

Why study cognition in the wild (and how to test it)?

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Abstract

An animal's behavior is affected by its cognitive abilities, which are, in turn, a consequence of the environment in which an animal has evolved and developed. Although behavioral ecologists have been studying animals in their natural environment for several decades, over much the same period animal cognition has been studied almost exclusively in the laboratory. Traditionally, the study of animal cognition has been based on well-established paradigms used to investigate well-defined cognitive processes. This allows identification of what animals can do, but may not, however, always reflect what animals actually do in the wild. As both ecologists and some psychologists increasingly try to explain behaviors observable only in wild animals, we review the different motivations and methodologies used to study cognition in the wild and identify some of the challenges that accompany the combination of a naturalistic approach together with typical psychological testing paradigms. We think that studying animal cognition in the wild is likely to be most productive when the questions addressed correspond to the species' ecology and when laboratory cognitive tests are appropriately adapted for use in the field. Furthermore, recent methodological and technological advances will likely allow significant expansion of the species and questions that can be addressed in the wild.

The natural habitat of an animal contains many potential sources of useful information. For a male rufous hummingbird *Selasphorus rufus* spending his breeding season in the Canadian Rocky Mountains, for example, each flower in his territory has a particular appearance, occupies a unique spatial location, contains a certain volume and concentration of nectar, and having been emptied, takes a specific length of time to refill. Considering the high metabolism of hummingbirds, as well as the pressing concerns of attracting a mate and defending his territory from rivals, we might expect that the hummingbird would take advantage of this environmental information in order to forage efficiently. The issue is how one might test the types of information hummingbirds acquire, and how they use them, during foraging.

Historically, addressing questions about the kinds of information animals in the wild can acquire and how they might use them has typically involved bringing the species of interest out of the wild and into the traditional home of experimental psychology, the laboratory (Balda & Kamil, 2006; Brodbeck, 1994; Chappell & Kacelnik, 2004; Pravosudov & Roth II, 2013). The study of cognition in the wild was, then, predominantly restricted to observational studies where cognitive abilities were attributed to an animal based on interpretations of that animal's behavior (Allen & Bekoff, 1999; Byrne & Bates, 2011; Byrne & Whiten, 1989).

Recently, however, questions as to the evolution and ecological role of cognition have come to the forefront of behavioral ecology, as behavioral ecologists seek to understand the evolution of the mechanisms underpinning behavior, in particular the evolution of cognitive abilities (e.g. Morand-Ferron, Cole, & Quinn, 2015; Rowe & Healy, 2014; Smith, Phillips & Reichard, 2015; Thornton & Lukas, 2012). However, rather than taking ecologically interesting animals into the laboratory, there is an

increasing focus on taking the experimental study of animal cognition out into the field to test cognition in its natural habitat.

The prospects for experimentally studying animal cognition in the field look better than ever before. Over 30 years of research in behavioral ecology has led to a vast literature on the flexibility of the behavior of animals in the wild, as well as the roles that using information could play in adaptive behavior. Additionally, after 4 decades, comparative cognition research in the laboratory has given us a firm grounding in the cognitive mechanisms that can underlie animal behavior. This strong grounding in these two research traditions provides an ideal foundation for researchers to investigate the role of cognition in the lives of wild animals.

Researchers from a range of fields are motivated to study cognition in the wild for a number of reasons; so, here, we discuss why researchers already working on cognition in the wild may choose to work outside of the laboratory and how to test hypotheses in the wild experimentally. Much of our discussion is directed to our own interests in the spatial and temporal cognition of wild hummingbirds, and lessons we have learned; however, a great deal of what we cover will be relevant to researchers addressing a broad range of species and other cognitive abilities.

Working in an animal's natural environment forces researchers to deal with ecological and logistic challenges rarely faced by researchers in the laboratory. Through the choice of a useful study species, ecologically-inspired experiments plus new technological advances, however, it is increasingly possible to probe the cognition of an ever-expanding range of wild animals.

Why study cognition in the wild?

This question is as broad as the question of why one should study animal cognition at all. The benefits and challenges of working in the field, however, lend themselves to asking certain questions rather more readily than others. In this section, we describe some of the various reasons why scientists choose to work in the field, both in terms of the aims of their research programmes, but also in terms of the practical benefits of working outside of the laboratory.

The Ecological Approach

Research programmes within the Ecological Approach involve the testing of hypotheses that concern how natural selection might have shaped animal cognition.

