

1 **How can we study the evolution of animal minds?**

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Abstract

During the last 50 years, comparative cognition and neurosciences have improved our understanding of animal minds while evolutionary ecology has revealed how selection acts on traits through evolutionary time. We describe how this evolutionary approach can be used to understand the evolution of animal cognition. We recount how *comparative* and *fitness methods* have been used to understand the evolution of cognition and outline how these methods could be extended to gain new insights into cognitive evolution. The fitness approach, in particular, offers unprecedented opportunities to study the evolutionary mechanisms responsible for variation in cognition within species and could allow us to investigate both proximate (ie: neural and developmental) and ultimate (ie: ecological and evolutionary) underpinnings of animal cognition together. Our goal in this review is to build a bridge between cognitive neuroscientist and evolutionary biologists, illustrate how their research could be complementary, and encourage evolutionary ecologists to include explicit attention to cognitive processes in their studies of behaviour. We believe that in doing so, we can break new ground in our understanding of the evolution of cognition as well as gain a much better understanding of animal behaviour.

34

35 **Introduction**

36 Niko Tinbergen (Tinbergen, 1963) proposed that biologists should try to understand animal
37 behaviours in the light of two different and complimentary perspectives: the *proximate* and
38 *ultimate* (see Bateson and Laland, 2013; Laland et al., 2011 for recent updates). While both
39 approaches have been employed in the study of animal cognition, most studies have done so
40 independently with little integration across fields. After some promising, integrative studies in
41 the 1980s and 1990s (see Kamil, 1998 for a review), the last decades have seen the establishment
42 of entirely independent lines of research with only a few notable exceptions. We now have a
43 deeper understanding of how animal minds work, but we know very little about the evolution of
44 or ecological pressures that shape cognition. Consequently, we know very little about what role
45 cognition, a collection of highly plastic and flexible traits, plays in adaptation and biological
46 evolution. We believe the time is ripe for evolutionary ecology studies to explicitly integrate
47 cognition to generate a much stronger understanding of how the mind evolves.

48

49 Proximate studies focus on the mechanisms underlying given behaviours and the developmental
50 biology of key structures. What stimuli trigger behaviours? How do neurons in the brain encode
51 stimuli and transform them into behaviour? What is the ontogeny of behaviour? In other words,
52 the proximate approach tries to understand how animal minds work. The current view for
53 cognitive neuroscientists is that the animal mind emerges from brain activity as the neural
54 machinery encodes, manipulates, stores and recalls information, which is together called
55 '*cognition*'. Cognition emerges when the brain transforms information into mental constructs or
56 representations (Barsalou, 2014). For *cognitive scientists*, cognition is a synonym of 'mind',
57 which, operationally, is divided in various *cognitive functions*, each function being implied in a
58 specific step of information processing (see also Figure 1). Perception (i.e. vision, olfaction,
59 audition, gustation and somesthesia) all contribute to the process by which mental
60 representations are built from environmental stimulation. Learning is the ability to associate
61 previously unrelated mental representations. Memory is the ability to store mental
62 representations either for a small amount of time (short term memory), a large amount of time
63 (long term memory) or in relation to a particular on-going task (working memory). Attention is
64 the mechanism allowing an individual to focus on only some mental representations among

65 many. Decision-making is the process enabling an individual to compare mental representations
66 and choose the most appropriate given the environmental context. Finally, executive functions
67 (reasoning, problem solving, flexibility, categorization etc...) enable an individual to perform
68 operations and manipulations of mental representations. Cognition is also sometimes divided
69 according to the nature of the representation; one can for instance talk about spatial or social
70 cognition.

71

72 The association between studies in psychology and neurosciences along with the advent of
73 powerful new neuroimaging technics (e.g. In vivo electrophysiology, Magnetic Resonance
74 Imaging (MRI), Positron emission Tomography (PET), optogenetic etc.) has lead us to better
75 understand how behaviours and decisions are linked to neural structures and neural activity in
76 several animal species including humans. Despite this in depth understanding, much less
77 progress has been made in understanding the evolutionary processes that have lead to the
78 patterns of cognition that we see.

79

80 Ultimate approaches focus on the evolutionary history of behaviours or traits and the selective
81 pressures that favour the evolution of those traits. Those using this approach have focused on
82 behaviours with only a few rare studies examining cognition *per se* (e.g. Bond and Kamil, 2002,
83 2006; Lyon, 2003; Théry and Casas, 2002). *Evolutionary biologists* and *behavioural ecologists*
84 have been primarily interested in the ecology and evolution of behaviour without examining the
85 cognitive mechanisms underlying these behaviours. What ecological or social contexts are
86 responsible for the evolution of a specific behaviour? What role does evolutionary history
87 (inheritance from a common ancestor) play in the evolution of that trait? What are the costs and
88 benefits of behaviours and what do they imply for selection on the animal's life history strategy?
89 To answer these questions behavioural ecologists have adopted the Neo-Darwinian theoretical
90 framework and developed tools and models to understand the extreme variability of behaviours
91 within and among species. However, this approach focuses on the aggregate outcome of
92 cognition and action (i.e. the behaviour) and has usually considered the animal mind as a black
93 box (Giraldeau, 2004). Indeed, much of behavioral or evolutionary ecology theory is based on
94 strategic decision-making. While in some cases these strategic decisions reflect physiological
95 trade-offs, many more cases reflect decisions made probably on the basis of processing external

96 information gathered by an individual. Attention in such studies is placed on the quality of
97 information and the outcome of a decision, but there is little understanding of how information is
98 processed and how cognitive abilities enhance or constrain decisions based on the available
99 information (Rowe, 1999, 2013). For example, social behavior, individual recognition, mate
100 choice, parental care, dispersal, foraging, and predator avoidance nearly always rely on gathering
101 external information. How well an individual gathers that information, how well it remembers
102 that information, and how it integrates different sources of information all depend on cognitive
103 capacities. To illustrate this notion (Figure 1) we can imagine a female who must choose the best
104 mate among males that each display a number of ornaments linked to various qualities (e.g. good
105 genes, parental care, nest defense, etc...). How does a female integrate the information provided
106 in each of the male's sexual signals with information about the external ecological environment
107 (e.g. are there many nest predators)? As the female comparison shops for the best male, how
108 many of the males can she remember? If she chooses to return to the second male she saw, will
109 she remember where he is and will she recognize him? This example illustrates just some of the
110 cognitive processes related to one behavior that would have fundamental consequences for
111 sexual selection theory. Many other behaviors and life history strategies will similarly depend on
112 cognitive capacities and actual measurement of cognitive abilities has the potential to
113 fundamentally alter our views of behavior.

