i.e., produce an informed phenotype) relative to a naive decision and can range from 0 (no impact) to 1 (life saving).

Information: a reduction in uncertainty that can be quantified in a Bayesian sense by comparing a prior knowledge state to a posterior state (sensu [1]). Information Ecology is not tied to any specific measurement but, for simplicity, we can estimate uncertainty in terms of the ‘probability of being wrong’ so that it ranges from 0 to 1. This probability is a product of the state space and previously obtained information. For example, without any prior knowledge, the probability of being wrong is higher for a four-sided dice than a two-sided dice (0.75 vs. 0.50). This uncertainty can be reduced with information (e.g., learning that the dice is weighted to always land on two would bring the uncertainty to 0 in both cases) and the quantity of information is measured as the reduction in uncertainty (0.75 or 0.50). Information ranges from -1 to 1, with negative information indicating a gain in uncertainty.

Information gain: the proportion of potential information that an animal is able to acquire that is specific to particular individuals and circumstances. Information gain accounts for the sensory system of the animal as well as their current knowledge state. Information gain would be 0 in cases where the information is inaccessible or was previously obtained; and would be as high as 1 if the animal is able to gain all the potential information. Information gain can be negative in the case of a well-informed individual who would gain uncertainty from an imperfect information source.

Information landscape: the distribution of information value for a particular individual and time. Peaks represent high-value information sources that would be worth acquiring. A landscape with many peaks represents an information-rich world, while a flat landscape indicates a world relatively devoid of valuable information. Information landscapes can be a useful heuristic for thinking about how and why animals might differ in their information foraging strategies.

Information value: the value of gaining information that varies across individuals

'ecologies' have been extremely successful at focusing research around a central question (sensory systems, cognition, or movement) in ecologically relevant settings, we wish to widen the scope to all types and stages of information use following the flow of information from one end of the flowchart to the other.

The Theory

An organism's information foraging strategy – the time and energy dedicated to gathering information at the expense of other biological processes – should be one that yields a net fitness benefit. Because information is a valuable resource, it has fitness consequences like any other valuable resource. This connects information to the array of rich theories surrounding resource acquisition including cost-benefit analyses and optimal foraging approaches. The costs of acquiring information include energy expenditure [44,45], search time [46], disease exposure [47], as well as the investment in neural or other physiological machinery to acquire and process information (e.g., brain tissue) [48,49]. The benefits of using information include the ability to produce an informed phenotype that allows more efficient behavior (e.g., accessing an otherwise inaccessible nut using a tool). Note that in social animals, the benefits of information can be frequency dependent, either positively (when it is better to have common information for coordination) or negatively (when it is better to have rare information, to avoid competition). Even if the costs and benefits cannot be measured directly, these variables can nevertheless be compared in a relative sense (see 'The Approach' section).

Broad adaptive questions about information use can be found at both ends of the Information Ecology framework (Figure 2). At the 'availability' end (Figure 1, in orange), Information Ecology is focused on the evolution of information foraging strategies: Why do some animals invest more in acquiring information than others? Why is information valuable to some animals but not others? We can then examine why some individuals have the machinery to acquire the information in the environment while others do not. For example, primates are more attuned to visual information [50], while most other mammals are more attuned to chemosensory information [51]. These differences reflect a particular taxon's evolutionary history. Sorting this out requires a comparative approach to understand the historical consequences [52] of information foraging.

Information Ecology can help extend existing theory. For example, consider two alternative ideas about the evolution of cognition and brain size – the social complexity hypothesis [53,54] and the ecological complexity hypothesis [55]. Both posit that some environments are cognitively more challenging than others (with the first focused on social challenges and the second focused on ecological challenges) and, consequently, taxa facing more of these challenges were selected for more-sophisticated cognition to solve them (e.g., [56]). Yet, in more complex social settings, there is more social information available and a greater opportunity to use social information to guide interactions. Similarly, in more complex foraging (or navigation or predation) environments, there is more foraging information available and greater opportunity to gain fitness advantages from the increased calories obtained through informed foraging. Instead of competing hypotheses, both are 'information complexity' hypotheses [57] proposing that certain types of challenges (social or ecological) create information peaks in the landscape that favor the evolution of active information foraging strategies. Posing this as an information problem not only identifies the common ground between these theories but also leads to evolutionary questions about the specific information animals are using and mechanistic questions about how they acquire and process that information.

