



What animals don't do or fail to find: A novel observational approach for studying cognition in the wild

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Abstract:	To understand how our brain evolved and what it is for, we are in urgent need of knowledge about the cognitive skills of a large variety of animal species and individuals, and their relationships to rapidly disappearing social and ecological conditions. But how do we obtain this knowledge? Studying cognition in the wild is a challenge. Field researchers (and their study subjects) face many variables that can easily interfere with variables of interest - confounding variables that are, some say, "impossible" to control for. In this review, I discuss the advantages and urgency of field-based studies on animal cognition and introduce a novel observational approach for field research that is guided by three questions: 1) What do foragers fail to find?, 2) what do they not do?, and 3) what do they only do when certain conditions are met? The approach is intended to give guidance to future data collection designs.

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What animals don't do or fail to find:

A novel observational approach for studying cognition in the wild

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field-based studies, chimpanzees, fruit, rainforest

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For Review Only

21 **Author Biography**

22 Karline Janmaat is a cognitive behavioral ecologist investigating the evolutionary function of
23 animal cognition. She is specialized in studying the cognitive strategies that human foragers
24 and wild apes and monkeys use in their daily search for food and has been observing them in
25 their rainforests for more than 20 years.

26

27 **Abstract (150 words)**

28 To understand how our brain evolved and what it is for, we are in urgent need of knowledge
29 about the cognitive skills of a large variety of animal species and individuals, and their
30 relationships to rapidly disappearing social and ecological conditions. But how do we obtain
31 this knowledge? Studying cognition in the wild is a challenge. Field researchers (and their
32 study subjects) face many factors that can easily interfere with their variables of interest.
33 Although field studies of cognition present unique challenges, they are still invaluable for
34 understanding the evolutionary drivers of cognition. In this review, I discuss the advantages
35 and urgency of field-based studies on animal cognition and introduce a novel observational
36 approach for field research that is guided by three questions: 1) What do animals *fail* to find?,
37 2) what do they *not do*?, and 3) what do they *only do when* certain conditions are met? My
38 goal is to provide guidance to future field researchers examining primate cognition.

39

40 **1 The comparative approach**

41 Comparison is fundamental in understanding the evolution of cognition (Box 1). Over the past
42 decades scientists from the fields of anthropology, psychology, and biology have employed
43 the comparative (phylogenetic) method to gain insights into the evolution of the animal
44 mind^{1,2,3,4} and to identify cognitive traits that are unique to humans and those that are shared

45 with other animals⁶. This work has focused on a variety of topics, ranging from comparisons
46 of primate skulls^{2,4,5} to that of gene-regulatory networks driving the earliest stages of cortical
47 development. Additional research on the evolution of cognitive traits is conducted by
48 inferring cognitive abilities from observed behaviors across species^{7,8}. By linking differences
49 in cognitive abilities with differences in current socio-ecological circumstances, hypotheses
50 about the evolutionary pressures that contributed to the positive selection of these abilities can
51 be tested and this can provide answers to the question of why the traits evolved^{3,4,9}. Drawing
52 inference about cognitive abilities from behavior is however not straightforward. Behavioral
53 scientists have therefore developed two approaches: the experimental approach and the
54 observational approach.

55

56 **2 How to study animal cognition?**

57 The first approach to infer cognitive mechanisms from behavior, often seen as the “gold
58 standard” in cognitive science, is the experimental approach. Shettleworth states: “It is almost
59 never possible to tell without experimental analysis what kinds of processes are reflected in a
60 given behavior”⁸ (p. 5). In lab or field-based experiments, scientists manipulate predictor
61 variables that are thought to influence the animal’s behavior. For example, by placing an
62 animal into a new environment and minimizing the number of landmarks it is familiar with,
63 we can test the animal’s ability to make novel short-cuts between newly-learned food
64 locations. This helps us to infer what type of mental representation of space the animal
65 made¹⁰. The second approach is to observe behavior in a natural environment without
66 manipulation (hereafter: an observational approach). In this particular example, we would
67 wait until an animal disperses into novel areas to know whether it can find novel short-cuts or
68 not. Clearly, experiments can make research more time efficient and at the same time make it
69 easier to distinguish between cause and effect. By comparing manipulated with un-
70 manipulated control conditions we can infer that it was only the manipulated variable that

71 affected the animal's response and not any other variable that happened to change
72 simultaneously with the variable of interest. This is particularly important when such
73 variables are naturally associated with each other. For example, if we play-back an alarm call
74 and the targeted monkey reacts, we can infer that it is only the sound that it reacted to and not
75 the smell or the body language of the animal that emitted the call¹¹. In other words, when
76 multiple sensory stimuli are always experienced simultaneously by the receiver in a natural
77 situation, an experiment is the only way to infer what information the receiver acts on.

78 Clearly, we have to assume causal relations are present¹², yet it is important to keep in
79 mind that causality can never be proven, whatever approach we take^{12,13}. Experiments simply
80 make it more likely that a change in one variable leads to a change in another variable, *ceteris*
81 *paribus* (other things being equal). Since other things rarely are equal, a balanced
82 experimental design is required. The difference between experimental and control conditions,
83 such as the vegetation density during a play-back of an alarm call in a tropical forest¹¹ may
84 not always be easy to measure. To better account for such a confounding variables(e.g., a
85 vegetation type that facilitates a predator's attack), we should balance the order and number
86 of control and experimental trials. In addition, we should randomize the assignment of
87 individuals to trials, to account for a difference between individuals. Though, this can be
88 difficult in most field and zoo experiments, where individuals cannot be separated from the
89 group. In addition, there is always a small probability that there was another variable acting
90 during the experiment that differed between both trials (caused by manipulation or chance,
91 e.g., a bird of prey flying by). Differences between experimental and control trials are less
92 likely to be balanced out when the number of trials one can conduct is limited due to
93 habituation effects or a small number of available subjects.

94 Differences between experimental and observational approaches are not always as clear
95 as is generally assumed. All experiments require observation, and experiments may not

96 control for all possible confounding variables. In these cases, experimental studies can by *a*
97 *posteriori* means statistically control for some confounding factors, such as motivation, that
98 could not be controlled for by the experimental design¹⁴⁻¹⁷. Similarly, observational studies
99 can, by *a priori* or *a posteriori* means, control for confounding variables, which increases the
100 likelihood of finding a cause and effect relationships substantially¹⁸⁻²⁰. In fact, some
101 experimental scientists describe experiments and non-experimental observational studies as
102 not categorically distinct methods, but rather place them at two ends of a continuum of
103 planned versus *post hoc* control for variation of predictor variables (see [21] for further
104 details).

105 In addition to being part of a continuum, both approaches are inseparable. The list of
106 experimental studies in cognitive science that were initially inspired by observational studies
107 on foraging, predator avoidance, and social behavior, is extensive^{14,22-28}. Yet, more
108 importantly, experiments have little value without previous field-based observational work.
109 To make sense of an animal's reaction to a manipulation, we first need to know how it reacts
110 to naturally occurring variation in that same variable. Furthermore, knowledge about failures
111 in experimental design²⁹ (e.g., due to distortions in broadcast speaker sound) only become
112 apparent once we know that the reaction to the manipulated variable is different from the
113 animal's reaction to naturally occurring variation in that same variable. Similarly, experiments
114 preceded by observational recordings of the subjects' behavior can help to explain cognitive
115 performance. Such combined approaches can, for example, help researchers avoid selecting
116 individuals that were recently involved in a social conflict before joining a cooperative
117 experimental task³⁰.

118 **3 Where to study cognition?**

119 It is not always considered ethically justifiable to manipulate wild and protected animals.

120 Therefore, many experiments that focus on highly endangered and protected animals, such as

121 great apes, take place in laboratories or zoos, where experimental manipulation does not
122 distract from or delay animals from, finding natural foods or detecting predators⁸. However,
123 that is often not the first argument brought forward to support this choice of research location.
124 When discussing the pros and cons of field- vs. captive-based studies in primatology,
125 Tomasello & Call³¹ wrote that “Other methodological challenges for field approaches to
126 primate cognition emanate from the impossibility of controlling all relevant factors under
127 “wild” conditions...”.

128 For example, if we refer back to the observation of the animal that dispersed to a new
129 area, we will never know whether the animal’s ability to make new shortcuts in the novel area
130 resulted from it using its own cognitive abilities, or by it simply following the new group
131 members it encountered³². This leads us to the question of where one can best study animal
132 cognition^{33,34}. Debates on what is the best environment to do so have been numerous^{23,37,38}. In
133 some fields of science, these debates led to the realization that a collaboration between lab
134 and field-based science, also termed the *synthetic* approach, is essential for improving
135 scientific insights^{9,39-42}.

136 In the field of primate cognition, which is most prominent in investigations on the
137 origins of human cognition, the debates, seem to have led to an alienation of each other’s
138 work. In fact, field and captive-based primatologists rarely read or cite each other’s
139 work^{33,34,35,36} (Box 2). This situation is unfortunate because it is especially the comparison of
140 natural habitat and captive studies can inform us about evolution^{40,41}.

141 A classic selection study in the field of evolutionary biology provides perhaps the best
142 example of a comparative field- and lab-based study that led to new insights. In this study, a
143 set of lab experiments found that in guppies (*Poecilia reticulata*) derived from high predation
144 localities had delayed senescence in comparison to counterparts from low predation localities,
145 while the field experiments showed the opposite effect³⁹. It was because of this difference in
146 results that evolutionary biologists came to understand that high predation risk leads to a

147 reduction in immune system investment, which has a different effect on the onset of
148 senescence in a parasite-free lab environment than in the field³⁹. This insight was only
149 obtained by studying the same species in the lab as well as in the wild.

150 Similar insights could be obtained in the field of primate cognition. For example,
151 studies on tool use can reach contrasting conclusions when the behavior of captive and wild
152 animals from the same species is compared. For example, bonobos (*Pan paniscus*), who (so
153 far) have not been observed to use tools in the wild to obtain food, were observed to use tools
154 in captivity⁴³. This difference in behavior helps us to obtain insight into the potential variables
155 that play a role in the development of cognitive abilities needed to perform complex forms of
156 tool use. Variables so far identified are 1) time available for exploration of objects, 2)
157 frequency of access to objects and 3) levels of distraction (by predation risk or a need to
158 search for food^{44,45}). Acknowledging these variables and linking them to ecological variables,
159 such as food availability, provides useful guidelines when designing statistical models that
160 investigate why some natural populations of primates use tools in some habitats, but not in
161 other habitats⁴⁶⁻⁴⁸.

162 Unfortunately, the number of cognitive abilities that have been studied in the same
163 primate species, both in the field and the lab, can often be counted on two hands. For
164 example, regarding studies that investigated whether chimpanzees are able to plan for the
165 future, defined as acting for a future motivational state²², I counted seven studies from
166 captivity (observational: 2^{49,50}, experimental: 5⁵¹⁻⁵⁵), and only one from the wild
167 (observational: 1¹⁹, experimental: 0). For episodic-like memory, defined as an ability to recall
168 “what”, “where” and “when” events occurred⁵⁶, I counted only two captive-based studies
169 (observational: 0, experimental: 2^{14,57}) and none in wild chimpanzees. The only study of
170 episodic-like memory in wild primates was done on capuchin monkeys using an experimental
171 approach⁵⁸.

