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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

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

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 redtail 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 a 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 that 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

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

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 rewarded 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.

948