The Approach

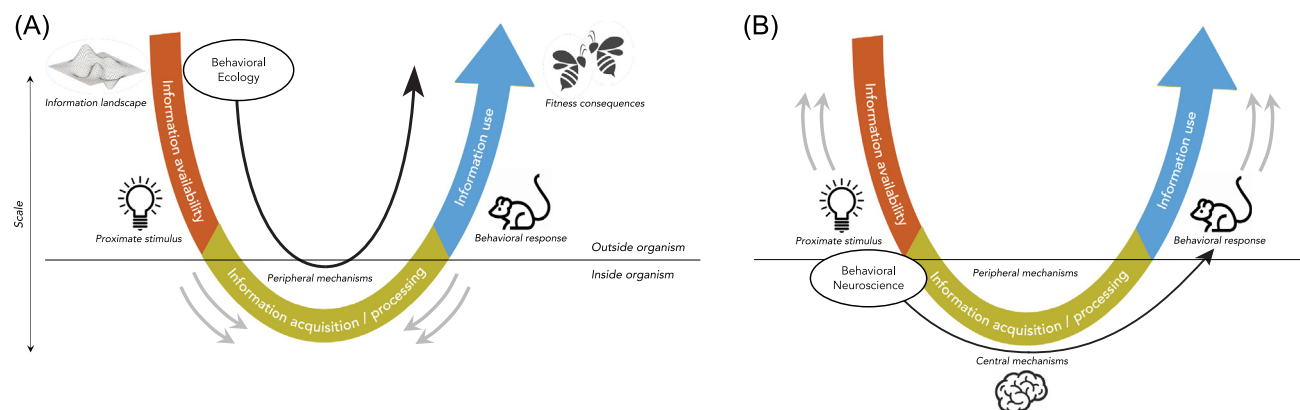
An Information Ecology framework examines how and why some organisms use an information-rich strategy while others use an information-poor one (or, ignore information altogether [58]). This

and circumstances. Values range from -1 to 1 and can be calculated as:

$$\text{Information value} = \frac{\text{Potential information} \times \text{Information gain} \times \text{Fitness gain} - \text{Acquisition costs}}{\text{Acquisition costs}}$$

Costs include search energy and time, opportunity costs, and risks (ranging from 0 to 1). In a comparative context, costs can also include the costs of producing and maintaining the sensory and cognitive machinery necessary for acquiring the information.

Potential information: the change in uncertainty that would come from using a potential information source (sensu [80]). This uncertainty reduction (or gain) is relative to a hypothetical naive individual (with the capability of sensing the information source) and therefore can be calculated by an observer without knowing about any particular individual. Ranges from -1 to 1.



Trends in Ecology & Evolution

Figure 2. Pushing information boundaries. The Information Ecology framework illustrates that different fields of research are addressing similar problems – each focused on different points along the flowchart. (A) Behavioral Ecology emphasizes the broad ends of the flowchart, focusing on the information available in the natural world and the fitness consequences of decisions (black arrow). Although Behavioral Ecology is becoming more experimental and more mechanistic, mechanisms (when considered) tend to be peripheral (not central). This approach will be strengthened by digging deeper into mechanisms of information acquisition and processing (gray arrows). (B) Behavioral Neuroscience emphasizes the mechanics at the smallest scale of the flowchart, focusing on how information is acquired and processed centrally in the brain (black arrow). Behavioral Neuroscience is increasingly including more natural stimuli, adding additional contexts, and expanding to nontraditional organisms to achieve greater ecological validity. This approach will be strengthened further by expanding the breadth of information availability and use to incorporate an adaptive perspective (gray arrows).

requires empirical data on where the information is, how specific information is acquired (e.g., sensory input), how it is processed (e.g., neurobiological mechanisms), and then, critically, how it is used in a natural setting. Furthermore, a ‘failure’ to use information will have different

