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

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20 Abstract

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

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

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

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

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

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

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

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

88

89 **Why study cognition in the wild?**

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

96

97 *The Ecological Approach*

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

100

101 *Cognitive Ecology*

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

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

115 hummingbird cognition in the wild has tested a range of *a priori* predictions about the
116 information to which hummingbirds “should” pay attention to in order to forage
117 effectively (Healy & Hurly 2013). Using field experiments that create a simplified
118 version of their natural environment, it is possible to investigate whether hummingbirds
119 can pay attention to various types of information present in the environment, as well as
120 the kinds of information they preferentially use during foraging. One of the challenges
121 of the cognitive ecology research programme, however, is to objectively identify *a*
122 *priori* predictions about types of information to which animals “should” pay attention.
123 With some knowledge of an animal’s natural history, it may seem straightforward to
124 generate predictions as to why animals should value certain cues over others. For
125 example, because the color and morphology of hummingbird-pollinated flowers have
126 evolved in response to hummingbird foraging (Temeles, Pan, Brennan & Horwitt,
127 2000), one might expect that hummingbirds pay considerable attention to flower color
128 when they first approach a flower (e.g. Grant, 1966). And, yet, in field experiments
129 where hummingbirds are trained to visit a flower of a particular color in a particular
130 location, when spatial and color cues are dissociated, hummingbirds consistently choose
131 flowers in the “correct” spatial location over flowers of the “correct” color (Hurly &
132 Healy, 2002; Hurly & Healy, 1996; Tello-Ramos, Hurly, & Healy, 2014).

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

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

141

142 *Behavioral Ecology*

143 An alternative ecological approach to studying the evolution of cognition
144 involves attempts to assess the value of a cognitive ability in terms of its impact on
145 survival and reproductive success, with the prediction that “better” cognition should
146 lead to increased fitness. This link between fitness and cognition had previously been
147 largely assumed, as researchers sought to understand the cognitive mechanisms
148 underlying behaviors that contributed to fitness, such as foraging (e.g., Bateson, 2002;
149 Brunner, Kacelnik, & Gibbon 1992), mate choice (e.g., Bateson, 1978; ten Cate,
150 Verzjiden, & Etman, 2006), and communication (e.g., Marler, 1997; ten Cate & Rowe,
151 2007).

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

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

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

169 Although some of these research programmes have involved tests of the
170 cognitive abilities of wild animals brought into the laboratory (e.g. Cole et al. 2012),
171 problem-solving tests are increasingly being presented to animals in the wild (Isden,
172 Panayi, Dingle, & Madden, 2013; Keagy, Savard, & Borgia, 2009; Morand-Ferron &
173 Quinn, 2011; Morand-Ferron, Cole, Rawles, & Quinn, 2011). For example, male
174 bowerbirds can be induced to solve batteries of problem-solving tasks, and their
175 performance can be compared to their mating success (Isden et al., 2013; Keagy et al.,
176 2009).

177

178 *The Anthropocentric Approach*

179 A large body of research addressed at investigating such aspects of cognition as
180 social cognition, numerosity, and causal understanding in wild animals is based less on
181 the ecology of a particular species and rather more on a search for human-like cognitive
182 processes in non-human animals (e.g. Taylor, Hunt, Medina, & Gray, 2009; Mayer et al.
183 2014; Smet & Byrne, 2013). This research is usually characterized by an interest in
184 "complex" cognition, generally defined with relation to human cognitive abilities, and
185 the degree to which such abilities are present in other species. Much of this work is
186 aimed at the identification of possible selection pressures that led to the evolution of
187 human intelligence (Maclean et al. 2012) through the description of the cognitive
188 abilities of species that are closely related to humans, or that share some biological or

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

191

192 *Practical benefits to working in the wild*

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

203

204 *Access to “natural” subjects and behaviors*

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

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

214 on experiments carried out on a grand scale impossible in the laboratory (Perdeck,
215 1958; Thorup et al., 2006).

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

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

226 Discoveries such as the role of the sun compass, the use of magnetic and
227 olfactory information (Wallraff, 2004; Wiltschko & Wiltschko, 2009), and the possible
228 use of different mechanisms inside and outside the familiar area (Guilford & Biro,
229 2014), have all relied on pigeons having access to real-world environments, and may
230 never have been discovered if the study of pigeon navigation had been restricted to the
231 scale of a laboratory testing room. Not only is the experimental study of homing
232 pigeons travelling through their natural environment a successful example of studying
233 animal cognition in the wild, it is a system that has also allowed a rare opportunity to
234 investigate the neurobiology of navigation over larger scales by studying the effects of
235 hippocampal lesions, often studied in small laboratory environments, on the large scale
236 navigation of homing pigeons (e.g., Bingman et al., 2005).