114
115 Understanding the evolutionary and ecological significance of cognition has been a major
116 challenge in biology as highlighted in several recent books (Dukas and Ratcliffe, 2009; Heyes
117 and Huber, 2000; Shettleworth, 2010) and review articles (Boogert et al., 2011; Dukas, 2004,
118 2008; Healy and Braithwaite, 2000; Kamil, 1998; MacLean et al., 2012; Pravosudov and
119 Smulders, 2010; Real, 1993; Thornton et al., 2012) and has led to a new field of research called
120 *cognitive ecology*. We argue that two factors will help to significantly advance our understanding
121 of animal cognition: 1) proximate and ultimate studies should develop lines of research that
122 allow direct integration of the two fields and 2) that evolutionary studies begin to apply their
123 research methods to cognition *per se* along with the behaviours that result from cognitive
124 processes. In doing so, we will gain a better understanding of how cognitive systems evolve and
125 how cognitive structures and function relate to the problems they evolved to solve.

126

127 In this review, we focus more on the contribution that evolutionary biology can offer cognitive
128 research since much less work has been done in this domain. Despite this bias towards what
129 evolutionary biologists could contribute (i.e. what we know less about), we also highlight new
130 contributions that cognitive neuroscientists could make to better integrate proximate and ultimate
131 understandings of cognition. In the first section, we review past work testing popular hypotheses
132 for cognitive evolution using comparative methods and highlight future directions to exploit
133 using these methods. We then illustrate how measuring selection on cognition within a species
134 provides a great opportunity to better understand the evolution of cognition and create direct
135 links with proximate studies of cognition (e.g. neurosciences, cognitive-psychology). We finish
136 by presenting two lines of research as case studies—food hoarding and brood parasitism—that,
137 in our view, have best integrated ecological challenges, natural behaviour and underlying
138 cognitive adaptation and which could serve as examples for future cognitive ecology research.

139

140 **Phylogenetic comparative studies of cognitive evolution**

141 Current tests of factors that influence the evolution of the brain have largely relied on
142 comparative methods. The phylogenetic comparative approach (Felsenstein, 1985, 2008;
143 Felsenstein and Felsenstein, 2004; Grafen, 1989; Harvey and Pagel, 1991; Ridley and Grafen,
144 1996) allows us to ask questions about how the evolution of a trait occurs through comparison of
145 extant species (although fossil evidence can be incorporated) while taking into account shared
146 ancestry estimated from a phylogeny. We can then ask questions such as what factors (e.g. social
147 or ecological) are associated with the evolution of a trait (e.g. brain size), if that trait evolves
148 directionally, how much common ancestry constrains evolution, and how the evolution of a trait
149 influences speciation rates.

150

151 The three major hypotheses of neurocognitive evolution that have been proposed focus on
152 identifying primary factors that have driven differences in brain size and cognitive function
153 across species. The first set of hypotheses suggest that cognition has evolved due to the value of
154 *ecological intelligence*; the ability to find and extract food (Byrne, 1997; Parker and Gibson,
155 1977), manage high spatiotemporal variation in food resources (Sol et al., 2005), or manage and
156 defend large territories (Clutton-Brock and Harvey, 1980). The second set of hypotheses propose
157 that cognition has evolved primarily due to its value in *social intelligence*; the ability to negotiate

158 and succeed through dominance in large groups (Dunbar, 1998; Whiten and Byrne, 1988) or
159 alternatively the ability to manage positive relationships and social partnerships (Dunbar and
160 Shultz, 2007, 2010; Emery et al., 2007). The third hypothesis, recently proposed to reconcile
161 ecological and social drivers, suggests that cognition evolved to *buffer* individuals against
162 environmental challenges by producing appropriate behavioural responses in new socio-
163 ecological contexts (Allman and Hasenstaub, 1999; Deaner et al., 2003; Sol, 2009).

164 Each of these hypotheses has been tested using comparative methods and each has found some
165 support. For example, brain size depends on diet in mammals (Eisenberg and Wilson, 1978;
166 Gittleman, 1986; Harvey et al., 1980; MacLean et al., 2014) suggesting a role of ecology.
167 Likewise, brain size and neocortex size are related to social group size (Barton and Dunbar,
168 1997; Dunbar, 1998; Dunbar and Bever, 1998; Gittleman, 1986; Marino, 1996) and other metrics
169 of social group structure in mammals (reviewed in Dunbar and Shultz, 2007) suggesting that
170 social drivers are also important to the evolution of the brain and cognition. Interestingly,
171 comparison of ecological and social factors in ungulates, showed that relative brain size is
172 influenced by social and ecological factors while relative neocortex size is only influenced by
173 sociality (Shultz and Dunbar, 2006). Finally, species with larger brains have been shown to
174 survive better in novel environments (Sol et al., 2005, 2007, 2008) in support to the cognitive
175 buffer hypothesis (Sol, 2009).

176 Comparative studies focused on brain size have also been largely criticised (Healy and Rowe,
177 2007; Lihoreau et al., 2012; Roth et al., 2010a). The high cognitive capacity of small-brained
178 invertebrates, such as bees and ants, suggests that high cognitive capabilities do not require large
179 overall brain size (Chittka and Niven, 2009). Measurements of brain size or brain structure
180 volumes are too coarse grained given that current neuroscience methods enable us to study fine
181 scale brain organisation and function (Healy and Rowe, 2007; Roth et al., 2010a). For instance,
182 cognitive neurosciences have revealed different brain networks and mechanism associated with
183 different cognitive abilities. Thus, instead of studying whole brain or neocortex size, comparative
184 studies should focus on neural circuits and functioning that are known to be involved in the
185 cognitive mechanism of interest when possible (Lihoreau et al., 2012).