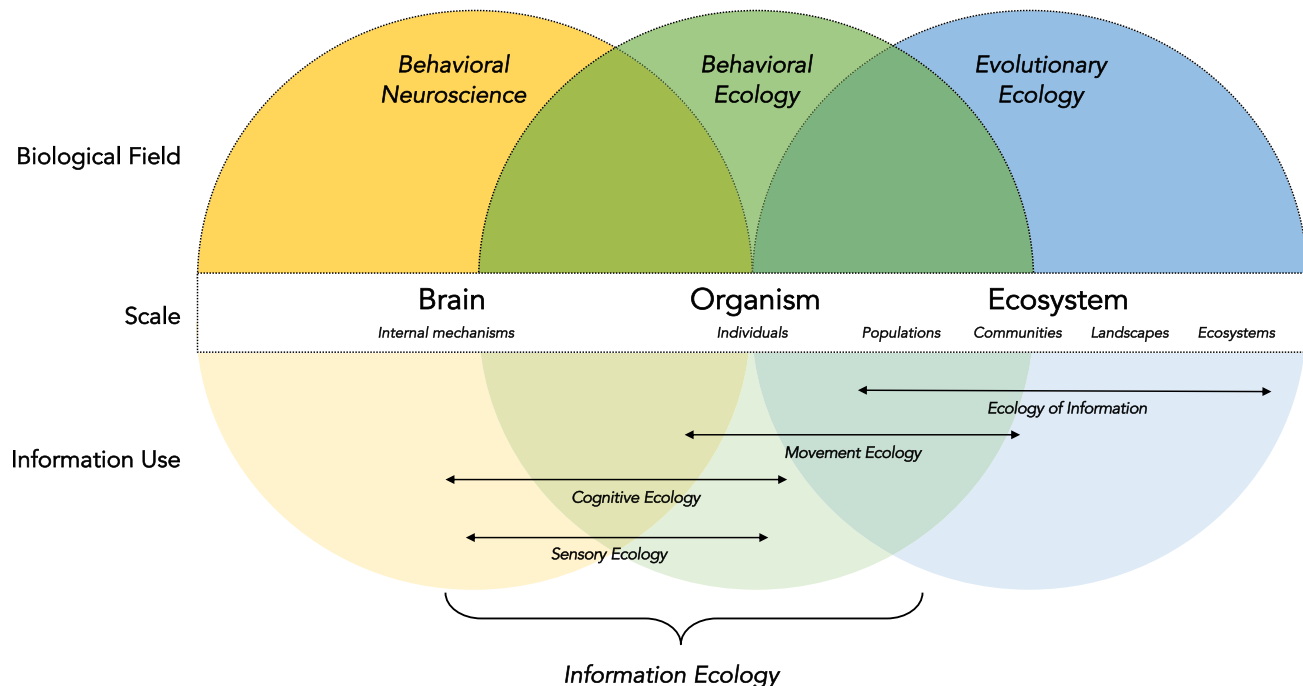
Box 1. Information links adaptive and mechanistic explanations

From Behavioral Neuroscience to Behavioral Ecology: sign- and goal-tracking

Individuals vary in the degree to which reward cues bias choice and control behavior. For example, in a Pavlovian conditioning paradigm developed in laboratory rodents, the appearance of a lever (‘cue’) predicts the delivery of food (‘reward’). One extreme, sign-trackers, attribute incentive motivational value (i.e., incentive salience [74]) to the cue itself; whereas the other extreme, goal-trackers, treat the cue merely as a predictor of the reward [69]. The same information (cue or reward) is perceived differently by different individuals. Importantly, in both rodents and humans, the tendency to sign-track has been associated with deficits in attentional and inhibitory control and a number of other traits reminiscent of psychiatric illness, including addiction and post-traumatic stress disorder [75]. Thus, it is important to understand the adaptive significance of sign-tracking and the factors that may render an individual more likely to exhibit this behavior. Sign-tracking is apparent across several taxa under laboratory conditions (e.g., fish, birds, and humans [71–74]), but individual differences in ecologically relevant settings have not yet been studied. Perhaps a sign-tracker’s attraction to the information source reflects an adaptive information foraging strategy under specific conditions (i.e., scarcity)? An information perspective sets a research agenda for broadening the environmental context for sign- and goal-tracking as well as the taxonomic diversity in which it is exhibited.

From Behavioral Ecology to Behavioral Neuroscience: the Bruce effect

The Bruce effect occurs when a pregnant female spontaneously aborts in response to a novel male [76]. The leading explanation for this phenomenon is that novel males in many species often commit infanticide; thus, females have been selected to terminate costly investment in an otherwise ‘doomed’ pregnancy [77]. As a counterstrategy to infanticide, the Bruce effect is an adaptive response for females [78]. However, consider a similar scenario where a novel male causes pregnant females to abort but not spontaneously. Instead, he induces her abortion through harassment and physical aggression, a process called feticide [79]. Feticide is adaptive for males, but not females. Two seemingly similar phenomena, the Bruce effect and feticide, have opposing adaptive explanations (i.e., one is adaptive for females, the other is not) that can only be distinguished with a mechanistic approach. First, how is the male detected by the reproductive physiology of a female? Is the information acquired through cognition, as in wild primates [78], or chemosensory channels, as in rodents [79]? Does the male activate the female’s hypothalamic-pituitary-adrenal (HPA) axis indicating his presence may be a stressful stimulus or not? An information perspective prompts us to answer questions not just about the novel male (information availability) and the aborted pregnancy (information use), but also about how female physiology responds to the information (information processing).