172 To encourage future comparisons and collaborations between captive and field-based
173 primatologists, I here apply the expression “unknown, unloved”. As a field-based
174 observational scientist, in this paper, I explain the advantages of the observational field-based
175 approach through examples of my own work. By doing so, I will describe some of the
176 advantages of field-based science as well as the challenges faced in captive-based science.
177 Yet my aim is not to devalue captive-based nor experimental research, or to pit us against
178 each other. Rather, my aim is to make captive-based and experimental scientists think
179 critically about the challenges of their approach and hopefully become more open to, or
180 familiar with, the potential and advantages of observational field-work (Box 2). The ultimate
181 aim of this paper is to achieve a better appreciation of the value and urgency of observational
182 field-based science and to encourage collaboration among scientists using different
183 approaches - enabling us to benefit from our distinct expertise.

184

185 **4 The importance and urgency of field studies**

186 **4.1 Obtaining insight into evolutionary function**

187 Two sources of information are required to study the origin and evolutionary function of a
188 cognitive ability. First, one needs knowledge of how species’ cognitive abilities compare.
189 This information has been gathered in a plethora of studies in comparative psychology^{3, 8,}
190 ^{9,24,34,59,60}. Here field and captive-based scientists can reach similar conclusions^{8,61,62}. Second,
191 one needs knowledge on the socio-ecological context in which species use particular
192 cognitive abilities, to subsequently compare the existence of such contexts across species.
193 Then, both types of knowledge can be used in phylogenetic analyses to test hypotheses about
194 which evolutionary pressures contributed to the positive selection of a cognitive ability^{3,4,7,60}.
195 Hence, it is not sufficient to only compare which animals use particular cognitive skills, but it

196 is also of the utmost importance to compare the conditions in which these animals employ
197 these skills.

198 Shettleworth⁸ defined cognition as the mechanisms by which animals acquire, process,
199 store, and act on information from the environment, making the understanding of an animal's
200 environment and its interaction with it crucial for understanding its cognition. This
201 environment can be created and controlled in a lab or zoo, though the field allows for
202 understanding how different mechanisms and environmental factors interact and integrate⁸,
203 and in what contexts cognitive mechanisms are employed and can lead to evolutionary
204 benefits.

205 206 4.2 External validity

207 One other advantage of field-based science is that it provides external validity, meaning that it
208 enables us to test whether cognitive abilities identified in captive settings are used by the
209 animals under natural conditions^{41,42}. Such validity not only increases our confidence that
210 mechanisms were successfully identified^{41,42}, but it also helps us to understand why animals
211 in captive setting sometimes perform poorly in cognitive tasks. One classic example of
212 experiments that lack external validity and result in surprisingly poor cognitive performances
213 can be found in the field of spatial cognition (discussed in [63]). In a variety of delayed-
214 matching-to-sample tasks, primates need to remember at which spatially distributed objects or
215 food dispensers they received food and at which they did not. Single locations can be
216 remembered very well when the intervals between exposure and memory testing (retention
217 interval) are as short as 2 minutes⁶⁴. However, larger numbers of locations appeared to pose a
218 problem. Initial findings suggested that monkeys are only able to remember a very small
219 number of spatial locations for short time durations^{62,65,66}. Some of these studies led to the
220 conclusion that remembering large numbers may be a unique trait in apes⁶⁷ or that memory
221 skills are better in particular species of lemurs compared to others⁶⁸. In many of these

222 experiments, food locations were not stable, the primates only had one exposure and the
223 retention intervals were often very short and did not match with variables impacting foraging
224 decisions in the wild^{63,65,67,68}. In the wild, visits to novel food sources such as newly-emerged
225 fruit are usually separated by one day to one week^{62,69,70}. Furthermore, only a few food
226 sources have not been visited before^{62,69,70}. For example, in chimpanzees, the average number
227 of fruit trees fed in per day that was “new” within our long consecutive follows of 28-44 days
228 was only four⁷¹, and across years our follows suggested that many locations had already been
229 learned in previous years⁶⁹. When Menzel and Junco^{72,73} tested Andean saddleback tamarins
230 (*Saguinus fuscicollis illigeri*, which is now referred to as *Leontocebus illigeri*), the
231 researchers were the first to use learning schedules that were similar to those likely used in the
232 wild. They introduced novel food locations one at a time with 24 hours between each novel
233 presentation and the testing phase. This approach resulted in 1) one-trial learning, 2) a
234 memory of up to 30 locations, and 3) food locations being remembered for up to 77 days^{72,73}.
235 These results strongly contrasted to earlier findings that lacked external validity.⁶⁶ Matching
236 the value of other variables that impact foraging decisions in the wild, such as social
237 variables, *i.e.* allowing primates to forage in a social group, improved memory
238 performances¹⁷ as well. The emission of food calls, in such social groups are likely associated
239 with positive emotions⁷⁴, which potentially contributed to the consolidation of memory traces.
240 Overall these considerations of natural foraging behavior likely contributed to the exceptional
241 performances of the tamarins tested^{72,73} and may explain differences in performance in other
242 species^{75,76}.

243

244 4.3 Motivation and challenging complexity

245 Rosati and colleagues²⁵ compared the cognitive performance of chimpanzees (*Pan*
246 *trogodytes*) and humans (*Homo sapiens*) by offering them a choice between a small
247 immediate reward and a large delayed reward²⁵. Humans surprisingly chose a larger reward,

248 with a delay of 2 minutes, only 20% of the time that a choice was offered, while chimpanzees
249 did so 70% of the time²⁵. We know, however, that humans are able to delay gratification and
250 can wait for larger rewards, and for example invest money to gain profits years later. Indeed,
251 when the researchers conducted an additional study, and changed the reward to offer money
252 instead of food, humans were more often willing to wait for a larger reward than for a smaller
253 immediate reward. The study is a perfect illustration of how important motivation is when
254 testing cognitive abilities. Currently, a growing number of studies suggest that a lack of
255 evidence for cognitive skills could have been a result of a lack of motivation or interest by the
256 study subject⁷⁷⁻⁷⁹. For example, studies that took into account bond strength in subject dyads,
257 before subjects were set up to participate in a cooperative task, are more likely to find
258 evidence for cooperative abilities compared to those studies that paired subjects up
259 randomly^{15,30,80,81}. Cognitive tasks with human demonstrators were completed more
260 successfully by enculturated or human-oriented apes, which had more contact with (and
261 perhaps more control over) human actions, compared to zoo-housed apes^{35,77,79,82}. Similarly,
262 chimpanzees who watched a chimpanzee demonstrator performed better in imitation tasks
263 than chimpanzees who watched a human demonstrator^{26, 79}. Scientists who conducted the
264 study suggested that the chimpanzees might lack the motivation to imitate another species⁷⁹.
265 Cognitive experiments that involved researchers dressed up as their study subject's species
266 and behaving like them suggested that the subjects were motivated to look at what the
267 (dressed up) researchers were doing and what they had "in mind"²⁷. This study by Krupenye
268 and colleagues²⁷ was the first in decades to find strong evidence that non-human apes have a
269 theory of mind.

270 Other studies indicated how important it is to challenge study subjects and to provide
271 many options when trying to test for cognitive skills^{83,84}. When Schubiger et al.⁸⁴ provided
272 common marmosets (*Callithrix jacchus*) and squirrel monkeys (*Saimiri sciureus*) with the
273 option to indicate where food was hidden in a two-choice task, for which the chance of

274 success is 50%, both species performed dramatically worse than when they were challenged
275 to remember one location out of nine⁸⁴. Similarly, when Girndt et al.⁸³ found that when apes
276 were offered a choice between pulling two prepositioned rakes to obtain food, where one of
277 the rakes would push the food into a trap, they failed to choose the correct rake above
278 chance⁸³. However, when they were challenged to use only one rake where they had to choose
279 to move the rake to either side (the side with the trap or the side without) to eventually pull
280 the food towards them, 80% of the apes made the correct choice in the first trial. In short,
281 these studies show how complexity in study design can drastically alter results and how more
282 complex or challenging tasks can trigger animals to perform better.

283 One clear advantage of testing cognitive skills of animals in their natural habitat
284 compared to those in captive settings is that wild animals need to be motivated and interested
285 to perform cognitive skills to obtain naturally occurring food and mates. This does not mean
286 that animals in the wild are always more motivated to employ a cognitive skill than animals in
287 captivity. For example, the motivation of wild animals to participate in field experiments is
288 described as being lower than in captive animals that are likely to have fewer distractions,
289 predetermined foraging plans, or fear of novel objects or food^{21, 28}. In addition, there are
290 observational field studies that suggest that motivation (e.g., to walk straight and fast toward
291 sleeping or feeding sites) was low at particular times and areas^{85, 86}. Furthermore, not all
292 cognitive skills may necessarily lead to increased access to food or mates. Yet, motivation to
293 employ cognitive skills to obtain food (which is the most common reward for cognitive tasks
294 in captivity) is likely to be overall lower in captive than in wild animals for the simple reason
295 that wild animals are not provisioned. Motivation in wild animals may be particularly high in
296 food-scarce periods, when foragers experience periods in which they catabolize major
297 amounts of body fat, lack particular nutritional compounds, and need to minimize group size
298 ⁸⁷⁻⁸⁹.

299

300 4.4 Lots of space: Body movement, experience, and cognitive development

301 The natural environment is characterized by its information complexity and a relatively large-
302 scale distribution of food and mates. For example, when an animal locates food, it receives
303 sensory information about odor, the sound of other foragers, and visual aspects of food
304 sources. When it has a memory of the food location and value, this knowledge needs to be
305 integrated with sometimes conflicting sensory information^{90,91}. Exposure to a variety of
306 information sources may lead to particular ontogenetic changes in the nervous system⁹². For
307 example, enabling the development of particular types of mental maps¹⁰. In cognitive science,
308 there is a growing consensus that sensory changes produced by motor actions are critical for
309 both development and maintenance of cognitive capacities⁹³. Animals that are never exposed
310 to a large variety of information and that lack the ability for large scale self-movement to
311 integrate environmental cues may show relatively lower performance levels than animals that
312 have those opportunities¹⁰. This effect can be observed in captive-bred golden lion tamarins
313 (*Leontopithecus rosalia*) that showed low spatial performance when they were released in a
314 large-scale space⁹⁴ compared to related tamarin species in the wild^{95,96}.

315 While group sizes in a captive environment increasingly approach natural values, group
316 sizes are still lower than those observed in natural habitats in many captive settings¹⁰⁸. In
317 addition, the total number of individuals that captive animals have had opportunities to learn
318 from in a life time are relatively low, due to lower rates of dispersion, migration and births .
319 Therefore, animals in the wild have the potential to learn social and ecological skills from a
320 potentially larger number of individuals⁹⁷⁻⁹⁹. Individuals do not need to rely on a small
321 number of group members that share their enclosure, especially when these other individuals
322 may all not possess the cognitive capacity at stake. Hence, one of the advantages of working
323 with wild animals is that cognitive abilities have likely developed to their full extent, due to a
324 particularly high variety of social and sensory input and large-scale movement abilities.

325 Moreover, wild animals are less likely to endure uncontrollable stress that is known to
326 result in aberrant behaviors and signs of depression in many captive animals¹⁰⁰⁻¹⁰⁴.
327 Enrichment conditions have improved substantially over the years, and most experiments are
328 conducted on a voluntary basis. Yet animals that are most often subject to cognitive tests,
329 such as primates, cetaceans, corvids, and elephants are all long-lived animals,¹⁰⁵⁻¹⁸ and a
330 history of uncontrollable stress, including social and nutritional stress and unnatural rearing
331 conditions (e.g., not being reared by the mother) can have long-term effects on brain
332 morphology¹⁰⁹⁻⁻¹¹⁰. The increased number of studies conducted with sanctuary animals,
333 especially on social cognition is particularly worrisome¹¹¹, as these animals have likely
334 endured high levels of social and nutritional stress before reaching these sanctuaries¹¹², but see
335 ¹⁰¹. For example, social deprivation during infancy is known to have negative effects on the
336 development of social skills and cognition¹¹³, resulting in shorter play bouts that lead to more
337 aggression in chimpanzee orphans compared to mother-reared chimpanzees¹¹⁴.