186

187 Efforts to address the problem that brain size may not be the same as cognitive abilities have
188 been made along two lines of comparative research: (i) spontaneous records of cognition-based
189 behaviours (e.g. innovation) in the wild and (ii) comparative psychology experiments in the lab.
190 The first line of research, also called ‘taxonomical counts of cognition in the wild’ (reviewed in
191 Lefebvre, 2011), enables the study of large samples of “spontaneous” behaviour occurring in the
192 selective environment or at least a natural or semi-natural habitat. This approach has confirmed
193 that relative brain size increases with increased tool use and frequency of innovation in birds
194 (Lefebvre et al., 1997, 2004) and primates (Lefebvre et al., 2004; Reader and Laland, 2002),
195 social learning in primates (Reader and Laland, 2002), or deception in primates (Byrne, 2004).

196

197 Taking the second approach, a few studies have begun comparing specific cognitive tasks among
198 a small number of related species that differ in social or ecological conditions. One of the most
199 advanced research programs of this kind, has been conducted on North American corvids (Balda
200 and Kamil, 2002; Balda et al., 1996; Kamil, 1998) using a large number of cognitive tests run in
201 the lab. Corvid species that rely heavily on food storing in the wild, such as Clark’s Nutcrackers
202 (*Nucifraga columbiana*), typically outperform other corvids in tasks requiring spatial cognition
203 (Olson et al., 1995); on the other hand, corvid species that are highly social, such as Pinyon Jays
204 (*Gymnorhinus cyanocephalus*), are better in cognition tasks mimicking social challenges such as
205 those designed to evaluate social learning, behavioural flexibility or transitive inference (Bond et
206 al., 2003, 2007, 2010; Templeton et al., 1999). Studies in primates have similarly addressed how
207 social structure is related to the evolution of cognitive abilities. Comparing species that differ in
208 their degree of sociality, Amici et al. (2008) have shown that species with fission-fusion social
209 organisation outperform species with very stable social groups in cognitive tasks requiring
210 inhibitory control and/or flexibility. Very recently, one of the most accomplished studies
211 merging phylogenetic and experimental cognition methods draws a slightly different picture
212 (MacLean et al., 2014). MacLean and his 57 collaborators realized the feat of gathering cognitive
213 performances of 36 animal species (from birds to rodents to apes) in two problem solving tasks
214 measuring self-control. Their results suggest that the major proximate mechanism underlying the
215 evolution of self control is the absolute brain volume rather than residual brain volume corrected
216 for body mass. They also report a significant relationship between cognitive performance and
217 dietary breadth but not social organization in primates. Thus, this massive comparative cognition

218 study challenges both the proxy of cognition (relative brain size) and the hypothesis (social brain
219 hypothesis) tested in many brain comparative studies and illustrates the danger of over
220 interpreting comparative cognition studies. Continued efforts to link specific cognitive functions
221 to their ecological and social settings present a promising avenue to understand the evolution of
222 cognition while recognizing that different cognitive abilities may evolve under different
223 environmental contexts.

224

225 A number of new directions using the comparative method have still not been sufficiently
226 exploited. First and foremost, analyses should begin to compare specific regions of the brain or
227 brain function rather than coarse measures of brain size. The increasing ease of using new
228 technology (e.g. MRI, PET) to measure brain structures, connectivity, and function that are
229 frequently measured in cognitive neurosciences could provide another link between the evolution
230 of cognitive processes and ecological or social factors that influence cognition. Second, only a
231 small range of questions using comparative methods have been addressed (see MacLean et al.,
232 2012 for a review). For example, comparative methods can be used to examine the sequence of
233 events in coevolution such that we could ask if the increase of a cognitive ability generally
234 precedes or succeeds specific social or ecological changes. Likewise, we could examine the
235 relative rates of evolution during the increase or decrease of a particular cognitive ability. Finally,
236 we can ask how shifts in cognition are associated with the speciation process itself (e.g.
237 Nicolakakis et al., 2003). Does the evolution of increased cognitive ability facilitate speciation?

238

239 **Intraspecific selection on neurocognitive traits: the fitness approach**

240 Measuring contemporary selection has proved a powerful approach to understanding the
241 evolution of traits and this method could be readily applied to the evolution of cognition. The
242 basic premise of this '*fitness*' approach follows Darwin's theory of evolution (1859) which
243 suggests that short term selection is the primary cause of evolutionary change and speciation.
244 Therefore a careful examination of selection can help us understand how a trait evolves.
245 Selection can come from a number of origins which largely fall under *natural selection*, which
246 includes the effects of abiotic influences and interspecific interactions on survival and
247 reproduction (Darwin, 1859; and modern synthesis in Huxley, 1942), or *social selection* (Lyon
248 and Montgomerie, 2012; West-Eberhard, 1983), which includes selection due to intraspecific

249 social interactions including the effects of mating behaviour (i.e. sexual selection, Darwin, 1871)
250 and kin cooperation (i.e. kin selection, Hamilton, 1964) among other intraspecific interactions.
251 There are two distinct advantages to the fitness method relative to the comparative method for
252 studying neurocognitive evolution. The first advantage is that studies of selection measure fitness
253 costs and benefits of specific traits which can provide a close match with measurements of
254 cognitive abilities and brain mechanisms currently studied in animal cognition and neurosciences
255 (Figure 2). Thus the fitness approach provides opportunities to integrate our proximate
256 understanding of cognition with new findings on the ultimate causes of cognitive evolution. The
257 second advantage is that examination of selection ideally includes identification of the agent of
258 selection or the specific social or ecological challenges that favour a specific trait. Adopting this
259 approach helps us acknowledge that there may be multiple factors that select for a given
260 cognitive ability and that each species will require only a subset of all cognitive skills given their
261 environment.