Trends in Ecology & Evolution

Figure 3. Relationship between Information Ecology and other ‘ecologies’. Information Ecology centers on how organisms use information to enhance fitness. Three other information-based approaches include Sensory Ecology (how organisms use information that they acquire through their unique sensory systems [34,35]), Cognitive Ecology (how organisms navigate their physical and social worlds using cognition [36,37]), and Movement Ecology (how organisms move across the landscape in ecologically relevant ways [38,39]). Information Ecology offers a larger umbrella term for information studies because it includes information not related to ‘movement’ and it emphasizes the entire flow of information rather than focusing on a single step (e.g., acquisition in Sensory Ecology or processing in Cognitive Ecology). Furthermore, by centering on information, Information Ecology highlights the questions (how and why animals use information) and methods (identify and manipulate information sources) that reach across scales. Another term ‘Ecology of Information’ was originally proposed to span scales from brains to ecosystems [41] – encompassing how information affects organismal fitness ‘Information Ecology’ (e.g., [42]), in addition to how information affects the dynamics of populations, communities, landscapes, and ecosystems (e.g., [43]). We divide this span and suggest using ‘Information Ecology’ for organismal-centered work (sensu [1]) and ‘Ecology of Information’ for ecosystem-level phenomena (as the name and description of the field suggest [41,43]).

interpretations depending on which step the failure occurred (e.g., whether the information was unavailable vs. whether it was available, but not acquired).

Information availability

Although information is pervasive, it is not universal. The entry point for Information Ecology is to have uncertainty, a necessary precondition [1,59] for the existence of **potential information** [1] (Figure 1). But, uncertainty alone does not guarantee an information source can reduce that uncertainty (e.g., anticipating a natural disaster). Information Ecology is focused on when information can reduce uncertainty in the external world. A key point is that potential information exists in the world whether or not an organism detects it (e.g., color information is still available even if the animal of interest is color blind). There are a number of competing ideas about how to measure and classify uncertainty and information, but this discussion is beyond the scope of this overview (but covered in [1,41,60,61]). For our purposes, it is sufficient to recognize that potential information exists in the external environment, we can measure it, and it can have value to organisms. This information can derive from the habitat, other animals, or an interaction between these two. Animals can even produce information by their own actions [20,62]. Mapping information availability requires that we know the habitat and social world better than the study subjects

with the caveat that we are restricted to the realm of information that we can access through our own senses and technology (as in UV light). We may be entirely unaware of the information sources that are available to other organisms [63]. Fortunately, technology is making information mapping much easier, particularly with respect to remote habitat and animal monitoring (in addition to direct observation) through remote sensing [64–66], often facilitated by artificial intelligence (AI) and machine-learning [21,22].

Animals do not (and cannot) use all the potential information they encounter. A taxon's evolutionary history may constrain their ability to detect or process the information. Or, the information may be accessible but have little relevance to a particular individual's behavior. **Information gain** quantifies how much of the potential information a particular individual is able to acquire, while **information value** incorporates the **fitness gain** that an individual would get from using the information to adjust their behavior [59,60,67]. Information value is highly variable and context dependent [68]; thus, the distribution of valuable information can be envisioned as an **information landscape** [69]. For social animals, some of the most valuable information comes through communication. Communication and information are inextricably linked as communication by definition is the transfer of information [70] (although see [71]).

To illustrate the application of these concepts, consider a hypothetical group of monkeys moving through the forest trying to avoid predators. If they have little information about where predators are, their prior uncertainty is high (~ 1). If a member of the group sees a leopard and produces an alarm call, other members now have low uncertainty about the location of a predator. Their posterior uncertainty is close to 0 (but not actually 0, because alarm calls are not perfectly reliable). We can estimate the drop in uncertainty, the potential information, to be ~ 0.9 . We are often interested in relative amounts of information, so estimates can suffice.

Estimating information value involves the perceptual capacities and opportunities plus the knowledge states of particular individuals to first estimate information gain. Many gain the entirety of the potential information (change from naive to knowledgeable, information gain = 1). For an individual that had already spotted the predator, the information gain is ~ 0 (because their uncertainty was already 0). For a deaf individual, the information gain is also 0. The fitness gain also varies – for an individual being stalked by the predator able to make a narrow escape, the fitness gain is essentially 1, that is, life-saving. For an individual safe in the trees, the fitness gain is close to 0. Fitness gain can vary in other ways – an injured animal might gain more from early evasive action than a healthy one. The information is acquired passively so the marginal cost of acquiring this particular piece of information is close to 0. Therefore, the potential information is 0.9 for everyone, but the information value of the alarm call ranges from 0 to 0.9 for different members of the group.