338

339 4.5 Urgency

340 Lastly, it must be emphasized that field studies are urgent. We can study animals in the
341 laboratory or zoo for the next 100 years, but we cannot say the same for many animals in the
342 wild. Natural habitat, especially of tropical forest primates, is disappearing at rapid speed¹¹⁵⁻
343 ¹¹⁷. This rapid decline of the rainforest environment and the primate populations that are
344 dependent on it creates a high level of urgency to study animals in their natural habitat.

345 When collecting behavioral data on wild animals, advanced technologies that enable
346 camera trap or audio triangulation methods are increasingly applied^{99,118-120}. Such
347 technological advances enable us to study behavior (through observations or experiments) in a
348 highly non-invasive manner and to avoid the risks associated with habituation, such as disease
349 transmission¹²¹. Such approaches make it possible to study wild animals without the need for
350 long-term commitment to protecting the habituated animals from poachers. It is, however, the

351 long-term commitments for studying wild populations that stanches their rapid decline, as
352 sheer researcher presence significantly decreases poaching and logging activities in the study
353 areas¹²². Field primatologists have a tradition of studying a diverse array of primate
354 species^{21,108} including many populations within these species^{123, 124}. The number of species
355 and populations clearly outnumber those in captivity¹⁰⁹, creating an inspiring potential for
356 comparative research that is disappearing in front of our eyes¹¹⁵⁻¹¹⁷.

357 Having summarized the advantages of field-based studies, the question still remains
358 whether it is actually possible to study cognitive abilities in the wild and how we can control
359 for confounding variables, especially when we work with highly endangered animals for
360 which experiments are rarely possible. Tomasello & Call³¹ were not the only ones to express
361 concern about the difficulties of studying animals in the wild. For example, Pritchard et al.²⁸
362 wrote: “As nearly all of this control is difficult if not impossible to achieve in the
363 experimental study of animals cognition in the wild, this can be a major downside to
364 attempting to investigate animal cognition in the wild”. In addition, MacDonald & Ritvo¹²⁰
365 wrote: “More importantly, obtaining sufficient control over extraneous variables is often
366 impossible.” In the following sections, I describe the approaches I used to deal with many of
367 these proposed difficulties. In addition, I provide guidelines (Fig.1) for future data collection
368 designs.

369

370 **5 Five steps to investigate cognitive abilities in wild animals by observation**

371 In his seminal work on the aims and methods of ethology, Tinbergen¹²⁵ expresses his concern
372 about the unequal ratio of experimental and observational studies, describing contempt for
373 simple observation as “a lethal trait in any science”. In the same paper, he writes “our science
374 will always need naturalists and observers as well as experimenters; we must, by a balanced
375 development of our science, make sure that we attract the greatest possible variety of talent,
376 and certainly not discourage the man with a gift for observation”. It is, therefore, striking that

377 an updated guideline for observational fieldwork to study animal cognition is lacking to date,
378 despite the many guidelines that are provided for experimental fieldwork^{9,28,29,31,41,42}.
379 Responding to this, as well as to Tinbergen's plea for a more balanced approach (Box 2), I
380 will focus on describing five steps that combine novel and traditional methods.

381

382 **5.1 Step 1. Choosing a study species**

383 The first step in starting an observational field study on animal cognition is to choose the
384 study species. The choice obviously firstly depends on one's questions. However, practical
385 guidelines can be provided (see also Martin & Bateson¹²⁶). Two important criteria proposed
386 by Pritchard et al.²⁸ are that the species should be "reliable" and "observable". Chimpanzees
387 fit these criteria exceptionally well. First, most primates show high levels of site fidelity and
388 can, therefore, be easily relocated across field seasons³². Second, chimpanzees are observable,
389 meaning they do not fly away, dive underwater or live underground but can relatively easily
390 be observed throughout the day. Furthermore, individual chimpanzees, as in most primate
391 species, can be identified without being marked. Another important criterion when choosing a
392 study species or population is that sufficient existing knowledge is available about the
393 behavior and the socio-ecological environment of the selected animals. The latter is essential
394 for the identification of crucial situations (Step 2) and the exclusion of alternative variables
395 (Step 3).

396

397 **5.2 Step 2. Identifying crucial situations**

398 To identify crucial situations in which animals would likely employ particular cognitive skills,
399 we can make use of the decades of field research on a large variety of species that reveal
400 insights into the challenges animals face in comparison to others in their natural habitat¹³¹.
401 For example, previous research shows that chimpanzees have a relatively costly form of long-
402 distance terrestrial locomotion compared to quadrupedal monkeys^{128,129}, and are

403 morphologically and/or physiologically limited in their digestion abilities¹²⁷. They cannot eat
404 highly toxic seeds (e.g., *Anthonota fragans*) or mature leaves, as can other primates such as
405 sooty mangabeys (*Cercocebus atys*¹⁸) and many Colobinae¹⁰⁶. Yet their large body and brain
406 rely on energy-rich tropical forest food, such as large crops of ripe fruit.^{129,130} Tai
407 chimpanzees spend 85% of their feeding time on ripe fruit,⁷⁴ and even in fruit scarce periods,
408 females still continue to eat ripe fruit 67% of their time¹³¹. Yet, ripe fruits are rare; in some
409 chimpanzee territories, ripe fruit-bearing tree density of edible species was estimated to be 17
410 times lower than that of trees that bear unripe fruits¹²⁷. Large ripe fruit crops that can “host”
411 an average chimpanzee party are even rarer and can have a complex distribution in space and
412 time¹²⁷. To deal with this challenge, we can hypothesize that wild chimpanzees create a
413 mental representation of food locations and values in time, through a large variety of
414 cognitive mechanisms, such as a memory of distant past events, flexible planning and keeping
415 track of proportions of fruit-bearing trees within species, *i.e.*, intuitive statistics¹²⁷. Hence, by
416 investigating the behavior of chimpanzees during their daily search for ripe fruit we can
417 expect to be able to identify the use of a number of cognitive skills. I provide a detailed
418 example of one more specific foraging situation below.

419 Identifying situations in which animals likely employ certain behaviors in their natural
420 habitat is nothing new and has a long tradition in the field of ethology^{8,38}. Many studies that
421 revealed that animals use cognitive abilities resulted from considerations of the benefits of
422 using them in the natural habitat^{56,132}. Making *a priori* predictions about the particular
423 information and skills animals in the wild “should” use is, however, not always
424 straightforward and requires extensive knowledge of their behavior as well as the
425 characteristics of their socio-ecological environment. For example, rufous hummingbirds
426 (*Selasphorus rufus*) choose flowers in the “correct” spatial location (where they previously
427 found food) over flowers of the “correct” color (at which they previously found food)^{28,133}.
428 Considering that hummingbird-pollinated flowers have evolved in response to hummingbird

429 foraging, it could be expected that they would pay more attention to color²⁸. However, if one
430 considers that flowers become depleted or differ in the amount of food they produce, a
431 prediction that the birds remember the location of the flowers instead of only the color may
432 better match observational findings²⁸. Dependent on the situation (e.g., the spatial scale),
433 animals should prioritize knowledge based on memory over particular forms of sensory
434 information, or the other way around^{28,92,134}.

435

436 5.2.1 A detailed example: Flexible planning- Returning to fruit trees at the right time

437 To identify a situation in which chimpanzees might use flexible route planning, I made use of
438 the following ecological and behavioral information. Rainforests are typically characterized
439 by a large biomass of fruit-consuming foragers that compete for fruit and can easily deplete a
440 large, productive, ripe fruit-bearing tree after it has been fed in by a chimpanzee¹³⁵.

441 Sympatric monkeys, though seldom ripe fruit specialists, do eat ripe fruit and can easily
442 deplete the few ripe fruits that are in a tree when chimpanzees are foraging elsewhere,
443 especially when these fruits are eaten by many other foragers. Figs (*Ficus spp.*), for example,
444 are eaten by more animal species than any other plant genus¹³⁶. When we visited chimpanzee
445 feeding trees, we found that sympatric species of monkeys, hornbills and squirrels were more
446 likely to be found foraging in a fig tree than in chimpanzee feeding trees of other fruits
447 species¹⁹.

448 Small fruits are also a sought-after resource. They can be eaten by a large number of
449 bird species, for example, because they are simply easier to swallow and can be eaten at faster
450 rates when processing surfaces (e.g., teeth) are small^{137,138}. Long-term phenology data of
451 chimpanzee feeding trees (11 yrs) further indicated that ripe fig fruits and small fruits are less
452 persistent¹⁹. These fruits are more ephemeral and stay in the trees for shorter periods than
453 other fruits.

454 The combination of this ecological and behavioral information helped to identify a
455 situation in which it could be beneficial to plan a return to fruit trees and to arrive earlier than
456 competitors at these types of fruits. First, the significant differences in ephemerality level of
457 chimpanzee food sources created a situation in which some of the first food they eat in the
458 morning (hereafter: breakfast food) would be more quickly depleted than others. Second, the
459 variation in distances between chimpanzee sleeping and breakfast sites created a situation in
460 which arrival times would be later at sites that are further away, and would thus likely result
461 in ending travel at a depleted tree if one would not plan to depart earlier to reach such trees.
462 Hence, the combination led to the prediction that chimpanzees would benefit from flexibly
463 planning their early morning departure times (see Step 4; “Question 3: Under what particular
464 conditions do chimpanzees plan?” for a description of how this was tested).

465 In a similar way, variation among food production rates of individual trees^{71,127,139}
466 creates a situation in which it could pay to be able to differentiate between individual food
467 trees and to remember feeding experiences across seasons or years. This discriminative ability
468 would then enable foragers to not approach just any tree at the start of a season but instead to
469 approach particularly those that are likely to bear large amounts of fruits. Hence, I chose the
470 situation where food production rates varied substantially, to investigate whether or not
471 chimpanzees use a memory of distant past events (see Table 1 for more examples of other
472 cognitive abilities).

473

474 **5.3 Step 3. Excluding as many alternative explanations as possible**

475 There are many variables that can explain a behavior. The cognitive mechanism of interest to
476 a researcher is only one of them⁸. For example, an animal that travels in a straight line
477 towards a food source may have navigated by using a mental representation of the food (using
478 a particular mental map), but it could at the same time have used sensory cues, such as the
479 fruit’s conspicuous color, or a searching rule (“go straight until you bump into a food

480 source”). These possibilities challenge cognitive scientists who want to infer the use of a
481 particular cognitive ability by observing behavior.

482 Hence, to test for particular cognitive abilities, it helps to think of many alternative
483 explanations, ideally before the start of data collection. While determining alternative
484 explanations, we are greatly aided by the growing number of studies on animal behavior in
485 the wild and historical knowledge from long-term field sites about individuals and their socio-
486 ecological environment^{21,127,140,141}. This development results in a growing biological
487 knowledge that can and should be used in data collection designs. For example, when
488 designing a statistical model to test for planning abilities by predicting nest departure time, I
489 could make use of a total of 46 field studies ranging from 1960 to 2013 to understand which
490 variables should be included to predict primate sleeping site departure time. In addition,
491 advances in data collection technologies such as high resolution, long-term bio-logging¹⁴²⁻¹⁴⁴
492 camera trapping^{96,119,145}, satellite and aerial imaging¹⁴⁶, and long-term field sites^{21, 140,141,147}
493 that have decades of contextual data to draw from, provide the data that can help to rule out
494 alternative explanations through statistical methods (Step 5).