Cognitive Ecology

During the 1980s and 1990s, the intersection of behavioral ecology and experimental psychology led to the new field of cognitive ecology (Dukas 1998; Dukas & Ratcliffe, 2009; Healy & Braithwaite 2000; see also the synthetic approach/cognitive ethology as used by Kamil 1998) as researchers began to base their hypotheses on the natural history of different species to test predictions about the cognitive abilities of those animals. This approach is perhaps best encapsulated by the work on spatial memory in food-storing and non-food-storing birds, where knowledge about the natural history of different species led to *a priori* predictions about how the ability of those birds to remember locations should vary, predictions that were largely supported (e.g., Biegler, McGregor, Krebs, & Healy, 2001; Hampton, Shettleworth, & Westwood, 1998; McGregor & Healy, 1999).

Although that work was located in the laboratory, ecologically-based questions have also been addressed in the field. For example, a long-running study of

hummingbird cognition in the wild has tested a range of *a priori* predictions about the information to which hummingbirds “should” pay attention to in order to forage effectively (Healy & Hurly 2013). Using field experiments that create a simplified version of their natural environment, it is possible to investigate whether hummingbirds can pay attention to various types of information present in the environment, as well as the kinds of information they preferentially use during foraging. One of the challenges of the cognitive ecology research programme, however, is to objectively identify *a priori* predictions about types of information to which animals “should” pay attention. With some knowledge of an animal’s natural history, it may seem straightforward to generate predictions as to why animals should value certain cues over others. For example, because the color and morphology of hummingbird-pollinated flowers have evolved in response to hummingbird foraging (Temeles, Pan, Brennan & Horwitt, 2000), one might expect that hummingbirds pay considerable attention to flower color when they first approach a flower (e.g. Grant, 1966). And, yet, in field experiments where hummingbirds are trained to visit a flower of a particular color in a particular location, when spatial and color cues are dissociated, hummingbirds consistently choose flowers in the “correct” spatial location over flowers of the “correct” color (Hurly & Healy, 2002; Hurly & Healy, 1996; Tello-Ramos, Hurly, & Healy, 2014).

Similarly, captive and wild nectivorous bats trained to feed from echoacoustically distinctive flowers also preferred to use spatial cues rather than the flowers’ unique acoustic shape when returning to feed at a rewarded flower (Thiele & Winter, 2005). As many flowers may look similar but each sits in a unique location, a possible post-hoc explanation for the preference of spatial rather than feature cues (e.g. color, shape) is not difficult. The previous examples however, serve to illustrate that

formulating *a priori* predictions about information use based on ecology and natural history can be less than straightforward.

Behavioral Ecology

An alternative ecological approach to studying the evolution of cognition involves attempts to assess the value of a cognitive ability in terms of its impact on survival and reproductive success, with the prediction that “better” cognition should lead to increased fitness. This link between fitness and cognition had previously been largely assumed, as researchers sought to understand the cognitive mechanisms underlying behaviors that contributed to fitness, such as foraging (e.g., Bateson, 2002; Brunner, Kacelnik, & Gibbon 1992), mate choice (e.g., Bateson, 1978; ten Cate, Verzijden, & Etman, 2006), and communication (e.g., Marler, 1997; ten Cate & Rowe, 2007).

Recently, however, interest has begun to include the direct investigation of the fitness consequences of cognition, inspired by the success of the work on the evolution of learning in *Drosophila*, in which flies respond to artificial selection on their associative learning abilities (e.g., Mery & Kawecki, 2003, 2005). Unlike the cognitive ecology focus on the ability of animals to learn particular ecologically relevant information, this more recent interest has tended to be directed towards “general” cognitive ability, typically assessed using one or more “problem-solving” tasks.

One commonly-used example is the “lid-flipping” task often presented to birds as a novel or innovative foraging task (e.g., Boogert, Giraldeau, & Lefebvre, 2008; Bateson & Matheson 2007; Liker & Bokony 2009). In this task, the bird must learn to remove a cover from a well containing food, where learning ability or innovativeness is typically assessed by the number of trials that a bird takes to learn to remove the lids

(see Griffin & Guez, 2014 for a recent review). Variation in an animal's performance across one or more of these generic tasks is used as a proxy for variation in this cognitive trait, allowing for the identification of correlations between "cognitive ability" and various aspects of life history (Morand-Ferron, Cole, & Quinn, 2015; Quinn, Cole, & Morand-Ferron, 2014; Thornton, Isden, & Madden, 2014).