262

263 To show that animal cognition evolves under direct natural or social selection requires that the
264 three necessary conditions for selection and evolution that Darwin (1859, 1871) outlined apply to
265 cognitive abilities (Dukas, 2004). Traits, or in this case cognitive abilities, will evolve if (1) there
266 is variability in cognition between individuals, (2) that this variability in cognitive ability is
267 heritable, and (3) that this variation is related to variance in fitness (survival, reproductive
268 success) under specific environmental conditions. Few studies have tackled these questions
269 specifically, but evidence from the literature supports the notion that cognition *should* evolve
270 under selection making the fitness approach fruitful.

271

272 *(1) Variation in neurocognitive ability*

273 Inter-individual variability in animal cognition studies is rarely reported, yet without variation,
274 cognition can not evolve. Studies in animal cognition generally focus on a small number of
275 individuals because of the time involved in training and testing subjects and this small sample
276 size precludes useful estimates of variation in cognitive abilities. However, a recent meta-
277 analysis of variation in individual performances at three common cognitive tasks for different
278 species revealed very high inter-individual variability (Thornton and Lukas, 2012). Individual
279 performances varied almost continuously from 25-100% success at a task in tests for species

280 with the largest sample sizes. Some of this variation is influenced by age, sex, developmental
281 conditions, or previous experience, so determining the extent of variation due to additive genes
282 rather than plasticity will require large sample sizes at single cognitive tasks.

283

284 Despite little direct evidence, there are a number of indirect measures of cognitive variability that
285 further support the notion that intraspecific variation in cognitive abilities should be widespread.
286 A growing number of recent studies focus on intraspecific variation in brain size including both
287 within and among population variation (for a review see Gonda et al., 2013). This variation is
288 also apparent in humans where inter-individual variation in brain structure and function has often
289 been considered “noise” until recently (Kanai and Rees, 2011). Perhaps the best evidence of
290 inter-individual cognitive variation comes from research on “general intelligence” in humans,
291 which has been extensively documented through the use of intelligence or ‘IQ’ tests and shows
292 high variation among individuals (Deary et al., 2010). Recent work has sought to tie variation
293 between IQ in humans to its neural substrate (Deary et al., 2010; Penke et al., 2012).

294

295 (2) *Heritability of neurocognitive abilities*

296 Heritability of traits is difficult to measure since many non-genetic effects (common environment,
297 parental care, maternal effects, etc...) contribute to resemblance between parents and offspring.
298 For example, twin studies show that brain structure or function (e.g. face recognition) is heritable
299 in humans (Peper et al., 2007; Wilmer et al., 2010; Zhu et al., 2010), yet non-genetic effects that
300 occur in utero can not be excluded (but see Trzaskowski et al., 2013). One of the most powerful
301 approaches to demonstrate that heritability of cognitive traits exists is through artificial selection
302 experiments where species show phenotypic changes in response to researcher imposed selection
303 criteria. Mery and Kawecki have shown that associative learning abilities for choice of
304 oviposition substrate can be inherited in *Drosophila melanogaster* (see Kawecki, 2010 for a
305 review; Mery and Kawecki, 2002, 2003, 2005). Marked differences in learning and memory
306 were shown between high learning and low learning selected *Drosophila* populations over 15
307 generations. Artificial selection of brain size in guppies (*Poecilia reticulata*) also suggests
308 heritability of brain size (Kotrschal et al., 2013a) with a divergence in relative brain size of 9%
309 between lines selected for large vs. small size over just two generations. Interestingly, large-
310 brained females outperformed small-brained females in a numerical learning test, which also

311 provides evidence for an association between increased brain size and higher cognition. These
312 results should be treated cautiously since disentangling true heritability from plasticity would
313 require more than 2 generations and a relaxation of selection to see if brain size differences
314 persist (see Healy and Rowe, 2013; Kotrschal et al., 2013b). Finally, the use of genome wide
315 association has recently been used to demonstrate a genetic basis of human general intelligence
316 and cognition. This approach has shown that a substantial proportion (between 40 and 66%) of
317 individual differences in human general intelligence is linked to genetic variation (Davies et al.,
318 2011; Benyamin et al., 2013; but see Chabris et al., 2012; Deary et al., 2012; Plomin et al., 2013).
319

320 *(3) The fitness benefits of cognition*

321 Selection on cognitive abilities will occur if there are fitness benefits to particular cognitive
322 phenotypes under a given set of environmental conditions. Addressing this question is
323 challenging because it requires both an estimate of cognitive performance or brain
324 structure/activity of a large number of individuals as well as fitness estimates, such as
325 reproductive success or survival, for the same individuals. Most cognitive tests are run under
326 laboratory conditions to control confounding effects on cognition and yet the best estimates of
327 fitness benefits should be measured in the wild where the importance of a specific cognitive
328 ability will also depend on the environmental context. Fitness measured in artificial selection
329 experiments on cognition or brain size have reported costs and benefits of improved cognitive
330 abilities in insects (Dukas, 2008; Kawecki, 2010) or increased brain size in fishes (Kotrschal et
331 al., 2013a), but the value of these traits in nature are unknown. In humans, general intelligence is
332 correlated with school achievement, job performance, health, and survival (Deary et al., 2010),
333 but not necessarily actual fitness (i.e. number of lifetime offspring that reproduce).
334

335 Two very recent studies have finally succeeded in measuring fitness consequences of problem-
336 solving abilities in wild populations of great tits (*Parus major*) (Cauchard et al., 2012; Cole et al.,
337 2012). Cole et al. (2012) took birds into short term captivity to perform an innovation task to get
338 food. Birds who solved the task had larger clutch sizes, but tended to desert their nest more often
339 if disturbed (Cole et al. 2012). Cauchard et al. (2013) conducted cognitive tests in the wild,
340 where birds had to remove an obstacle that blocked access to their nestbox. Those who could
341 solve the puzzle had higher survival of offspring to fledging. Both studies found individual