495 Another way to rule out alternative explanations is through observational control. This
496 control is achieved by quantifying the information animals could use, such as the sensory cues
497 that food or mates emit (see an example below). We can also pose the question, what do
498 animals fail to do? (see Question 1 below). These lines of complementary scientific progress
499 allow us to reason more wisely about the variables that most likely affect an animal’s
500 behavior.

501

502 5.3.1 An example – Are primates using sensory cues or memory?

503 One of the most difficult challenges facing field-based scientists who investigate spatio-
504 temporal memory or route planning is to rule out the use of sensory cues as an alternative
505 explanation for observed behavior. For example, some plant species that rely on seed

506 dispersal can substantially increase the amount of scent emitted from ripe fruit, such that
507 primates can distinguish them more easily from unripe fruits¹⁴⁸, and likely detect them from
508 larger distances. One of the most frequently used methods in primatology to rule out the use
509 of sensory cues is to estimate the distances at which the study species can perceive food or
510 other animals^{36,69,85,118,149}. Being primates ourselves sometimes helps to make these distances
511 more realistic. On an olfactory level, humans, similar to non-human primates are sensitive to
512 isoamyl acetate, the major component in a large variety of fruit odours^{71,150,151}. Although, the
513 exact link between olfactory receptor genes and odorous ligands is still unclear, humans also
514 have a comparable and even slightly larger estimated number of functional olfactory receptor
515 genes than other primates¹⁵². On a visual level, comparative studies indicate that visual acuity
516 thresholds are lower for human than for nonhuman primates, which have typically smaller
517 eyes and hence smaller retinal image size^{153,154}. This enables us to assume that if humans
518 cannot see something, neither can most other diurnal primates. Of course, the human
519 observer's senses may be adapted to different light levels and may not be as trained as those
520 of the study subjects, yet detection distance estimations could make certain simulated
521 detection distances (e.g., >100m) highly unlikely, leaving the use of spatial memory as the
522 most likely explanation.¹⁵⁵

523 Perhaps a better option to rule out the use of sensory cues as an alternative explanation
524 is to incorporate certain behavioral processes, such as feeding competition, to one's
525 predictions. An example of such an approach is the study of Tujague & Janson³⁶, who
526 investigated the approach speed of tufted capuchin monkeys (*Sapajus nigritus*) towards food
527 trees. They ingeniously predicted that the number of individuals that can benefit from early
528 arrival at food trees would increase initially with fruit amount, but would eventually plateau
529 or even decline as food availability becomes large enough to allow all group members to feed.
530 Their data supported the idea that the monkeys were considering the amount of fruit as well as
531 the level of competition they would face at the feeding tree. The tested effect made it highly

532 unlikely that the monkeys had simply been guided by sensory cues, as this would have
533 predicted a linear effect of fruit amount on speed, as opposed to the nonlinear relationship
534 they found.

535 The easiest observational way to rule out search strategies that are guided by sensory
536 cues is to investigate only approach behavior towards foraging goals that do not emit a strong
537 smell or have a conspicuous color, such as water holes,^{144,156} or to focus on food species or
538 types that do not emit any smell or visual cue that indicates edibility^{18,36}. Another option is to
539 investigate what animals fail to find because food sources are depleted or did not yet produce
540 food. Asking this question can be particularly informative when investigating cognitive
541 mechanisms that can help animals to find food or mates.

542

543 Question 1: What do chimpanzees fail to find? - Informative failing

544 To test whether chimpanzees employ intuitive statistics to improve foraging efficiency, our
545 team followed five female chimpanzees in the Tai National Park in Cote d'Ivoire, totaling 275
546 days in three food-scarce periods (Fig. 2). During these periods we, marked all trees that the
547 chimpanzees fed in or inspected and recorded their location with a GPS. To know the history
548 of tree visits and to be able to detect the beginning of fruit-feeding periods, we decided to
549 prioritize on the duration of our follows instead of the number of individuals we followed⁷¹.

550 The expectation was that the chimpanzees would use intuitive statistics to more often inspect
551 highly synchronous fruit species, for which they had a high success rate of finding fruits.
552 Hence, we predicted that their inspection behavior would be guided by botanical knowledge.
553 Importantly, we focused on inspections of *empty trees*. These trees did not bear any fruits, nor
554 did they have fruits on the ground, and they could not emit any sensory cues like color or
555 smell, or cues emitted by foraging animals that could have triggered the chimpanzees to look
556 up. By recording when the female chimpanzees looked up at the crown and failed to find
557 food, we gained insight into their expectations about finding food. Since fruits, and thus

558 sensory cues, were absent, we argued that their behavior must have been guided by their
559 botanical knowledge, and was thus able to exclude relevant explanatory variables, such as the
560 use of smell or vision, by *observational control*. In other words, by recording failing behavior,
561 it was possible to determine what chimpanzees were likely expecting – making their failures
562 become informative (*informative failing*). Since the number of inspected trees that were
563 empty was substantial (38% of all inspected trees), we could analyze what influenced the
564 probability of inspecting empty trees. In addition, we measured fruiting synchrony levels of
565 the different fruit species from 11 years of phenology data. To rule out the alternative
566 explanation that the chimpanzees were simply conditioned and were more likely to inspect
567 trees that belonged to species at which they fed earlier more often, we included fruit-bearing
568 tree density as a control in our statistical model. This also enabled us to control for the
569 possibility that the chimpanzees were sensitive to the absolute number of fruit-bearing trees
570 they had encountered, regardless of their proportion. Controlling for this, we found that it was
571 the synchrony level and thus the proportion of trees that bore fruits that had a significant
572 effect on inspection probability of empty trees⁷¹. Hence by recording informative failing
573 behavior we found evidence that chimpanzees used intuitive statistics, *i.e.*, they had
574 expectations about the different success rates of food finding of particular species, irrespective
575 of their density. This ability to distinguish between proportions of food items was later tested
576 and confirmed in an independent study in captive chimpanzees,^{157,158} providing an example of
577 how field and captive-based studies on the same species can complement each other and
578 strengthen the evidence for an animal's cognitive ability.

579

580 **5.4 Step 4. Increasing detection probability of the cognitive abilities of interest**

581 In the same way that behavior can be an expression of many different mechanisms; a
582 cognitive mechanism can express itself through many different behaviors. For example,
583 primates may exhibit their use of a spatio-temporal memory of a food source by 1) rapid

584 travel^{18,159}, 2) highly linear travel^{86,160}, 3) making significant changes in travel
585 direction^{69,161,162}, 4) changing travel direction at long distances before arrival⁷⁴, or by 5)
586 revisiting after particular intervals^{56,163}. Although such behavioral diversity may appear
587 overwhelming at first, it can also be an advantage that can help fieldworkers gain insight into
588 the decision-making of the animal and detect the use of certain cognitive abilities by applying
589 the rules of parsimony. Before data collection, it can help to design a protocol that considers a
590 suite of behaviors known to potentially express the cognitive skill of interest. Such a protocol
591 should also record behaviors that indicate what animals do not do, or only do when certain
592 conditions are met. To explain this in more detail, I show two examples from my studies on
593 chimpanzees.

594

595 Question 2: What do chimpanzees not do? - Quasi-experiments

596 To find out whether chimpanzees employed an across-seasons or year-long memory of the
597 fruiting states of individual trees, I investigated the probability that chimpanzees would
598 inspect individual trees that they had fed in during previous years. To control for confounding
599 variables, such as sensory cues, I not only investigated what chimpanzees did, but also what
600 they did not do (when they did not inspect, *i.e.* the non-events²¹). In an experimental
601 approach, it is as important to know when the animal reacts as well as when it does not react
602 and to record the non-events²¹. Similar to an experiment, I sampled the context prior to the
603 observations in the “testing” phase and investigated whether the context was decisive of
604 whether the study subjects did or did not react (event vs. non-event). Yet, contrary to
605 traditional experiments, I did not manipulate but rather conducted a so-called *quasi-*
606 *experiment*. This is defined by Janson²¹ as a realm of focused observations taken under
607 conditions that account for variation in one or a few hypothesized causal variables, without
608 any actual manipulation of those variables. Thus, I used data from unique follows of one adult
609 female during the three subsequent years. The first year our team followed and marked all the

610 feeding trees visited by the target female during 28 consecutive days. During the second and
611 third years, we followed the same female for eight continuous weeks, which included the
612 same period as the first year to ensure we would cover the same fruiting seasons. Then I
613 analyzed the female's ranging routes in 2011 in relation to the locations of the feeding trees
614 from 2009 and 2010. Next, I investigated which variables influenced the probability that the
615 chimpanzee female inspected one of these trees on the first approach within the respective
616 fruiting season. I recorded when the female inspected but also when she did not inspect (the
617 non-event) all the trees that she approached to within the detection distance but did not feed
618 on (*i.e.* trees that were unlikely to bear edible fruit).

619 By recording events as well as non-events, we were able to calculate the inspection
620 probability of trees that were approached the year(s) after. We found that after controlling for
621 confounding variables, both the number of feeding visits (familiarity) in the previous years
622 and the maximum amount of fruits found in the feeding trees in previous years had an effect
623 on inspection probability⁶⁹. Therefore, we were able to find evidence that this chimpanzee
624 used an across-seasons memory when deciding which fruit trees to monitor by recording what
625 the study animal did, but by also recording what she did not do. These findings support
626 experimental studies in captivity, which showed that chimpanzees can remember tool
627 locations for at least 3 years⁵⁹. In this case the fieldwork provided ideas about the adaptive
628 value of such a memory of distant past events, as fruit-bearing trees have fruiting intervals
629 that range from 1 to 16 years^{69,127}.

630 The initial idea for a quasi-experimental approach was developed during a study on
631 spatial memory in mangabeys (*Lophocebus ugandae*)^{18,21}. To determine whether this species
632 uses spatial memory of feeding trees' fruiting states, we pre-sampled the context by traversing
633 a monkey group's home range. We then selected a large number of fruit-bearing and empty
634 trees from the same species prior to following the monkeys. It was only after this pre-

635 sampling that we recorded which trees the monkeys did and did not visit. Since my team
636 followed the group for continuous periods of up to 100 days, we were able to compare the
637 visiting probability of fruit trees that had been depleted by the mangabey group earlier in the
638 observation period with the visiting probability of trees that did not bear fruit yet. Since both
639 tree crowns and fruit fall areas were empty, sensory cues could not explain why depleted trees
640 were avoided, and the best explanation of the observed results was that the monkeys were
641 indeed using a spatial memory of fruiting states¹⁸. Both studies on foraging cognition in
642 chimpanzees and mangabeys indicated that recordings of non-events are equally informative
643 as recording what animals do. A similar approach is widely used in the fields of ecology
644 (resource selection¹⁶⁴) and epidemiology referred to as case-control studies¹⁶⁵.