Although some of these research programmes have involved tests of the cognitive abilities of wild animals brought into the laboratory (e.g. Cole et al. 2012), problem-solving tests are increasingly being presented to animals in the wild (Isden, Panayi, Dingle, & Madden, 2013; Keagy, Savard, & Borgia, 2009; Morand-Ferron & Quinn, 2011; Morand-Ferron, Cole, Rawles, & Quinn, 2011). For example, male bowerbirds can be induced to solve batteries of problem-solving tasks, and their performance can be compared to their mating success (Isden et al., 2013; Keagy et al., 2009).

The Anthropocentric Approach

A large body of research addressed at investigating such aspects of cognition as social cognition, numerosity, and causal understanding in wild animals is based less on the ecology of a particular species and rather more on a search for human-like cognitive processes in non-human animals (e.g. Taylor, Hunt, Medina, & Gray, 2009; Mayer et al. 2014; Smet & Byrne, 2013). This research is usually characterized by an interest in "complex" cognition, generally defined with relation to human cognitive abilities, and the degree to which such abilities are present in other species. Much of this work is aimed at the identification of possible selection pressures that led to the evolution of human intelligence (Maclean et al. 2012) through the description of the cognitive abilities of species that are closely related to humans, or that share some biological or

ecological characteristic with humans, such as a relatively large brain or a fission-fusion social structure.

Practical benefits to working in the wild

To date, of course, most studies of animal cognition have been conducted in the laboratory, and for good reason. The malleable environment of the laboratory allows the precise control over information available to animals during training and testing, while control over the husbandry of laboratory animals, including training regimes and diet, allows some degree of control over the motivation and previous experience of experimental subjects. As nearly all of this control is difficult if not impossible to achieve in the experimental study of animal cognition in the wild, this can be a major downside to attempting to investigate animal cognition in the wild. That said, there are ways in which this apparent cost to working with wild animals in their natural habitat may be mitigated.

Access to “natural” subjects and behaviors

Perhaps the first of these, and one that motivates many keen to investigate the evolution of cognition, is that by working with animals in the wild, one can potentially access a much wider range of study species than just those suited to the laboratory. Additionally, this might mean gaining access to investigating the mechanisms that underlie “natural” behaviors, which are not easily produced or tested in the laboratory.

In some cases, the behavior of interest is carried out on a scale that excludes it from being studied in any real way in the confines of the laboratory environment. For example, determining whether avian migrants truly know the location of their wintering grounds, rather than just the distance and direction to fly in order to reach them, relies

on experiments carried out on a grand scale impossible in the laboratory (Perdeck, 1958; Thorup et al., 2006).

Similarly, the homing flights of pigeons are impressive because of the distances involved. Pigeons released in unfamiliar territory, many kilometres from their home loft, can reliably find their way home using multiple sources of information from their surroundings to fix their position and chart a homeward trajectory (Wallraff, 2005).

Although the small-scale spatial cognition of pigeons can be investigated successfully in the laboratory (Cheng, Spetch, Kelly, & Bingman, 2006), such data do not confirm how it is that pigeons manage to home successfully over longer distances. Only by studying the behavior of pigeons navigating home from unfamiliar locations have researchers made significant headway in understanding what environmental information the pigeons use.

Discoveries such as the role of the sun compass, the use of magnetic and olfactory information (Wallraff, 2004; Wiltschko & Wiltschko, 2009), and the possible use of different mechanisms inside and outside the familiar area (Guilford & Biro, 2014), have all relied on pigeons having access to real-world environments, and may never have been discovered if the study of pigeon navigation had been restricted to the scale of a laboratory testing room. Not only is the experimental study of homing pigeons travelling through their natural environment a successful example of studying animal cognition in the wild, it is a system that has also allowed a rare opportunity to investigate the neurobiology of navigation over larger scales by studying the effects of hippocampal lesions, often studied in small laboratory environments, on the large scale navigation of homing pigeons (e.g., Bingman et al., 2005).

One key feature of the laboratory species commonly used to investigate animal cognition, such as pigeons, rats, and zebra finches, is their ability to thrive in captivity.

Pigeons and rats in the laboratory can also readily be trained to search for food or to modify their behavior to gain reward, e.g., through pressing levers (e.g., Adams & Dickinson, 1980) or pecking at lights (Brown & Jenkins, 1968), while zebra finches readily sing, choose mates, and build nests, allowing access to the cognitive abilities that underlie these behaviors (e.g., Bailey et al. 2014; Muth & Healy, 2014).