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

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

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

254

255 *Access to “natural” environments*

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

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

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

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

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

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

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

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

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

326

327 *Stress and motivation*

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

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

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

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

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

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

365

366 **Testing cognition in the wild**

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

371

372 *What can animals in the wild learn?*

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

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

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

390 The cognitive ecological approach, in which researchers test *a priori* predictions
391 about cognitive ability based on species' ecologies, has also been used to determine
392 what animals can learn. For example, arrays of artificial flowers presented in birds'
393 territories with specific delays before each flower is refilled have been used to show that
394 rufous hummingbirds can learn which flowers refill after 10 and which refill after 20
395 min: birds return to the 10-min flowers after 10-15 min and to the 20-min flowers after
396 20-25 min (Henderson et al., 2006). Rufous hummingbirds will also learn to visit
397 particular patches at the times of day when the artificial flowers in those patches contain
398 reward (Figure 1; Tello-Ramos, Hurly, Higgott, & Healy, 2015). Although, as in
399 problem-solving tasks, birds can "succeed" or "fail" depending on whether they visit the
400 rewarded flowers or not, the pattern of the birds' successes and failures demonstrated
401 one of the kinds of information to which these birds can pay attention during foraging,
402 in this case, intervals of time (also see Fetterman & Killeen, 1995 for a laboratory
403 analogue of this time-place foraging task).

404

405 ***What have wild animals learned?***

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

413 For example, in the Tello-Ramos et al. (2015) time-place learning experiment,
414 hummingbirds increasingly visited the appropriate patch of flowers for each hour of the
415 4 hours during which flower patches were available each day (Figure 1; Tello-Ramos,
416 Hurly, Higgott & Healy, 2015). It is not clear, however, how the hummingbirds did this.
417 For example, they might have learned the location of the rewarded patch or the
418 appearance of the rewarded flowers. They may have used interval timing, circadian
419 timing, or have remembered the order in which the patches refilled. To determine which
420 of these possibilities the birds did use and, more generally, to identify what cognitive
421 abilities an animal has used to solve a particular task, other kinds of experiments are
422 required.

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

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

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

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

451

452 **The relevance of ecology**

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

457

458 ***Species choice***

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

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

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

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

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

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

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

495 Amenability can, however, go beyond just a lack of neophobia. The ability to
496 move animals, to change their environment with artificial landmarks or sounds, or to
497 control the sensory environment that those animals experience also depends on the
498 relevant species. It is far easier, for example, to move a desert ant to a new location to
499 investigate the animal's response to dealing with self-motion and visual cues in conflict
500 (e.g., Collett & Collett, 2009), than to conduct the same experiment with a large
501 mammal. Logistical issues of this nature are just one of the reasons that the navigation
502 mechanisms used by wild desert ants are well understood (Collett, Chittka, & Collett,
503 2013), whereas the mechanisms underlying similar abilities in many larger species are
504 not. With a considered choice of a study species—one that is reliable, observable, and
505 amenable to experimental investigation—it is much easier to investigate cognition
506 without having to bring animals into the laboratory.

507

508 ***Experimental design***

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

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

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

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

538

539

540 Role of Technology

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

547 Passive integrated transponder (PIT) tags, for example, can be used to identify
548 individuals interacting with experimental apparatus in the wild (Brewer, Redmond,
549 Stafford, & Hatch, 2011; Morand-Ferron & Quinn, 2011). These tags are activated by
550 an electromagnetic field that can be fitted to any number of objects (such as feeders,
551 platforms, or nest boxes), allowing the experimenters to automatically log the identity
552 and performance of an animal, including the duration spent by an individual at an
553 apparatus. This automated approach allows the collection of high quality data from
554 hundreds of animals, a feature rarely if ever possible in the laboratory. For example,
555 90% of the great tit *Parus major* population in the Wytham Woods in the UK has been
556 fitted with leg-ring PIT tags, making it possible to describe the social network of several
557 sub-populations within that area and then to track the social transmission of the solution
558 of novel tasks through a population (Aplin et al., 2015).

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

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

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

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

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

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

595

596 **Conclusions**

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

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

609

610

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923 **Figure legends**

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

936

937 **Figure 2.** An example of using transformations to test what information hummingbird
938 use to estimate the distance of a goal from landmarks. During training (left),
939 hummingbirds could remember the distance of the flower (+) to the landmarks (black
940 circles), in terms of the absolute distance of the flower (dashed arrow) or the apparent
941 size of the landmarks (grey). In the test (right), where the size and position of the
942 landmarks is increased, these cues now indicate different locations. From Pritchard et al.
943 (2016)a.

944

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