342 variation in cognitive performance of birds (solvers vs. non solvers), so selection should act on
343 problem solving abilities. Fitness costs of higher cognition (e.g. higher desertion rates; Cole et al.
344 2012), could produce a trade-off that helps maintain variation in cognitive abilities among
345 individuals. These results are very promising, and should be diversified to a much broader range
346 of cognitive abilities and expanded to measures of brain structure or function (Figure 2).
347 Furthermore, following pioneering research linking food hoarding behaviour and spatial memory
348 (see Pravosudov and Roth II, 2013 for a review, and see Case Study 1 below), understanding
349 why cognition evolves will also require us to directly link cognitive performance (e.g. memory)
350 to ecological challenges that the animals face in their natural environment (e.g. finding a food
351 store). This last point is critical because if there are correlations among different cognitive
352 abilities then measurement of selection (i.e. higher fitness) on one ability could be due to
353 correlational selection on a different cognitive trait that is the actual target of selection.

354

355 **Case Studies**

356 As detailed above, there is now some evidence for selection of cognitive abilities in wild animals,
357 including humans. The next challenge for cognitive ecology is to identify which cognitive
358 functions are critical for a species in their natural environment. While for most species we are
359 still at the point of forming hypotheses on which cognitive abilities are critical (as we did for
360 mate choice in Figure 1), there are a few studies that have moved well beyond this stage. Here
361 we present two lines of research as examples of successfully linking natural behaviour, cognitive
362 function and ecological agents of selection.

363

364 *(1) The evolutionary ecology of spatial memory*

365 Food hoarding animals rely on food caching and later retrieval of caches to survive winter and
366 should have evolved excellent spatial memory abilities and associated neural structures (i.e.
367 hippocampus). Based on this simple ecology-driven hypothesis, a flourishing literature on the
368 cognitive ecology of food storing has emerged over the last thirty years. This work has
369 successfully combined proximate and ultimate understandings of spatial cognition and serves as
370 an example for future studies of the evolutionary ecology of cognition (see Brodin, 2010 for an
371 historical review).

372 The first studies of the evolutionary and ecological significance of spatial memory employed the
373 comparative framework, with the prediction that scatter food hoarding species should surpass
374 non-hoarding species in spatial memory tasks and should have a relatively bigger hippocampus.
375 However, results from these early studies were equivocal and difficult to interpret. The
376 superiority of spatial capabilities in hoarding species was not always clear (reviewed in Healy et
377 al., 2009). Furthermore, and more concerning, the comparative approach suffers from a number
378 of confounding factors, such as morphological differences between species, that could never
379 clearly be separated from performance in cognitive tasks (but see (Kamil, 1998) for methods).

380

381 Problems with comparative analyses have been very elegantly solved by focusing on intra-
382 specific variation in a number of landmark studies comparing populations exposed to different
383 ecological contexts. In one of the earliest of such studies, Pravosudov and Clayton (2002)
384 demonstrated that black-capped chickadees (*Poecile atricapilla*) living in harsh winter climates
385 (i.e. Alaska) cache more food, have higher spatial memory capabilities, and have a larger
386 hippocampus that contains more neurones than individuals of the same species in populations
387 from milder climates (i.e. Colorado). While the appearance of adaptation is clear, such
388 differences could reflect either local adaptation shaped by natural selection or result from
389 plasticity in brain structure and behaviour generated from the local environment. The persistence
390 of among population differences in brain structure and caching behaviour in common garden
391 experiments, during which 10 days-old chicks from these different populations were hand-raised
392 in identical environmental conditions, strongly argues for a role of natural selection in shaping
393 local adaptation for spatial memory, neural density, and neurogenesis in the hippocampus (Roth
394 et al., 2010b, 2012).

395

396 Recent analyses using this within species comparative approach in this and other species have
397 further pushed our understanding of the links between cognition and evolutionary ecology and
398 between proximate and ultimate understandings of cognitive evolution. Research in mountain
399 chickadees (*Poecile gambeli*) along an altitudinal gradient has shown similar patterns of
400 differentiation in food storage, spatial memory, and hippocampal characteristics as with
401 contrasted populations in the black-capped chickadee (Freas et al., 2013). Other studies have
402 extended this work on spatial memory differences across populations in caching behaviour to

403 differences between behavioural strategies within a population (LaDage et al., 2013). In side-
404 blotched lizards (*Uta stansburiana*), males adopt one of three different mating strategies that rely
405 to different degrees on spatial memory for territory defence and the distribution of available
406 females across territories. Accordingly, characteristics of the dorsal cortex and hippocampus
407 show differences among genetically determined alternative male strategies within a population
408 (Ladage et al., 2009; LaDage et al., 2013). Work on hippocampal size contrasts among
409 populations has recently been extended by fine scale studies of neural structure (Roth et al.,
410 2010a, 2012) and differential gene expression (Pravosudov et al., 2013) within the hippocampus
411 among contrasted populations of birds. The next step should be to measure the influence of
412 spatial cognition and the underlying hippocampal structures or function on fitness in these
413 contrasted environments.

414

415 *(2) Cognitive mechanisms of host-parasite arm races in brood parasites*

416 Avian brood parasites lay their eggs in the nest of other individuals from the same or different
417 species to avoid the costs of parental care but imposes a cost on the host (reviewed in Davies,
418 2011). These reciprocal selection pressures have often led to an arms race of detection and
419 mimicry in egg appearance – a true cognitive battleground. Studies of avian brood parasitism
420 provide measures of selection on cognitive traits (recognition, rejection, deception), clear
421 identification of the agent of selection, examination of how cognition influences the
422 coevolutionary arms race, and neural traits associated with host-parasite life history.