Should one want to investigate the cognitive abilities of a non-typical species, then one has first to consider the logistical implications of appropriate housing and welfare, before considering whether that species can then either perform the relevant behavior or be capable of being trained to do so. Food-storing birds, especially the tits and chickadees, have proved to be a very successful example of wild animals that do well (although they do not reproduce) once in the laboratory. They also both store food readily and can be trained to perform a variety of rewarded tasks (e.g., Healy 1995; McGregor & Healy 1999; Pravosudov & Roth II 2013). For many species, the housing issue alone is sufficient to exclude laboratory testing, whereas for others the question itself is more appropriately addressed in the field.

Access to “natural” environments

The information available to an animal in the wild is very different from the information available to an animal in the laboratory. In some respects, this may seem to be obvious. What may be less obvious is that the difference in information between the laboratory and the wild can be qualitative as well as quantitative.

Typically, differences between the laboratory and the wild are discussed in quantitative terms: the laboratory is barren or sparse, whereas the field has more confounded variables. The implication is that there is more information available to the animal in the wild, more potentially confounded cues, which make understanding how

animals use a particular source of information more challenging. Even critiques of the laboratory environment rely on this logic, arguing that the lack of information makes the laboratory somehow unnatural, which then limits its value for testing ecologically relevant cognition (e.g., Jacobs & Menzel 2014).

What may be less often appreciated, however, is that the environment of the laboratory can structure the kinds of information that animals acquire. Take, for example, the use of local and global cues in a spatial cognition task. An animal trained in the laboratory to search for a hidden piece of food near a landmark (a local cue) learns that information in a very specific wider environment. Often animals are tested in a relatively small test room or maze, rarely more than a few metres across, and almost always delimited by walls or other distinct boundaries that can provide “global” information. This global information can affect how the animal uses the landmark to remember the food’s location. For example, as a single landmark by itself can provide distance and not direction information, global cues, such as the size and shape of the room, can be used to provide the direction information necessary for the landmark to reliably indicate the location of the reward.

If an animal’s ability to use a landmark depends on the available global information, and global information differs between different environments, then the environment in which an animal is trained could shape how that animal uses a landmark. Obviously the lab and the field are very different environments, but even within the laboratory, differences in rooms or mazes could result in animals acquiring different information. The available global information could depend, for example, on the size of the testing area: both redbellied splitfin fish *Xenotoca eiseni* and chicks will use the geometry of an enclosure to orient themselves, but both species appear to weight this geometric information more heavily in smaller enclosures than in larger enclosures

(Chiandetti et al., 2007; Sovrano et al., 2005, 2007). If landmark use does depend on global cues as well as local cues, then this effect of enclosure size could result in animals in larger enclosures using different information when they search for a reward relative to a landmark than does an animal that searches for reward in smaller enclosures.

The influence of the properties of the test environment on shaping how animals use landmarks has implications for what studies in the laboratory tell us about animals in the outside world. For example, if landmark-use experiments were to be conducted in the wild, the global information available to the wild animal, and as a result the information it learns about the rewarded location, could be very different from that learned by an animal trained to do a similar task in the laboratory. The “wild” is large, open and predominantly wall free. And, although insurmountable boundaries such as cliffs and rivers may be present, free-living, wild animals are very rarely enclosed in a small space by such boundaries. As a result, as an animal in the wild moves through its environment, its perception of its surroundings is likely to be very different from that of an animal moving around in a small walled room.

For laboratory-tested animal, features such as boundaries and the shape of the environment are likely to be more salient. And, when landmarks are moved between trials, the apparent changes in the global information in the laboratory may appear more severe than if landmarks were to be moved an equivalent distance in the wild (Pritchard, Hurly, & Healy, 2015). Rather than acting as a neutral background against which stimuli can be precisely controlled, the environment of the laboratory can, thus, play an active role in the kinds of information that animals learn. This might suggest that researchers testing animals solely in the laboratory would also have an interest in the outcome of analogous experiments conducted on free-living animals.

The difference between the laboratory environment and the natural conditions under which an animal usually learns about its environment is not just physical. Social factors can affect what animals in the wild can learn or how they express their learning in behavior. Solitary individuals may be able to readily solve a task or attend to a source of information in the laboratory, but in the wild, an animal's performance may be affected by a number of social factors. Individuals may be distracted by the needs to defend territory, defend mates from competitors, or fend off undesired suitors. Dominant individuals may monopolize access to foraging or mating opportunities, preventing lower ranked individuals from acquiring novel information or using the information that they have acquired (Gajdon, Fijn, & Huber, 2004; Morand-Ferron et al., 2011). What animals can do in the laboratory may be quite different from what they are able to do in the wild.