645

646 Question 3: Under what particular conditions do chimpanzees plan?

647 To further increase the probability of detecting the use of cognitive abilities by wild
648 chimpanzees I continued to test what chimpanzees do only when certain conditions are met. I
649 was inspired by Noser & Byrne⁸⁵, who found evidence that chacma baboons (*Papio ursinus*)
650 departed their sleeping cliffs earlier in fig season than in periods when they fed on other less
651 sought-after food. Combining this knowledge with the finding of significant differences in
652 ephemerality levels of chimpanzee food, I investigated whether chimpanzees plan to leave
653 their sleeping nest earlier to feed on highly sought-after ephemeral fruits than when they feed
654 on other fruits. I predicted that nest departure times would be influenced by a number of
655 variables, including the ephemerality level of the fruits (fruit size and type), the fruit genus
656 (figs or other fruits), and a large number of control variables suggested from earlier studies
657 that affect primate sleeping site departure time¹⁹. We found that the chimpanzees departed
658 earlier to feed on figs, but only when the fig trees were far away¹⁹. Since arrival time for
659 distant figs was similar to arrival time at nearby figs, we concluded that chimpanzees left their
660 sleeping nest earlier to feed on figs that were far away, to make up for travel time and to

661 arrive at about the same time as when the fig trees were close to their feeding trees. Perhaps
662 more intriguing was the finding that the females sometimes departed as much as two hours
663 later when they fed on other kinds of fruits. We concluded that chimpanzees delayed their
664 departure when there was little competition with other species, such as for *Panda oleosa* nuts
665 that can only be opened by chimpanzees through tool use. In this case, female chimpanzees
666 (all with young and vulnerable offspring) reversed their behavior relative to moving toward
667 fig trees, avoiding early-morning departures when they could not easily reach food by
668 climbing short distances through the canopy but had to travel long distances along the forest
669 floor where leopards are active¹⁹.

670 Alternative explanations for a given behavior can always be brought forward *a*
671 *posteriori*. For example, one could argue that the chimpanzees that happened to depart early
672 could eat from the fig tree, while the ones that happen to depart later missed out on the figs,
673 and hence had to feed on other foods. To discard such explanations, it is crucial to decide *a*
674 *priori* to record a suite of behaviors that can indicate planning behavior. For example, the
675 above explanation can be made highly unlikely if one considers first, the distances the
676 chimpanzees travelled, second, their speed of approach, third, the skittish behavior of the
677 early risers treading along the forest floor in the dark, and four, the finding that no fig trees
678 were inspected nor entered before feeding on the other fruits (see [19]) for a discussion of
679 other alternative explanations). First, having recorded the distances and arrival times, we
680 found that the females arrived at about the same time at the breakfast figs that were far away
681 and those that were nearby, making it unlikely that late departures simply resulted in females
682 missing out on figs and ending up eating another kind of fruits. Second, travel speed data
683 informed us that chimpanzees travelled to fig trees more quickly than towards other breakfast
684 sites, supporting that they planned their trips. Third, the observed skittish behavior of the early
685 risers makes it highly unlikely that females would “happen” to depart early for no reason.
686 Lastly, if the chimpanzees simply missed out on finding figs after late departures, we should

687 have observed that they inspected or entered depleted trees before feeding, which was not the
688 case. Arguably, each of the above behaviors could potentially be explained by yet another set
689 of alternative explanations; however, following the rule of parsimony, we concluded that
690 flexible planning is the simplest explanation for this combination of behaviors.

691 It was especially important to think of potential interactive effects when understanding
692 the chimpanzees' decision-making and the roles of competition and predation risk. In this
693 case, we tested for an interactive effect between fruit type and distance from the nest to the
694 feeding tree and tested what chimpanzees do (e.g., depart early for figs) when certain
695 conditions (e.g., a long distance) are met. Studies that investigate the interactive effects of
696 ecological variables on animal behavior can infer complex cognitive abilities. Other examples
697 can be found in the tool use context. Wild chimpanzees were observed to be more likely to
698 select heavy tools to crack nuts, yet only when they would crack nuts on the ground, but not
699 when they had to take the tool up into a tree to crack nuts on a branch²⁰. Similarly, the same
700 chimpanzees were more likely to select heavy tools, but not when the tools were far away
701 from the anvil and had to be transported over long distances²⁰.

702 The more dimensions an animal needs to take into account, the more likely those
703 particular combinations have never been encountered before and will therefore be *novel*,
704 especially when competition frequently changes these conditions. Chimpanzees reuse the
705 same tools¹⁶⁶. Hence tools are likely to be found at different locations each time a
706 chimpanzee revisits the same cracking site. The same level of complex thinking applies to
707 chimpanzee decisions to depart earlier to feed in a distant fig tree compared to those that are
708 nearby. It is true that we do not know where the chimpanzees had been before we started
709 observing them and thus the early departure for distant figs could have resulted from the
710 chimpanzees having learned associations between the time of day and the distance to certain
711 fig trees and a low or high availability of figs (time-place associations⁸). However, we do

712 know that fig trees get depleted after 1.9 feeding visits on average and that Taï chimpanzees
713 make their nest at different locations 98% of the time. Hence, the opportunity for conditional
714 prior learning is limited, making the use of flexible route planning and conditional decision-
715 making a more plausible explanation of the observed behavior¹⁹. Similar novel situations are
716 likely to occur in conditional decision making in the social realm, such as whom to mate with,
717 groom or be social with, as ranks and group compositions continuously change¹⁶⁷.

718 Not knowing what the animals have done before observations take place can make it
719 difficult to exclude associative learning explanations in field studies, yet it is important to bear
720 in mind that the same problem applies to captive-based studies where we rarely know what
721 animals have experienced before their arrival in the zoo or laboratory¹⁶⁸. Perhaps one could
722 argue that the higher probability of prior associative learning in wild animals will lead to more
723 false positives (type I errors) in field-based compared to captive-based studies. However,
724 cases where cognitive abilities in captivity were only confirmed after many experimental
725 studies²⁷, suggest that captive studies are more prone to false negatives (type II errors). This
726 further stresses the importance of studying the same mechanisms in captivity as well as in the
727 wild.

728

729 **5.5 Step 5. Controlling by Statistical Design – Controlling the uncontrollable**

730 Lastly, we can use advanced statistical methods to investigate the cognitive abilities of wild
731 animals. The latest developments in the field of hierarchical or generalized linear mixed
732 modelling¹⁶⁹⁻¹⁷¹ enable us to use repeated observations conducted on the same individuals.
733 This makes it unnecessary to average or aggregate months of data collected on one individual
734 to one single data point, which has dramatic consequences for sample size, power, and
735 statistical analyses. The ability to use repeated observations of the same individuals has
736 become especially valuable for scientists who investigate an animal's long-term memory by

737 obtaining a complete picture of the animal's experience over time and by observing one
738 individual for extensive periods. These studies only allow for a limited number of study
739 subjects within the duration of most scientific funding periods.

740 For example, in 2004, my colleague and I collected 18 months of data on 7 to 8 individual
741 male and female mangabeys, respectively. To analyze the data we were not able to do much
742 more than simple Mann-Whitney U tests¹⁷³. Statistical tests that are appropriate for small
743 datasets make it impossible to take more than two predictor variables into account¹⁷⁴. Mixed
744 or hierarchical modeling techniques such as Generalized Linear Mixed Modelling¹⁷³ (SI; Fig.
745 S1) enable behavioral scientists to use more data, and thus to include many categorical as well
746 as quantitative predictor variables (to be tested or controlled for) and their interactive effects
747 to predict behaviours^{169,170}. Hence, these techniques enable us to draw much stronger
748 conclusions using purely observational data on animal behavior than was possible in the past.

749 We furthermore no longer need to throw away data that were recorded close in space or
750 time to avoid a spatio-temporal dependency of data points. While the approaches are still
751 under development, there are several ways in which scientists can account for autocorrelation
752 between data points taken at short intervals of time or space^{71,171}, allowing researchers to use
753 most or all of their original data. In short, we can embrace all or most of our data and use it to
754 control for many if not all relevant factors. These statistical models, in addition, provide large
755 flexibility with regard to the response variables with diverse distributions (Table 2¹⁶⁹) and also
756 with regard to unbalanced data collection.

757

758 5.5.1 An example controlling for evening travel distance to test for future planning

759 Since chimpanzees make their sleeping nests at different locations in the forest, I could
760 investigate whether chimpanzees position their nest closer or more *en route* to ephemeral

761 fruits. The difference between evening arrival direction and morning departure direction from
762 chimpanzee nests can be influenced by many variables. For example, when figs are rare, a
763 small difference in degree may be caused by the fact that the chimpanzees were traveling
764 towards the fig tree in the evening, but were unable to reach it before dusk, because the fig
765 tree was far away. This could have resulted in chimpanzees making a nest on the way to the
766 morning feeding tree without the use of future planning skills. Therefore, controlling for
767 overall travel distances between the last evening and early morning breakfast locations and
768 the possibility that the nest positioning simply reflected a failed attempt to reach a late night
769 feeding site was crucial. By use of statistical control we found that chimpanzees made their
770 nest more *en route* to fig trees used in the morning as opposed to other morning feeding sites
771 and were indeed planning for the next day¹⁹.

772

773 **6 Conclusions and Future Directions**

774 Being selective in the data we record is something field scientists have been trained to do for
775 decades^{125,175}. The information one could record while studying an animal in its natural
776 habitat is often so overwhelming that choices needs to be made about the variables to record
777 to best answer the research questions. During this process, priority is often given to behaviors
778 that the target animal performs, such as the trees it visits, how long it eats, how many other
779 animals are present, or whom it grooms. To record when it does not perform certain
780 behaviors (e.g., when it does not approach or inspect a tree, pick up a tool or groom an
781 individual, or when it fails to find food or mates) does usually not have obvious value.
782 Furthermore, such recordings can require a time investment; one needs to first sample the
783 context (e.g., mark all the trees with and without fruit in the home range), and this will take
784 away time from the behavioral observations one can do within a limited study duration. By
785 providing examples of studies in which such investments paid off, I hope to have created an
786 understanding that this extra time spent can be worthwhile for future studies.

787 I hope that such future studies will include collaborations between field and captive-
788 based scientists. Specifically, where similar questions will be asked for the same species in
789 the laboratory and in the field. I envision a variety of joint goals.

790 First, captive-based studies can provide insights into the role of genetic predispositions
791 in the development of capacities, such as episodic-like memory, by being able to confront the
792 animals with challenges they have never faced in the wild (e.g., presenting ice lollies¹⁴) while
793 field studies can enable us to investigate the evolutionary value of that same mechanism and
794 enlighten us on the type of predispositions we can expect^{18,58,176}.

795 Second, collaboration can help us to better understand the extent of cognitive plasticity.
796 For this, it is essential to study the capacities of populations that live in different
797 environmental conditions¹⁷⁷⁻¹⁷⁹. The field offers a wide range of variability^{48,180}. Hence,
798 comparative studies on cognitive performances of wild and captive animals provide a wealth
799 of opportunities to determine which factors are important for the development of particular
800 cognitive skills.

801 Third, collaboration can improve the rigor of field science and to study animals in
802 conditions where experiments are not feasible. To return to an earlier example of alarm calls,
803 determining whether a monkey reacts to a call or to another sensory signal, such as a caller's
804 body movement, is a challenge when you are unable to do experiments. Having more
805 knowledge on the detection distances of these signals could enable field scientists to exclude
806 visual cues and could enable us to extend the research to species and locations where
807 experiments are not feasible. Studies on such sensory abilities, especially on olfactory
808 detection fields, are surprisingly limited to date (but see [150,151,153,154,181,182]) and
809 would greatly strengthen the conclusions field-based science can draw.

810 Fourth, field scientists can provide ideas for new captive-based testing contexts, or a
811 way to control for biases in performances. For example, many cooperation studies involve
812 food-sharing activities^{80,81}, which likely results in an unintended bias for high cooperative
813 performance scores in food-sharing species. Having detailed knowledge on the behavior of
814 wild animals, provides an opportunity to control for levels of food-sharing behavior in a
815 comparative phylogenetic analysis, as well as ideas for new contexts in which to test for
816 cooperative abilities in captive animals.