423

424 Studies of avian brood parasitism have done an outstanding job of quantifying the fitness costs
425 and benefits to each player of the host-parasite arms race—often linked to recognition of
426 parasites (Davies, 2011; Lyon and Eadie, 2008). A parasite's fitness is so intricately tied to
427 acceptance by hosts that they must adapt to new host defences either by identifying and changing
428 to a new host or surpassing host defences. Hosts, on the other hand, pay a cost of parasitism, but
429 the evolution of new defences (often a cognitive ability) must be balanced against the frequency
430 of parasitism and the costs of producing better defences (Davies and Brooke, 1988, 1989a,
431 1989b; Lotem, 1993; Lotem et al., 1995; Rothstein, 1982). Costs of new defences include
432 developing the cognitive or morphological structures for new defences as well as the added risk
433 of expressing those defences (e.g. rejecting own eggs), and these costs influence the evolution of

434 recognition abilities. Plasticity in host recognition reveals the importance that making an
435 incorrect choice can have for the evolution of egg rejection. For example, some common cuckoo
436 hosts avoid rejecting their own eggs (recognition error) when parasites are not present by only
437 increasing rejection rates when adult cuckoos are seen in the vicinity of the nest (Davies and
438 Brooke 1988). In South American coots, intraspecific parasitism leads to egg rejection, but an
439 interspecific parasite, the blackheaded duck, that imposes no parental care costs is only rejected
440 when ecological conditions render incubation more costly (Lyon and Eadie, 2004). Globally,
441 studies of avian brood parasites have provided an excellent understanding of the selective
442 environment generated by host-parasite interactions that influences the evolution of recognition
443 and rejection of eggs.

444
445 Mimicry-recognition-rejection arms races reveal the link between cognitive abilities and the
446 evolutionary dynamics of host-parasite systems. Arms races in avian brood parasites related to
447 egg mimicry push host recognition systems to identify parasites while avoiding recognition
448 errors (Davies and Brooke, 1988; Rothstein, 1982). The accuracy of identifying a mimetic egg
449 depends on visual discrimination abilities and recent studies have begun to specifically integrate
450 this process using ‘visual modelling’—information on cone sensitivity and objective measures of
451 egg colour patterns—to understand rejection behaviour, or the lack thereof, in some species
452 (Cassey et al., 2008; Spottiswoode and Stevens, 2010). Recent findings show that visual
453 detection of parasites can improve by integrating multiple sources of information (Spottiswoode
454 and Stevens 2010). Egg cues (de la Colina et al., 2012; Langmore et al., 2009; Spottiswoode and
455 Stevens, 2010; Sennungsen and Holen, 2010), external cues of parasite presence (Davies and
456 Brooke, 1988), or counting the number of eggs laid (Lyon, 2003) have all been shown as means
457 to improve the decision to reject parasite eggs. Use of multiple and disparate cues to improve the
458 accuracy of rejection behaviour would require executive functions to weigh these different
459 criteria in a rejection decision and future research could examine this cognitive ability. Not all
460 host species reject eggs or chicks, which implies that physiological or cognitive limitations may
461 also influence the detection of a parasitic egg (Davies and Brooke, 1988; Lotem, 1993; Lotem et
462 al., 1995; Rodríguez-Gironés and Lotem, 1999; Rothstein, 1982).

463

464 An understanding of the cognitive mechanisms underlying rejection have also played an
465 important role in understanding why despite close visual mimicry in eggs, nestlings are rarely
466 mimetic. One hypothesis is that unlike egg recognition where comparisons between multiple host
467 eggs and a single parasitic egg makes discrimination possible, having only a single parasite chick
468 in the nest (e.g. common cuckoos) could have severe long term fitness costs if birds *learn* the
469 appearance of their chicks (Lotem, 1993). Indeed, learning does seem to play a role in
470 identification and discrimination of eggs (Rothstein, 1974, 1978; Strausberger and Rothstein,
471 2009) and possibly chicks (Colombelli-Négrel et al., 2012; Shizuka and Lyon, 2010). A possible
472 solution in some species, such as the North American coot, might be to use extra cues such as
473 hatch order and soft rejection (e.g. lower feeding) to help identify parasitic chicks while reducing
474 the risk of mis-imprinting (Shizuka and Lyon, 2010, 2011). These models and empirical results
475 show that the cognitive mechanisms underlying how a species is able to recognize its eggs and
476 chicks plays an important role in the evolution of the host-parasite arms race.

477

478 Finally, a few studies have also begun to investigate the link between neurophysiology and the
479 ecology of brood parasites. Initial studies focused primarily on whole brain size or hippocampus
480 size in brood parasites and their non-parasitic relatives since each species should face different
481 ecological imperatives. Generally, whole brain size tends to be smaller in brood-parasites than
482 their closest relatives (Corfield et al., 2013; Iwaniuk, 2004; Overington, 2011), which could be
483 linked to less complex cognitive function needed in the absence of parental care in brood
484 parasites (Boerner and Krüger, 2008). Hippocampus size, however, varies predictably with the
485 need for excellent spatial memory in brood parasites. Brood parasites have an enlarged
486 hippocampus in the breeding season (Clayton et al., 1997), the sex that searches for nests tends
487 to have a larger hippocampus than the other sex (Reboreda et al., 1996; Sherry et al., 1993), and
488 brood parasites have a relatively larger hippocampus than closely related non-parasites (Corfield
489 et al., 2013; Reboreda et al., 1996). Furthermore, recent analysis has uncovered a specific region
490 of the hippocampus that is enlarged in parasitic species relative to others (Nair-Roberts et al.,
491 2006), suggesting brain regions may have evolved to manage the specific needs of brood
492 parasites relative to other spatial memory. These studies provide a rare example of direct linkage
493 between ecology and neurophysiology on a well understood fitness landscape. An exciting next

494 step in such systems could be to examine variation in neural structure with variation in the ability
495 of different hosts – either across or within a species – to reject parasitic eggs or chicks.