Stress and motivation

Even if the species of interest could be brought into the laboratory and the scale of the laboratory and the information available to the animals were appropriate for understanding the behavior of interest, the animal itself may still experience the laboratory task very differently than if it were presented with an analogous task in the wild. This is because confining or handling some animals, or presenting them with unfamiliar tasks, can result in those animals becoming stressed (Balcombe, Barnard, & Sandusky, 2004). Such stress may affect the animal's motivation and/or behavior (Baenninger, 1967), preventing it from either learning a task appropriately or not at all (Bowman, 2005). This can then lead to the conclusion that the animal cannot learn information that it actually did learn or to the interpretation that the behavioral response

is a result of impaired cognition, rather than that the impairment is due to a stress response.

For example, male rats *Rattus norvegicus* outperform female rats in spatial tests when tested in the Morris water maze. The acute stress of performing the task, however, can result in females being much more thigmotactic (swimming close to the maze wall) than males (Harris, D'Eath, & Healy, 2008). Although this can look like a sex difference in spatial cognition (the time taken to find the hidden platform), once the time spent in thigmotaxis is removed, males and females take just as long to swim to the platform, thus demonstrating they have learned its location equally well.

Of course, animals in the wild are by no means free of stress. Indeed, avoiding predators and having to find sufficient food to avoid starvation are significant stressors. However, as animals tested in the wild are not confined during training or testing and can disengage with the experiment when they choose, if they do engage, then the experimenter can assume they are motivated to do so. Their performance even under conditions of daily life stressors may better reflect their true capacities under natural conditions than those of animals tested in the laboratory, while also avoiding the development of behavioral artefacts such as stereotypical flight patterns or obsessive biting or licking (Mason, 1991).

Laboratory conditions, on the other hand, might lead to confined animals being more motivated or habituated to solve cognitive tasks than wild animals. For example, captive kea *Nestor notabilis* learned how to lift a tube more readily than did kea in the wild (Gajdon, Fijn & Huber, 2004). Wild spotted hyenas *Crocuta crocuta*, too, were less successful at approaching and solving a novel task than were captive hyenas (Benson-Amram, Weldele, & Holekamp, 2013). The possible difficulties in directly comparing data collected in the laboratory with data collected in the wild were seen

when the performance of the same great tits tested in similar tasks in the laboratory and then in the wild were not correlated (Morand-Ferron et al., 2011).

Testing cognition in the wild

Testing animal cognition outside the laboratory affects the kinds of questions that researchers can ask and how they are able to ask them. There are two major types of questions typically addressed concerning animal cognition in the wild: those that concern what an animal can learn and those that concern what an animal has learned.

What can animals in the wild learn?

Questions that address what an animal can learn usually involve measuring the performance of an animal on an experimental task in which the use of a particular cognitive ability is deemed necessary for success; if an animal performs the task, then the animal is considered to possess that cognitive ability. Such an approach is often employed in problem-solving tasks, in which animals learn to acquire a reward through performing a novel action or series of actions. These “problems” can be easily modified in form to suit the manipulative skills of the species of interest (e.g., lids that can be prised off using a bill, a nose, teeth, and so on) and the use of this kind of task has led to demonstrations of problem-solving abilities from a wide range of species (Griffin & Guez, 2014).

However, as problem solving tasks are usually concerned with motor learning, the nature of any information that the animals have acquired about the task is rarely investigated. Instead, researchers more often focus on the role that manipulative skill, persistence, and inhibition play in success (e.g., Benson-Amram & Holekamp, 2012; Griffin & Guez, 2014; Griffin, Diquelou, & Perea, 2014), investigating why individuals

vary in their ability to solve a task rather than analysing the information that the animals have acquired about the task itself (Thornton & Lucas, 2012).

The cognitive ecological approach, in which researchers test *a priori* predictions about cognitive ability based on species' ecologies, has also been used to determine what animals can learn. For example, arrays of artificial flowers presented in birds' territories with specific delays before each flower is refilled have been used to show that rufous hummingbirds can learn which flowers refill after 10 and which refill after 20 min: birds return to the 10-min flowers after 10-15 min and to the 20-min flowers after 20-25 min (Henderson et al., 2006). Rufous hummingbirds will also learn to visit particular patches at the times of day when the artificial flowers in those patches contain reward (Figure 1; Tello-Ramos, Hurly, Higgott, & Healy, 2015). Although, as in problem-solving tasks, birds can "succeed" or "fail" depending on whether they visit the rewarded flowers or not, the pattern of the birds' successes and failures demonstrated one of the kinds of information to which these birds can pay attention during foraging, in this case, intervals of time (also see Fetterman & Killeen, 1995 for a laboratory analogue of this time-place foraging task).