817 Finally, there is a new interdisciplinary field emerging to study the adaptiveness of
818 cognitive abilities⁹. Cognition clearly is essential for a wide range of behaviors that are
819 needed for survival and reproduction^{8,9}. This raises the question of why there is individual
820 variation and plasticity in cognitive performance. Experiments in the lab suggest that some
821 cognitive traits are heritable, yet only a few studies so far have dared to address the question
822 of the consequences of lower levels of cognitive performance and how cognitive abilities or
823 performances are linked to life-history traits or fitness⁹. This challenging question can clearly
824 only be answered by combining our best possible collaborative skills.

825 I envision collaborations where scientists using both approaches better familiarize
826 themselves with the values of each other's work. In particular, I hope that improved field-
827 based approaches produce results that obtain a higher status than is sometimes assigned by
828 captive-based researchers. I especially hope the guidelines provided here, will trigger young
829 scholars to go to the field and reset the balance between field and captive based studies (Box
830 2). By identifying crucial contexts, collecting data on a suite of behaviors (e.g., recording
831 what animals do not do, or only do when certain conditions are met), controlling for
832 interfering variables by conducting observational control (e.g., recording what animals fail to
833 find), and by combining this technique with well-thought-out statistical models, based on
834 decades of biological knowledge, we are able to infer conclusions about the cognitive

835 abilities of wild animals. What is important to always remember is that every approach has
836 benefits and challenges. Consequently, using complementary approaches is more likely to
837 yield novel insights in primate cognition and move the field in exciting new directions.
838 Perhaps we are even on our way to make the “impossible” possible.

839

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853 Box 1: Cognition

854 Cognition, defined as the mechanisms by which animals acquire, process, store, and act on
855 information from the environment⁸, can result in declarative knowledge (knowing that) and
856 procedural knowledge (knowing what to do⁸). For example, when an animal is searching for
857 food it could have knowledge about the exact locations of, and directions between, the food and
858 a small hill, or it could simply only know that if it wants to find food, it needs to turn right
859 when it reaches the small hill. Knowing what an animal knows and what cognitive mechanisms
860 it uses is not simply derived from observing what an animal does. Hence, behavioral science
861 has developed experimental and observational approaches to infer cognition from behavior.
862 Different types of cognition can lead to a variety of knowledge that can help an animal to find,
863 access, and guard food and mates. For example, to find food, animals may use foraging
864 cognition³³, *i.e.* mechanisms that acquire, process, store and act upon 1) sensory information
865 about the cues emitted by foods^{91,69,119,183}, 2) spatial information of the locations and efficient
866 route of travel^{18,157,184}, 3) temporal information of the timing of a visit, or return^{58,176,185}, 4)
867 ecological information of the characteristics of food sources and competitors (e.g., level of
868 ephemerality, synchrony, fruit production and depletion rates^{19,71,70, 74,186,187}), and 5) social
869 information about the decisions or knowledge of group members^{33,188,189}. All these information
870 types can either result in declarative or procedural knowledge. A cognitive scientist's challenge
871 is to find out by looking at the outside what type of knowledge is processed on the inside.

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874 Box 2: The imbalanced distribution and diffusion of knowledge in Primate**875 Cognition**

876 A recent study investigated how knowledge derived from research in either captive or natural
877 environments is represented in the literature on primate cognition, and to what degree captive
878 and field approaches for data collection are used in these two types of studies¹⁹⁰. For this
879 study, Glabischnig¹⁹⁰ selected 16 review and theoretical papers focusing on primate cognition
880 and the types of studies (field vs. captive) that were cited by the respective authors were
881 counted (Table S1, S2).

882

883 Distribution of type of studies across all cited publications

884 Glabischnig¹⁹⁰ found 583 (66.55%) references to studies conducted on primates in
885 captive environments and 293 (33.45%) references to studies in natural environments (Table
886 S1, S2). These figures suggest a highly unbalanced availability or distribution of knowledge
887 on primate cognition from natural versus captive environments. Captive-based studies largely
888 applied experimental techniques and only 15% used purely observational methods in their
889 research. In contrast, studies in natural environments mainly applied observational methods
890 and used experimental techniques in 28% of cases (rates include studies that incorporated
891 both, experiment and observation, Table S1).

892 Captive-based studies were cited at a higher rate than field-based studies by captive-
893 oriented primatologists (317 captive *versus* 48 natural studies cited). Citations of their field-
894 based colleagues showed a more equal distribution (266 captive *versus* 240 natural studies
895 cited). This was also reflected by the average ratio of captive-based/field-based studies for
896 captive-oriented (8.27) and field-oriented primatologists (1.28; Table S2). In addition, there is
897 a notable difference in the kind of field-based studies that were referenced by the two
898 different types of researchers. While field-oriented researchers cited experimental studies in

899 the wild more than 30% of cases, their captive-oriented colleagues cited the same type of
900 study about 8% of the time (percentages include also studies that include field experiments as
901 well as a combination of experimental and observation studies; Table S3).

902 There is one outlier among the publications from field-oriented primatologists with a
903 high lab/field ratio (ratio: 4.59; Table S2). Interestingly, this publication is a collaborative
904 paper between field and captive oriented researchers. The collaboration seems to have
905 resulted in a lower ratio of lab/field studies than the average ratio for captive oriented
906 primatologists, as well as a much higher absolute count of field study citations than any paper
907 from captive oriented primatologists (Table S2).

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912 References

- 913
- 914 [1] Romanes GJ. 1884. *Mental evolution in animals*. New York: Appleton.
- 915 [2] Harvey PH, Krebs JR. 1990. Comparing brains. *Science* 249: 140–146.
- 916 [3] Reader SM, Hager Y, Laland KN. 2011. The evolution of primate general and cultural
917 intelligence. *Philos Trans R Soc Lond B Biol Sci* 366 (1567): 1017-1027.
- 918 [4] DeCasien AR, Williams, SA, Higham JP. 2017. Primate brain size is predicted by diet but not
919 sociality. *Nat Ecol Evol* 1: 0112.
- 920 [5] Falk D. 2012. Hominin paleoneurology: where are we now? *Prog. Brain Res* 195: 255-272.
- 921 [6] Hansen DV, Lui JH, Parker PR, Kriegstein AR. 2010. Neurogenic radial glia in the outer
922 subventricular zone of human neocortex. *Nature* 464 (7288), 554-561.
- 923 [7] Deaner RO, Isler K, Burkart J, Van Schaik C. 2007. Overall brain size, and not encephalization
924 quotient, best predicts cognitive ability across non-human primates. *Brain Behav Evol* 70 (2): 115-
925 124.
- 926 [8] Shettleworth SJ. 2010. *Cognition, evolution, and behavior*. Oxford University Press.
- 927 [9] Morand-Ferron J, Cole EF, Quinn JL. 2016. Studying the evolutionary ecology of cognition in
928 the wild: a review of practical and conceptual challenges. *Biol Rev* 91(2): 367-389.
- 929 [10] Jacobs LF, Menzel R. 2014. Navigation outside of the box: what the lab can learn from
930 the field and what the field can learn from the lab. *Mov Ecol* 2(1): 3.
- 931 [11] Schel AM, Zuberbuehler K. 2009. [Responses to leopards are independent of experience](#)
932 [in *Guereza colobus* monkeys](#). *Behaviour* 146:1709-1737.
- 933 [12] Popper KR. 1959. *The logic of scientific discovery*. University Press.
- 934 [13] Hume D. 1793. *Untersuchung über den menschlichen verstand*. Jena. Verlag der
935 akademischen Buchhandlung. p. 49-84.
- 936 [14] Martin-Ordas G, Haun D, Colmenares F, Call J. 2010. Keeping track of time: evidence
937 for episodic-like memory in great apes. *Anim Cogn* 13 (2): 331-340.

- 938 [15] Engelmann JM, Herrmann E, Tomasello M. 2015. Chimpanzees trust conspecifics to
939 engage in low-cost reciprocity. *Proc R Soc B* 282(1801): 20142803.
- 940 [16] Crockford C, Wittig RM, Mundry R, Zuberbühler K. 2012. Wild chimpanzees inform
941 ignorant group members of danger. *Curr Biol* 22(2): 142-146.
- 942 [17] Schel, AM, Machanda Z, Townsend SW, Zuberbühler K, Slocombe KE. 2013.
943 Chimpanzee food calls are directed at specific individuals. *Anim Behav* 86 (5): 955-965.
- 944 [18] Janmaat KRL, Byrne RW, Zuberbühler K. 2006. Evidence for a spatial memory of
945 fruiting states of rainforest trees in wild mangabeys. *Anim Behav* 72 (4): 797-807.
- 946 [19] Janmaat KRL, Polansky L, Ban SD, Boesch C. 2014. Wild chimpanzees plan their
947 breakfast time, type, and location. *Proc Natl Acad Sci USA* 111 (46): 16343-16348.
- 948 [20] Sirianni G, Mundry R, Boesch C. 2015. When to choose which tool: multidimensional
949 and conditional selection of nut-cracking hammers in wild chimpanzees. *Anim Behav* 100:
950 152-165.
- 951 [21] Janson CH. 2012. Reconciling rigor and range: observations, experiments, and quasi-
952 experiments in field primatology. *Inter J Primatol* 33 (3): 520-541.
- 953 [22] Raby CR, Clayton NS. 2009. Prospective cognition in animals. *Behav Processes* 80(3):
954 314–324.
- 955 [23] Tomasello M, Call J. 2008. Assessing the validity of ape-human comparisons: A reply to
956 Boesch (2007). *J Comp Psychol* 122 (4): 449-452.[http://dx.doi.org/10.1037/0735-](http://dx.doi.org/10.1037/0735-7036.122.4.449)
957 [7036.122.4.449](http://dx.doi.org/10.1037/0735-7036.122.4.449).
- 958 [24] Balda RP, Kamil AC. 1989. A comparative study of cache recovery by three corvid
959 species. *Anim Behav* 38:486–495.
- 960 [25] Rosati AG, Stevens JR, Hare B, Hauser MD. 2007. The evolutionary origins of human
961 patience: temporal preferences in chimpanzees, bonobos, and human adults. *Curr Biol* 17
962 (19): 1663-1668.

- 963 [26] Horner V, Whiten A, Flynn E, de Waal FBM. 2006. Faithful replication of foraging
964 techniques along cultural transmission chains by chimpanzees and children. Proc Natl Acad
965 Sci USA 103: 13878-13883.
- 966 [27] Krupenye C, Kano F, Hirata S, Call J, Tomasello M. 2016. Great apes anticipate that other
967 individuals will act according to false beliefs. Science 354 (6308): 110-114.
- 968 [28] Pritchard DJ, Hurly TA, Tello-Ramos MC, Healy SD. 2016. Why study cognition in the
969 wild (and how to test it)? J Exp Anal Beh 105(1): 41-55.
- 970 [29] Wittig RM, Crockford C. 2018. Chimpanzees: Investigating cognition in the wild. In
971 Bueno-Guerra N, Amici F, editors. Field and laboratory methods in animal cognition.
972 Cambridge: Cambridge University Press, p. 115-145.
- 973 [30] Engelmann JM, Herrmann E. 2016. Chimpanzees trust their friends. Curr Biol 26 (2):
974 252-256.
- 975 [31] Tomasello M, Call J. 2011. Methodological challenges in the study of primate cognition.
976 Science 334 (6060): 1227-1228.
- 977 [32] Janmaat KRL, Olupot W, Chancellor RL, Arlet ME. 2009. Long-term Site Fidelity and
978 Individual Home Range Shifts in *Lophocebus albigena*. Intern J Primatol 30(3): 443-466.
- 979 [33] Zuberbühler K, Janmaat KRL. 2010. Foraging cognition in nonhuman primates. In: Platt
980 ML and Ghazanfar AA, editors. Primate neuroethology. New York: Oxford University Press
981 p. 64-83.
- 982 [34] Rosati AG. 2017. Foraging Cognition: Reviving the Ecological Intelligence Hypothesis.
983 Trends Cogn Sci <http://dx.doi.org/10.1016/j.tics.2017.05.011>.
- 984 [35] Leavens DA, Bard KA, Hopkins WD. 2017. The mismeasure of ape social cognition.
985 Anim Cogn, 1-18, <https://doi.org/10.1007/s10071-017-1119-1>.
- 986 [36] Tujague MP, Janson CH. 2017. Wild capuchin monkeys anticipate the amount of ripe
987 fruit in natural trees. Anim Cogn 20(5): 841-853.