Critically, using simple estimates of each component of information value based on detectable features of the world (e.g., proximity to a predator), we can make directionally accurate estimates of how information value varies. Thus, we can generate and test predictions about who should (and should not) attend to information sources. We can rely on strategies that Behavioral Ecologists have developed for dealing with probabilistic and variable phenomena (like fitness or sociality); start with simple categorical comparisons (using average or maximum values) where consistent differences in information value are likely and move to more detailed measurements and complex comparisons as areas for further exploration are revealed.

Information acquisition and processing

Assuming information exists, an organism next needs to acquire and process it. This is the primary focus for Behavioral Neuroscientists investigating sensation, perception, attention, and

cognition. Information acquisition can happen along any of the sensory modalities (e.g., olfactory, visual, auditory, tactile, taste). Furthermore, animals can acquire information actively or passively and through either individual exploration (personal information) or they can get it from others (social information) [62,72]. And, this information can be acquired and/or embedded across different timescales (e.g., seconds to millenia). However, animals may not acquire all (or any) of the available information, possibly because the information is (i) outside their sensory abilities, (ii) they fail to encounter it, (iii) they have already acquired it, or (iv) the information is not valuable enough to warrant sufficient attention. Information Ecology considers each of these possibilities in asking why animals do and do not acquire information.

To measure the acquisition and processing of information, we need to record internal states, which is most achievable in the controlled laboratory settings of Behavioral Neuroscience. Innovative technology and semi-invasive methods are helping field studies to record internal processes with increasing precision, while preserving naturalistic behavior in field settings. Combined with experimental approaches in the wild (e.g., by adding an information source), the field studies of Behavioral Ecology are increasingly able to identify where the information flow breaks down [31]. However, field studies still have a long way to go toward understanding the neurobiology that underpins many of the behaviors we observe.

Information use

Finally, we want to know if animals use this information to achieve an informed phenotype that is more fit than an uninformed one. This process involves ‘decisions’ that are often cognitive but can also be noncognitive (e.g., reflexive, affective, developmental, or genetic). Documenting information use can be as simple as comparing phenotypes/behaviors in informed versus uninformed settings. But this is just the first step into the blue arrow (Figure 2A). Perhaps the most interesting aspect of information use is identifying any fitness consequences of those decisions. Therefore, we need to link the behavioral response to fitness outcomes – how does it impact survival and reproduction? This can only be done in the wild, and combining captive and wild studies on the same (or similar) species can be particularly valuable, as different settings are better suited to address different stages of the information system (i.e., processing and acquisition in captivity, use and fitness consequences in the wild) [73].

Concluding remarks

The explicit focus on information in animal studies is growing rapidly, making this a perfect time to propose a research agenda that tracks the flow of information in animals. This is facilitated by technological and methodological advances that make it easier to document and manipulate the information landscape. By bridging mechanistic questions focused on causation (typically tackled in captivity) with functional questions focused on fitness consequences (typically tackled in the wild), Information Ecology regains the ‘missing middle’ of organismal biology. It integrates diverse research under one umbrella to build a stronger and more efficient investigation of behavior. As we grow these links, we can begin to answer entirely new questions (see Outstanding questions).

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Declaration of interests

No interests are declared.

Outstanding questions

Are there efficiency gains for more active information foragers? That is, does investing in one type of information processing reduce the cost of processing other information, thereby creating information generalists? Some species appear to favor information solutions and such efficiency gains could be a reason why.

How can the revolution in machine-learning and AI be harnessed to understand information foraging? AI allows us to map the information landscape in unprecedented new ways. This strengthens our ability to test hypotheses about information foraging strategies across animals.

What are the precise costs of information foraging? Better estimates of these costs will give us more predictive power.

Morphological specializations can constrain flexibility and evolvability, but do we see similar consequences of neurobiological specialization for information processing? Can the neurobiology of information processing restrict the generalizability and evolvability of information use?

How often do animals ‘fail’ to use available information? Are they failing to use information due to some sensory constraint? Or, due to the adaptive avoidance of high-cost/low-benefit information? More evidence of absence is needed.

How many ways are there to solve the same information processing problem? Can convergent information use in two species have similar neurobiological underpinnings? A broader comparative understanding of information processing would be helpful.

How did humans become the ultimate ‘information foragers’? More comparative work is needed to better understand why some species more than others have become active information foragers.

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