What have wild animals learned?

One of the challenges to asking what animals can learn is that researchers might make assumptions about the cognitive mechanisms necessary to solve a particular task (Sulikowski & Burke, 2015). Although a task might be designed to test a particular cognitive ability, such as episodic-like memory or spatial memory, the cues that animals actually use might not match those assumed by the experimenters. By themselves, tests of whether animals can solve a task actually may tell us very little about the information that the animals use to solve the task.

For example, in the Tello-Ramos et al. (2015) time-place learning experiment, hummingbirds increasingly visited the appropriate patch of flowers for each hour of the 4 hours during which flower patches were available each day (Figure 1; Tello-Ramos, Hurly, Higgott & Healy, 2015). It is not clear, however, how the hummingbirds did this. For example, they might have learned the location of the rewarded patch or the appearance of the rewarded flowers. They may have used interval timing, circadian timing, or have remembered the order in which the patches refilled. To determine which of these possibilities the birds did use and, more generally, to identify what cognitive abilities an animal has used to solve a particular task, other kinds of experiments are required.

One form such an experiment might take is to train an animal to reach a performance criterion and then to present the animal with an unrewarded test trial in which some component of the task has been manipulated. For example, a hummingbird that has been trained to use a pair of landmarks to locate a rewarded flower could use a number of different distance and direction cues from those landmarks to remember the flower's position (Figure 2). By modifying the landmarks and removing the flower, these different cues can be put into conflict and the way in which the hummingbird responds when it searches for the absent flower can be used to determine the cues to which it had attended.

More naturalistic cues, such as those used in playback experiments, may require very little training of an animal, as they have been "trained" by their previous experience during their life. Apparently simple experimental designs can provide insight into what wild animals have learned of their surroundings. Playbacks were used to show, for example, that on return from migration, male hooded warblers *Setophaga citrina* not only recognized the songs of their neighbors, but that they also remembered

the locations of their neighbors' territories, treating the song of a neighbor apparently sung in the "wrong" territory as they would the song of a stranger (Godard, 1991).

Multiple playbacks can also be used to assess whether the information that an animal has learned is the same for different stimuli, using a habituation-dishabituation paradigm. For example, Diana monkeys *Cercopithecus diana Diana*, habituated to the sound of leopard-specific alarm calls through repeated playback, remained habituated when played the sound of a leopard growling, but dishabituated when played the shriek of an eagle, when the monkeys once again responded with an alarm call. A parallel result was found for monkeys that had habituated to eagle-specific alarm calls: they did not respond to the eagle shriek, but dishabituated when played the leopard growl (Zuberbühler, Cheney, & Seyfarth, 1999). This pattern of results strongly suggests that the monkeys associated both the sound of the alarm calls and the predator noises with some internal representation of each predator.

The relevance of ecology

Whether the question is what an animal *can* learn or what it is that it *has* learned, the ease with which these questions can be addressed in the wild may be constrained by the ecology of the species being studied. By taking ecology into account early on, however, researchers can avoid or find ways around such constraints.

Species choice

The ecology of a species is very likely to affect how readily the cognitive abilities used by that species can be studied in the wild, especially in experimental tests of hypotheses about animal cognition (Thornton, 2014). This is much less of an obstacle when using observational methods (Byrne & Bates, 2011). Perhaps frustrating for many

potential researchers of animal cognition in the wild is the multiplicity of reasons why a particular species might be unsuitable.

Ideally, animals suitable for the experimental study of cognition in the wild should be reliable, observable, and amenable. Reliable animals are those that can be found easily on multiple occasions and will perform the behavior of interest sufficiently frequently to allow collection of adequate data. Animals that are rare or perform behaviors that occur sporadically would not be reliable and may be challenging to study in the wild.

Rufous hummingbirds have been a useful example for studying cognition in the wild because they are very reliable. Throughout the breeding season, males are almost always found within their individual feeding territories, which they fiercely defend from rivals (Kodric-Brown & Brown, 1978). As they are highly motivated to find food and typically feed every 10-15 min, it is relatively simple to collect sufficient data even though their breeding season may be as short as 6 weeks.