- 988 [37] Boesch C. 2007. What makes us human (*Homo sapiens*)? The challenge of cognitive
989 cross-species comparison. *J Comp Psychol* 121: 227–240.
- 990 [38] Röell DR 2000. *The World of Instinct: Niko Tinbergen and the Rise of Ethology in the*
991 *Netherlands (1920-1950)*. Uitgeverij Van Gorcum. p.166-171.
- 992 [39] Reznick DN, Ghalambor CK 2005. Selection in Nature: Experimental Manipulations of
993 Natural Populations. *Integr Comp Biol* 45(3): 456-462.
- 994 [40] Wilson DS, & Whitehouse H. 2016. Developing the field site concept for the study of
995 cultural evolution. *Cliodynamics* 7(2).
- 996 [41] Kamil AC. 1988. A synthetic approach to the study of animal intelligence. Leger DW
997 editor. *Behavioral mechanisms in evolutionary ecology*. University of Nebraska Press, p.
998 230-257.
- 999 [42] Kamil AC. 1998. On the proper definition of cognitive ethology. In: Balda RP,
1000 Pepperberg IM, Kamil AC, editors. *Animal cognition in nature: The convergence of*
1001 *psychology and biology in laboratory and field*. San Diego, Academic Press. p. 1-28.
- 1002 [43] Van Schaik CP, Deaner RO, Merrill MY. 1999. The conditions for tool use in primates:
1003 implications for the evolution of material culture. *J Hum Evol* 36(6): 719-741.
- 1004 [44] Haslam M. 2013. ‘Captivity bias’ in animal tool use and its implications for the
1005 evolution of hominin technology. *Philos Trans R Soc Lond B Biol Sci* 368(1630): 20120421.
- 1006 [45] Toth N, Schick KD, Savage-Rumbaugh ES, Sevcik RA, Rumbaugh DM. 1993. Pan the
1007 tool-maker: investigations into the stone tool-making and tool-using capabilities of a bonobo
1008 (*Pan paniscus*). *J Archaeol Sci* 20 (1): 81-91.
- 1009 [46] Meulman EJ, Sanz CM, Visalberghi E, van Schaik CP. 2012. The role of terrestriality in
1010 promoting primate technology. *Evol Anthropol* 21(2): 58-68.
- 1011 [47] McGrew, WC, Ham RM, White LJT, Tutin CEG, Fernandez M. 1997. Why don't
1012 chimpanzees in Gabon crack nuts? *Int J Primat* 18(3): 353-374.

- 1013 [48] Barrett BJ, Monteza-Moreno CM, Dogandižić T, Zwyns N, Ibañez A, Crofoot MC.
1014 2018. Habitual stone-tool aided extractive foraging in white-faced capuchins, *Cebus*
1015 *capucinus*. bioRxiv. <http://dx.doi.org/10.1101/351619>.
- 1016 [49] Osvath M. 2009. Spontaneous planning for future stone throwing by a male chimpanzee.
1017 *Curr Biol*, 19(5): R190-R191.
- 1018 [50] Osvath M, Karvonen E. 2012. Spontaneous innovation for future deception in a male
1019 chimpanzee. *PloS one*, 7(5): e36782.
- 1020 [51] Mulcahy NJ, Call J. 2006. Apes save tools for future use. *Science* 312: 1038–1040
1021 (doi:10.1126/science.1125456).
- 1022 [52] Osvath M, Osvath H. 2008 Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*)
1023 forethought: self-control and pre-experience in the face of future tool-use. *Anim Cogn* 11:
1024 661–674.
- 1025 [53] Beran MJ, Perdue BM, Bramlett JL, Menzel CR, Evans TA. 2012. Prospective memory
1026 in a language-trained chimpanzee (*Pan troglodytes*). *Learn Motiv* 43(4): 192-199.
- 1027 [54] Dufour V, Sterck EHM. 2008. Chimpanzees fail to plan in an exchange task but succeed
1028 in a tool-using procedure. *Behav Process* 79: 19–27.
- 1029 [55] Osvath M, Persson T. 2013. Great apes can defer exchange: a replication with different
1030 results suggesting future-oriented behaviour. *Front. Com. Psychol* 2: 698
1031 (doi:10.3389/fpsyg.2013.00698).
- 1032 [56] Clayton NS, Dickinson A. 1998. Episodic-like memory during cache recovery by scrub
1033 jays. *Nature* 395 (6699): 272.
- 1034 [57] Menzel CR. 2005. Progress in the study of chimpanzee recall and episodic memory. In:
1035 Terrace HS, Metcalfe J, editors. *The Missing Link in Cognition: Origins of Self-Reflective*
1036 *Consciousness*. Oxford. Oxford University Press. p. 188–224.
- 1037 [58] Janson CH. 2016. Capuchins, space, time and memory: an experimental test of what-
1038 where-when memory in wild monkeys. *Proc R Soc*, 283(1840): 20161432.

- 1039 [59] Martin-Ordas G, Berntsen D, Call J. 2013. Memory for distant past events in
1040 chimpanzees and orangutans. *Curr Biol* 23 (15): 1438-1441.
- 1041 [60] MacLean EL, Hare B, Nunn CL, Addess, E, Amici F, Anderson RC, ... & Boogert NJ
1042 2014. The evolution of self-control. *Proc Natl Acad Sci USA*, 111(20) :2140-2148.
- 1043 [61] Tolman EC.1948. Cognitive maps in rats and men. *Psychol Rev* 55(4): 189.
- 1044 [62] Kramer G. 1952. Experiments on bird orientation. *Ibis* 94(2): 265-285.
- 1045 [63] Cunningham EP 2003. The use of memory in *Pithecia pithecia* 's foraging strategy.
1046 *PhD* thesis, City University of New York.
- 1047 [64] Martin-Ordas G, and Call J. 2011. Memory processing in great apes: the effect of time
1048 and sleep. *Biol Letters* 7(6): 829-832.
- 1049 [65] Harlow HF, Mears C. 1979. The human model: Primate perspectives. New York: Wiley.
- 1050 [66] Tinklepaugh OL. 1932. Multiple delayed reactions with chimpanzees and monkeys.
1051 *Comparative Psychology* XIII (2) 207-243.
- 1052 [67] Gallistel CR, Cramer AE. 1996. Computations on metric maps in mammals: getting
1053 oriented and choosing a multi-destination route. *J Exp Biol* 199(1): 211-217.
- 1054 [68] Rosati AG, Rodriguez K, and Hare B. 2014. The ecology of spatial memory in four
1055 lemur species. *Anim Cogn* 17: 947-961.
- 1056 [69] Janmaat KRL, Ban SD, Boesch C. 2013. Chimpanzees use long-term spatial memory to
1057 monitor large fruit trees and remember feeding experiences across seasons. *Anim Behav* 86
1058 (6): 1183-1205.
- 1059 [70] Cunningham E, Janson C. 2007. Integrating information about location and value of
1060 resources by white-faced saki monkeys (*Pithecia pithecia*). *Anim cogn* 10(3): 293-304.
- 1061 [71] Janmaat KRL, Ban SD,Boesch C. 2013. Taï chimpanzees use botanical skills to discover
1062 fruit: What we can learn from their mistakes. *Anim Cogn* 16 (6), 851-860.
- 1063 [72] Menzel EW, Juno C. 1982. Marmosets (*Saguinus fuscicollis*): Are learning sets learned?
1064 *Science*, 217(4561): 750-752.

- 1065 [73] Menzel EW, Juno C. 1985. Social foraging in marmoset monkeys and the question of
1066 intelligence. *Philos. Trans. R. Soc. Lond. B*, 308(1135): 145-158.
- 1067 [74] Ban SD, Boesch C, Janmaat KRL. 2014 Taï chimpanzees anticipate revisiting high-
1068 valued fruit trees from further distances. *Anim Cogn* 17(6):1353–1364.
- 1069 [75] Prétôt L, Bshary R, Brosnan SF. 2016. Comparing species decisions in a dichotomous
1070 choice task: adjusting task parameters improves performance in monkeys. *Anim Cogn*, 19(4):
1071 819-834.
- 1072 [76] Salwiczek LH, Prétôt L, Demarta L, Proctor D, Essler J, Pinto AI, Wismer S, Stoinski T,
1073 Brosnan SF, Bshary R. 2012. Adult cleaner wrasse outperform capuchin monkeys,
1074 chimpanzees and orang-utans in a complex foraging task derived from cleaner client reef fish
1075 cooperation. *PLoS ONE* 7:e49068.
- 1076 [77] Call J, Tomasello M. 1996. The effect of humans on the cognitive development of apes.
1077 In: Russon AE, Bard KA, Parker ST, editors. *Reaching into thought*. New York: Cambridge
1078 University Press. p 371–403.
- 1079 [78] Buttleman D, Carpenter M, Call J, Tomasello M. 2007. Enculturated chimpanzees
1080 imitate rationally. *Dev Sci* 10 (4): 31-38.
- 1081 [79] Buttleman, D, Carpenter M, Call J, Tomasello M. 2013. Chimpanzees, Pan troglodytes,
1082 recognize successful actions, but fail to imitate them. *Anim Behav* 86 (4): 755-761.
- 1083 [80] Melis AP, Hare B, Tomasello M. 2006. Engineering cooperation in chimpanzees:
1084 tolerance constraints on cooperation. *Anim Behav* 72: 275–286.
- 1085 [81] Suchak M, Eppley TM, Campbell MW, de Waal FBM. 2014. Ape duos and trios:
1086 Spontaneous cooperation with free partner choice in chimpanzees. *PeerJ*, 2, e417.
- 1087 [82] Damerius LA, Forss SIF, Kosonen ZK, Willems EP, Burkart, JM, Call J, Galdikas BMF,
1088 Liebal K, Haun DBM, van Schaik CP. 2017. Orientation toward humans predicts cognitive
1089 performance in orang-utans. *Sci Rep* 7: 40052.