496

497 The above studies provide some of the best examples of how discrimination ability links with
498 cognitive decision making under natural ecological conditions. While many of these host-
499 parasite studies have not specifically been framed in terms of cognitive ecology, the focus on
500 discrimination, recognition, learning, and decision making are all clearly linked to cognition and
501 could further link to both specific cognitive abilities studied in other organisms and to
502 neurophysiological studies. Together with the strong understanding of the fitness costs and
503 benefits of host-parasite coevolution, these systems provide an excellent opportunity to link
504 cognition, neurophysiology, and evolutionary biology.

505

506 **Conclusion**

507 We have highlighted two ways to investigate the evolution of cognitive processes in animals: the
508 comparative approach focuses on evolutionary history while the fitness approach examines
509 contemporary selection. Much of our knowledge on the evolution of cognition comes from the
510 comparative approach and the full application of recently developed phylogenetic tools should
511 allow for interesting new results in this line of research. However, since cognition presents all
512 the characteristics of traits under selection (variation, heritability and fitness benefits), we believe
513 that taking the fitness approach to cognitive function will allow us to better explore the
514 evolutionary mechanisms that shape animal minds. Furthermore, the fitness approach more
515 easily allows us to integrate proximate and ultimate factors underlying animal cognition in a
516 single study, as suggested fifty years ago by Tinbergen (Tinbergen, 1963).

517

518 **4- Future directions**

519 The integration of evolutionary biology with cognitive sciences provides a very promising
520 avenue of research that could revolutionize our understanding of animal mind. Here we
521 highlighted how methods and new research questions in evolutionary biology could contribute to
522 our current understanding of the proximate basis of cognition. We believe the (unranked) top
523 priorities for the future are:

- 524 1) Identify cognitive functions that are crucial for species currently studied by evolutionary
525 ecologists and behavioural ecologists.
- 526 2) What are the fitness consequences of cognitive performance in the wild and what are the
527 ecological contexts under which that ability is favoured?
- 528 3) Are cognitive performance and/or neurocognitive processes consistent across different
529 environments for a given species? Are they consistent for a given individual if we can measure
530 cognitive abilities in the wild?
- 531 4) Can we create more ecologically relevant cognitive performance tasks that help link cognitive
532 abilities or brain structure to specific ecological challenges?
- 533 5) What environmental or social factors are associated with the evolution of specific cognitive
534 abilities or neural structures across species and what role do these abilities play in the speciation
535 process?
- 536 6) Are different cognitive abilities related to each other (i.e. positive correlation or trade-off)? Is
537 there compelling evidence for general intelligence in non-human animals?
- 538 7) Problem solving is the one “cognitive” task that has been related to fitness in wild animals.
539 However the cognitive mechanisms underlying this task remain unclear (Healy, 2012; Rowe and
540 Healy, 2014; Thornton et al., 2014). What are the fitness benefits of other well characterized
541 cognitive capacities such as visual cognition or associative learning?
- 542 8) What are the implications of cognitive performance for theory in evolutionary ecology and
543 conversely what does an ecological perspective on cognition tell us about neurocognitive
544 development?

545

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548

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846 **Figure captions**

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849 **Figure 1: Mate choice and cognitive capacities that could hypothetically play a role**

850 In bi-parental breeding songbirds, choosing an appropriate mate according to available male
851 stock, previous breeding experience and actual environmental conditions is a behaviour that will
852 have drastic fitness consequences for any female and that is likely to rely on the interplay
853 between various cognitive functions. Recognition of ornaments linked to different male qualities
854 (e.g. good genes, parental care, nest defense, etc.) uses perception (visual and auditory) to detect
855 male signals and categorization to group and identify male quality according to their ornaments
856 (1). The use of previous breeding experience relies on past learning linking male ornaments and
857 reproductive success from previous experiences (2). Mate choice itself, integrates all information
858 available to the female including current ecology, mate options, and past experience supposedly
859 through decision-making mechanisms (3). Finding the chosen mate, once the decision has been
860 taken, probably relies on spatial memory to relocate the territory defended by the chosen male
861 and endogenous attention to detect the chosen male from among the background of other males
862 and environmental features (4).

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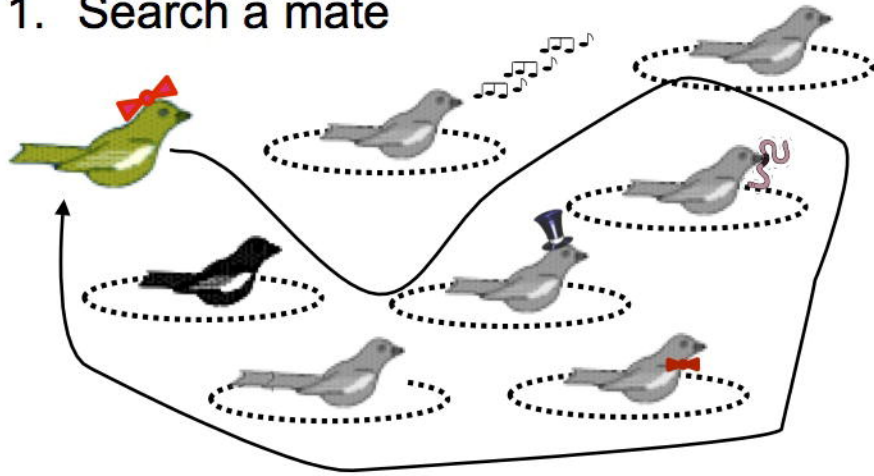
865 **Figure 2: How to study brain and cognition selection?**

866 Ideal evolutionary ecology studies of cognition should integrate socio-ecological (left panel, 1),
867 neurocognitive (middle panel, 2) and fitness (right panel, 3) variables. Such an approach seeks to
868 truly merge behavioural and evolutionary (green background) and cognitive neuroscience
869 (yellow background) methods. As examples:

870 1) Socio-ecological contexts of selection could correspond to natural gradients in sociality
871 (ie: Population density, gregariousness), habitat quality (ie: level of fragmentation,
872 urbanization) and/or distribution of resources (ie: harshness of the environment).
873 Experimental manipulations of ecological factors, such as variation in food
874 supplementation or reintroduction in a novel environment, are of particular interest to
875 isolate ecological causes of selection.