Observable animals are those that can be identified and whose behaviors can be readily recorded. Identifying and quantifying cognitive abilities depends on recording performance of the same individuals. The ease with which this is done may range from relatively straightforward irrespective of the animal (e.g., recording the sounds an animal makes for addressing questions concerning acoustic communication) or vary in complexity depending on the animal. For example, to investigate the use of landmarks in navigation, one might require sophisticated data-loggers to track the paths of animals across great distances (Guilford et al., 2011) or require little more than a pencil and a notebook (e.g., desert ants; Muller & Wehner, 1988).

Finally, amenable animals are those willing to partake in the relevant field experiments. One stumbling block to working on some species may be the degree to

which the animal displays neophobia when presented with an experimental apparatus. Although neophobia may be fascinating in itself, it can make training animals to interact with apparatus a lengthy and difficult experience. Although animals may habituate to experimental equipment with time and suitably graded exposure, working with less neophobic species, such as Kea (Gajdon et al., 2004) or New Zealand robins *Petroica longipes* (Garland, Low, & Burns, 2012) can make running experiments in the wild a much smoother experience.

Amenability can, however, go beyond just a lack of neophobia. The ability to move animals, to change their environment with artificial landmarks or sounds, or to control the sensory environment that those animals experience also depends on the relevant species. It is far easier, for example, to move a desert ant to a new location to investigate the animal's response to dealing with self-motion and visual cues in conflict (e.g., Collett & Collett, 2009), than to conduct the same experiment with a large mammal. Logistical issues of this nature are just one of the reasons that the navigation mechanisms used by wild desert ants are well understood (Collett, Chittka, & Collett, 2013), whereas the mechanisms underlying similar abilities in many larger species are not. With a considered choice of a study species—one that is reliable, observable, and amenable to experimental investigation—it is much easier to investigate cognition without having to bring animals into the laboratory.

Experimental design

Having chosen a suitable species, the next hurdle for investigating cognition in the wild is the form in which to present the relevant question. If one is interested in whether an animal *can* use certain types of information, for example, then even in the laboratory there are already a variety of testing paradigms. For instance, to determine

which cues an animal uses to return to a location, there is often a convergence on standardized paradigms, such as the radial maze or the Morris Water Maze, although these devices can come in different forms (e.g., Bond, Cook & Lamb, 1981; Flores-Abreu et al., 2014; Hilton & Krebs, 1990; Spetch & Edwards, 1986). In the wild, in order to ensure an animal's participation, these paradigms, at least in their laboratory form, may well be unsuitable, forcing field experimenters to "think outside of the box." As the variety in the laboratory suggests, conformity to established paradigms need not be strictly enforced, and novel experimental designs can be used to address familiar questions.

One way to encourage the participation of wild animals in experiments is to attempt to tie the experiment into the day-to-day life of the animal. This might be done by using a paradigm that utilizes a familiar context, such as a naturalistic foraging task (Healy & Hurly, 1995), sexual display, or predator avoidance. Taking advantage of these natural behaviors can result in increasing the motivation of animals to take part or they may require less training to reach high levels of performance, which may give the animals the best chance of answering the cognitive question posed by the experimenter.

For investigating social learning in wild vervet monkeys, for example, the knowledge that dominant males and females are more likely to access resources before the rest of the troop helps in the design of experimental apparatus, whereby the dominant monkeys act as demonstrators to the rest of the troop (van de Waal, Renevey, Favre, & Bshary, 2010). In this way, researchers have found that the monkeys paid more attention to dominant females, who will spend their lives in their natal troop, than to males, who disperse to other groups upon maturity. The importance of phrasing a question in a meaningful way to the study animal can also be key to motivating animals in the wild to attempt the task.

Role of Technology

The enthusiasm for investigating cognition in the wild is being greatly benefitted by recent advances in technology, which are enabling access to many more species and questions that require animals to be followed over long distances, for long periods of time, or to be described in detail. Three types of technology, in particular, are transforming the collection of data in the wild: automatic experimental apparatus, biologgers, and computer vision.

Passive integrated transponder (PIT) tags, for example, can be used to identify individuals interacting with experimental apparatus in the wild (Brewer, Redmond, Stafford, & Hatch, 2011; Morand-Ferron & Quinn, 2011). These tags are activated by an electromagnetic field that can be fitted to any number of objects (such as feeders, platforms, or nest boxes), allowing the experimenters to automatically log the identity and performance of an animal, including the duration spent by an individual at an apparatus. This automated approach allows the collection of high quality data from hundreds of animals, a feature rarely if ever possible in the laboratory. For example, 90% of the great tit *Parus major* population in the Wytham Woods in the UK has been fitted with leg-ring PIT tags, making it possible to describe the social network of several sub-populations within that area and then to track the social transmission of the solution of novel tasks through a population (Aplin et al., 2015).

Other technologies, on the other hand, allow researchers to record otherwise inaccessible behavior. Biologging technologies, such as accelerometers or geolocators, can be attached to an animal and will not only provide the location of the animal, but also give information on their rate of movement (Aguilar Soto et al., 2008), yield

environmental information such as light or temperature, whether the animal is in the water or not (Guilford et al., 2009), and can even include cameras, which allow access to the behavior of the animal in new ways (Bluff & Rutz, 2008; Rutz, Bluff, Weir, & Kacelnik, 2007). In particular, biologging technologies can enable data collection from species difficult to observe by any other means, such as marine animals and long distance migrants. In the context of investigating cognition in the wild, biologging technology has already been put to use in manipulations of animal navigation (e.g., Biro, Meade, & Guilford, 2004; Cochran, Mouritsen, & Wikelski, 2004), and it seems likely that these devices will become increasingly useful in the future.

Although less often used so far, computer vision also has significant potential for studying ‘wild’ cognition. Unlike PIT tagging and biologging, which involve attaching devices to animals, computer-vision technology allows researchers to track and record the behavior of animals without requiring the animal to carry any equipment.

One application of this technology is the ability to track the movements and paths of animals in 3D, based on the view of multiple calibrated cameras. Although thus far the use of this technology in animal behavior research has mostly been restricted to the laboratory (but see Clark, 2009; Thierault et al., 2014; de Margerie et al., 2015), it has been used recently to track the flight paths of hummingbirds as they searched for a previously visited flower (Pritchard et al., 2016b, Figure 3). Although birds could be tracked only when they were in view of both cameras, the computer-vision technology applied to the data after collection meant that the experiments themselves did not require any expensive equipment, but still allowed examination of navigation in the wild in ways that previously have been restricted to the laboratory.

In addition to providing economical tracking solutions, similar methods can be used to reconstruct the visual information available to animals navigating in the wild.

Using multiple overlapping photographs of an area, for example, three-dimensional reconstruction techniques can be used to generate a three-dimensional model of natural environments, which alongside the reconstructed paths of an animal, allow researchers access to the “view from the cockpit” of animals travelling through their worlds (Stürzl, Grix, Mair, Narendra, & Zeil, 2015). These data can be used alongside experiments and computational modelling to quantify and manipulate information available to animals in their natural environments in unprecedented ways.

Conclusions

The study of cognition in the wild, especially spatial navigation, seems likely to continue gathering momentum as technological advances increase our access to ever more species and their behaviors in the field. We are optimistic about the implications of such work.

Studying animal cognition in the wild can help biologists and psychologists interested in the evolution of cognition to understand the role that cognitive mechanisms play in the natural lives of animals. As the cognitive abilities of more species are studied in the environment in which such processes evolved, the prospects of a truly comparative study of cognition look bright. Comparing species that are either closely or distantly related, in similar or different environments, as well as quantifying the fitness consequences of variations in cognition under natural conditions, will greatly enhance our understanding about how cognitive abilities respond to natural selection.

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Figure legends

Figure 1. Results of a time-place learning experiment testing whether hummingbirds could learn to associate different rewarded locations with different times. A territorial hummingbird had the option of visiting any of four patches each containing six artificial flowers. The flowers in only one patch contained reward at any one time, each for one hour a day. In order to visit the correct patch at the correct time, hummingbirds could learn the time of day each patch was rewarded or the order in which patches were rewarded. The figure represents the percentage of first visits made to each patch over the five days by 8 birds (mean). Each panel shows the visits made to each of the patches over the four hours that the patches were placed in the hummingbird's territory. The vertical dash lines indicate the times at which a patch became empty and the next patch contained reward. The horizontal black bars represent the duration over which the flowers in that patch contained reward. After (Tello-Ramos et al. 2015).

Figure 2. An example of using transformations to test what information hummingbird use to estimate the distance of a goal from landmarks. During training (left), hummingbirds could remember the distance of the flower (+) to the landmarks (black circles), in terms of the absolute distance of the flower (dashed arrow) or the apparent size of the landmarks (grey). In the test (right), where the size and position of the landmarks is increased, these cues now indicate different locations. From Pritchard et al. (2016)a.

Figure 3. A three-dimensional reconstruction of the flight path of a hummingbird, as he comes in to feed from an artificial flower (triangle). The x, y, and z axes represent the flower's position in metres relative to one of the cameras.