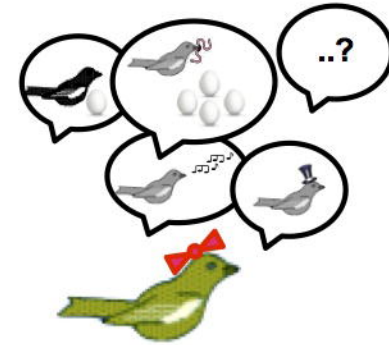
- 876 2) Cognitive abilities can be measured in the wild using foraging tasks. This approach has
877 been successfully adapted to measure perception, problem solving, learning, behavioural
878 flexibility and spatial cognition. Such methods rely on individual identification usually
879 mediated by visual tags (i.e. colour rings) or passive integrated transponders (PIT) tags.
880 However, some cognitive functions are difficult to measure in the wild and one may want
881 to have a better control on motivational state and environmental parameters. Short-term
882 period of captivity seems appropriate in such a framework and potentially enable us to
883 use up-to-date psychophysics protocols and equipment developed in comparative
884 cognition labs. Development of embedded cameras or microphones has the potentials to
885 reveal spontaneous cognitive capabilities like tool use, social cognition or vocal
886 communication. Likewise, neurologgers or transmitters enable us to measure brain
887 activity (electroencephalogram, single unit activity) in free ranging wild animals. Spatial
888 and whole brain measurement could also be assessed using MRI or PET devices through
889 short term scanning protocol.
- 890 3) The fitness benefit is traditionally assessed through evaluation of reproductive success or
891 a measure of survival. Behaviour associated with reproductive success (i.e. mating,
892 parental care) can also be used as proxies of fitness.
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1. Search a mate



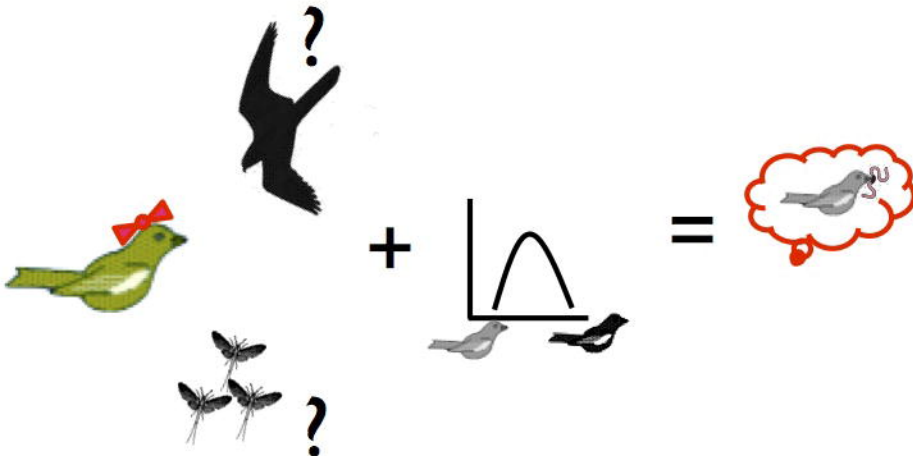
Perception, Categorization

2. Use previous mating experience



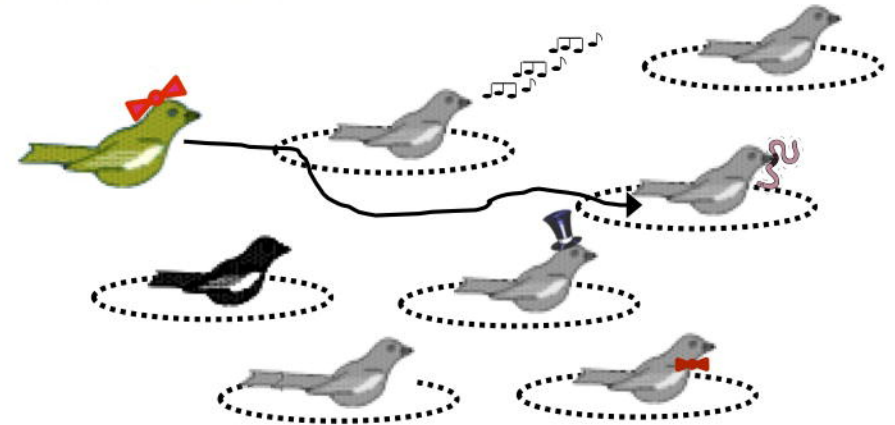
Learning, Memory

3. Integrate environmental information



Decision Making

4. Find chosen mate

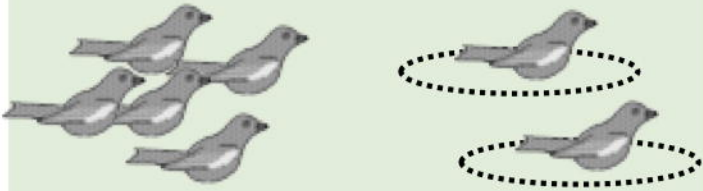


Spatial Memory, Attention

Socio-ecological context of wild populations

Natural gradient

Sociality



Habitat quality



Experimental gradient

Reintroduction



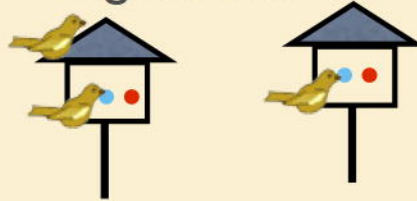
Food availability



Measure of brain and cognition

In the wild

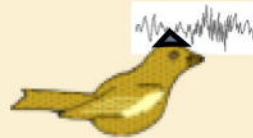
Cognitive Task



Embedded camera



Embedded neurologger



In short-term captivity

Psychophysics



Neuroimaging



Fitness and life history

Reproductive success



Survival



Behaviors

Parental care



Mate choice