- 1090 [83] Girndt A, Meier T, Call J. 2008. Task constraints mask great apes' ability to solve the
1091 trap-table task. *Journal of Experimental Psychology: Anim Behav Proc* 34 (1), 54.
- 1092 [84] Schubiger MN, Kissling A, Burkart JM. 2016. How task format affects cognitive
1093 performance: A memory test with two species of New World monkeys. *Anim Behav* 121: 33-
1094 39.
- 1095 [85] Noser R, Byrne RW 2007. Travel routes and planning of visits to out-of-sight resources
1096 in wild chacma baboons, *Papio ursinus*. *Anim Behav* 73: 257–266.
- 1097 [86] Jang, H., Boesch, C, Mundry, R. Janmaat KRL (in review) Travel linearity and speed of
1098 human foragers and chimpanzees during their daily search for food in tropical rainforests. *Sci*
1099 *Rep*
- 1100 [87] Vogel ER, Knott CD, Crowley BE, Blakely MD, Larsen MD, Dominy NJ 2012. Bornean
1101 orangutans on the brink of protein bankruptcy. *Biol Lett*, 8(3): 333-336.
- 1102 [88] Knott CD. 1998. Changes in orangutan caloric intake, energy balance, and ketones in
1103 response to fluctuating fruit availability. *Intern J Primatol* 19(6): 1061-1079.
- 1104 [89] Anderson DP, Nordheim EV, Boesch C, Moermond TC. 2002. Factors influencing
1105 fission-fusion grouping in chimpanzees in the Tai National Park, Cote d'Ivoire. In: Boesch C,
1106 Hohmann G, Marchant LF, editors. *Behavioural Diversity in Chimpanzees and Bonobos*.
1107 Cambridge: Cambridge University Press. p. 90-101.
- 1108 [90] Garber PA, Dolins FL. 1996. Testing learning paradigms in the field: evidence for use of
1109 spatial and perceptual information and rulebased foraging in wild moustached tamarins. In:
1110 Norconk MA, Rosenberger AL, Garber PA editors. *Adaptive radiation of neotropical*
1111 *primates*. New York: Plenum Press. p. 201–216.
- 1112 [91] Bicca-Marques JC, Garber PA. 2004. Use of spatial, visual, and olfactory information
1113 during foraging in wild nocturnal and diurnal anthropoids: A field experiment comparing
1114 *Aotus*, *Callicebus*, and *Saguinus*. *Am J Primatol* 62(3):171–187.

- 1115 [92] Stewart J, Stewart JR, Gapenne O, Di Paolo EA, editors 2010. Enaction: Toward a new
1116 paradigm for cognitive science. MIT Press.
- 1117 [93] O'Regan JK, Noë, A. 2001. A sensorimotor account of vision and visual consciousness.
1118 Behav. Brain Sci. 24: 939–973.
- 1119 [94] Menzel CR, Beck BB. 2000. Homing and detour behavior in golden lion tamarin social
1120 groups. In: Boinski S, Garber PA, editors. On the move: how and why animals travel in
1121 groups. Chicago: University of Chicago Press. p. 299–326.
- 1122 [95] Garber PA 1989. Role of spatial memory in primate foraging patterns: *Saguinus mystax*
1123 *and Saguinus fuscicollis*. Am J Primatol 19(4): 203-216.
- 1124 [96] Porter, LM, Garber PA. 2013. Foraging and spatial memory in wild weddell's
1125 saddleback tamarins (*Saguinus fuscicollis weddelli*) when moving between distant and out-of-
1126 sight goals. Internat J Primatol 34(1): 30-48.
- 1127 [97] Lee PC, Moss CJ. 1999. The social context for learning and behavioural development
1128 among wild African elephants. In: Box HO, Gibson KR, editors. Mammalian social learning:
1129 comparative and ecological perspectives. Cambridge: Cambridge University Press. p. 102-
1130 125.
- 1131 [98] Estienne V, Stephens CR, Boesch C. 2017. Extraction of honey from underground bee
1132 nests by central African chimpanzees (*Pan troglodytes troglodytes*) in Loango National Park,
1133 Gabon: Techniques and individual differences. Am J Primatol 79 (8): e22672.
- 1134 [99] Thornton A, McAuliffe K. 2006. Teaching in wild meerkats. Science, 313(5784), 227-
1135 229.
- 1136 [100] Hosey GR. 2005. How does the zoo environment affect the behaviour of captive
1137 primates? Appl Anim Behav Sci 90 (2): 107-129.
- 1138 [101] Wobber V, Hare B. 2011. Psychological health of orphan bonobos and chimpanzees in
1139 African sanctuaries. PLoS One 6 (6): e17147.

- 1140 [102] Birkett LP, Newton-Fisher NE. 2011. How abnormal is the behaviour of captive, zoo-
1141 living chimpanzees? PloS One, 6 (6): e20101.
- 1142 [103] Brand CM, Boose KJ, Squires EC, Marchant LF, White FJ, Meinelt A, Snodgrass JJ.
1143 2016. Hair plucking, stress, and urinary cortisol among captive bonobos (*Pan paniscus*). Zoo
1144 Biol 35 (5): 415-422.
- 1145 [104] Zhang ZY, Mao Y, Feng XL, Zheng N, Lü LB, Ma YY, ... & Hu XT. 2016. Early
1146 adversity contributes to chronic stress induced depression-like behavior in adolescent male
1147 rhesus monkeys. Behav Brain Res 306: 154-159.
- 1148 [105] Kemper CM, Gibbs SE. 1997. A study of the life history parameters of dolphins and
1149 seals entangled in tuna farms near Port Lincoln, and comparisons with information from other
1150 South Australian dolphin carcasses. Australia (Australian Nature Conservation Agency).
1151 South Australian Museum.
- 1152 [106] Salomons HM, Mulder GV, van de Zande L, Hausmann MF, Linskens MH, Verhulst
1153 S. 2009. Telomere shortening and survival in free-living corvids. Proc R Soc B 276 (1670):
1154 3157-3165.
- 1155 [107] Trimble MJ, Van Aarde RJ, Ferreira, SM, Nørgaard CF, Fourie J, Lee PC, Moss CJ.
1156 2011. Age determination by back length for African savanna elephants: extending age
1157 assessment techniques for aerial-based surveys. PloS One 6 (10): e26614.
- 1158 [108] Rowe N, Myers M. 2016. All the world's primates. Pogonias Press, Charlestown. p. 1-777.
- 1159 [109] Arnsten AF. 2009. Stress signalling pathways that impair prefrontal cortex structure
1160 and function. Nature reviews. Neuroscience 10 (6): 410.
- 1161 [110] Bogart SL, Bennett AJ, Schapiro SJ, Reamer LA, Hopkins WD. 2014. Different early
1162 rearing experiences have long-term effects on cortical organization in captive chimpanzees
1163 (*Pan troglodytes*). Dev Sci 17 (2): 161-174.
- 1164 [111] Wobber V, Herrmann E, Hare B, Wrangham R, Tomasello M. 2014. Differences in the
1165 early cognitive development of children and great apes. Dev Psychobiol 56 (3): 547-573.

- 1166 [112] Hicks TC, Darby L, Hart J, Swinkels J, January N, Menken S. 2010. Trade in orphans
1167 and bushmeat threatens one of the Democratic Republic of the Congo's most important
1168 populations of eastern chimpanzees (*Pan troglodytes schweinfurthii*). *Afr Primates* 7 (1): 1-
1169 18.
- 1170 [113] Nelson CA, Zeanah CH, Fox NA, Marshall PJ, Smyke AT, Guthrie D. 2007. Cognitive
1171 recovery in socially deprived young children: the Bucharest early intervention project.
1172 *Science* 318: 1937–1940.
- 1173 [114] Van Leeuwen EJ, Mulenga IC, Chidester DL. 2014. Early social deprivation negatively
1174 affects social skill acquisition in chimpanzees (*Pan troglodytes*). *Anim Cogn* 17 (2): 407-414.
- 1175 [115] Craigie ID, Baillie JE, Balmford A, Carbone C, Collen B, Green RE, Hutton JM. 2010.
1176 Large mammal population declines in Africa's protected areas. *Biol Conserv* 143 (9): 2221-
1177 2228.
- 1178 [116] Junker J, Blake S, Boesch C, Campbell G, du Toit L, Duvall C, Ekobo A, Etoga G,
1179 Galat-Luong A, Gamys J, Ganas-Swaray J, Gatti S, Ghiurghi A, Granier N, Hart J, Head JS,
1180 Herbinger I, Hicks TC, Huijbregts B, Imong IS, Kuempel N, Lahm S, Lindsell J, Maisels F,
1181 McLennan M, Martinez L, Morgan B, Morgan D, Mulindahabi F, Mundry R, N'Goran PK,
1182 Normand E, Ntongho A, Okon DT, Petre CA, Plumptre A, Rainey H, Regnaut S, Sanz C,
1183 Stokes E, Tondossama A, Tranquilli S, Sunderland-Groves J, Walsh P, Warren Y,
1184 Williamson EA, Kuehl HS. 2012. Recent decline in suitable environmental conditions for
1185 African great apes. *Divers Distrib* 18 (11): 1077-1091.
- 1186 [117] Estrada A, Garber PA, Rylands AB, Roos C, Fernandez-Duque E, Di Fiore A., ...
1187 Rovero F. 2017. Impending extinction crisis of the world's primates: Why primates matter.
1188 *Science Advances* 3 (1): e1600946.
- 1189 [118] Kalan AK, Piel AK, Mundry R, Wittig RM, Boesch C, Kühl HS. 2016. Passive
1190 acoustic monitoring reveals group ranging and territory use: a case study of wild
1191 chimpanzees (*Pan troglodytes*). *Front Zool*: 13(1): 34.

- 1192 [119] van Pinxteren BO, Sirianni G, Gratton P, Després-Einspenner ML, Egas M, Kühl H,
1193 Lapuente J, Meier A, Janmaat KRL. 2018. Sooty mangabeys scavenge on nuts cracked by
1194 chimpanzees and red river hogs—An investigation of inter-specific interactions around
1195 tropical nut trees. *Am J Primat*, e22895.
- 1196 [120] MacDonald SE, Ritvo S. 2016. Comparative cognition outside the laboratory. *Comp*
1197 *Cogn Behav Rev*, 11.
- 1198 [121] Köndgen S, Kuehl H, Kouamé N'Goran P, Walsh PD, Schenk S, Ernst N, Biek R,
1199 Formenty P, Mätz-Rensing K, Schweiger B, Junglen S, Ellerbrok H, Nitsche A, Briese T,
1200 Lipkin WI, Pauli G, Boesch C, Leendertz FH. 2008. Pandemic human viruses cause decline
1201 of endangered great apes. *Curr Biol* 18(4): 260-264.
- 1202 [122] Campbell G, Kuehl H, Diarrassouba A, N'Goran PK, Boesch C. 2011. Long-term
1203 research sites as refugia for threatened and over-harvested species. *Biol Lett* 7 (5): 723-726.
- 1204 [123] Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin C, EG,
1205 Wrangham RW, Boesch C. 1999. Cultures in chimpanzees. *Nature* 399 (6737): 682-685.
- 1206 [124] Van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A,
1207 Utami SS, Merrill M 2003. Orangutan cultures and the evolution of material culture. *Science*
1208 299 (5603): 102-105.
- 1209 [125] Tinbergen N 1963. On aims and methods of ethology. *Z Tierpsych* 20(4): 410-433.
- 1210 [126] Martin P, Bateson PPG. 2007. *Measuring behaviour: an introductory guide*.
1211 Cambridge: Cambridge University Press.
- 1212 [127] Janmaat KRL, Boesch C, Byrne R, Chapman C, Goné Bi ZB, Head JS, Robbins M M,
1213 Wrangham R, Polansky L. 2016. The spatio-temporal complexity of chimpanzee food: How
1214 cognitive adaptations can counteract the ephemeral nature of ripe fruit. *Am J Primatol* 78 (6):
1215 626-645.
- 1216 [128] Pontzer H, Raichlen DA, Rodman PS. 2014. Bipedal and quadrupedal locomotion in
1217 chimpanzees. *J Hum Evol* 66: 64-82.

- 1218 [129] Taylor CR, Rowntree VJ. 1973. Running on two or on four legs: which consumes more
1219 energy? *Science* 179(4069): 186-187.
- 1220 [130] Wrangham RW, Conklin-Brittain NL, Hunt KD. 1998. Dietary response of
1221 chimpanzees to seasonal variation in fruit abundance. I. Antifeedants. *Int J Primatol* 19: 949–
1222 970.
- 1223 [131] Porter L, Garber P, Boesch C, Janmaat KRL. (in press). Finding fruit in a tropical
1224 rainforest: a comparison of the foraging patterns of two distinct fruit-eating primates across
1225 years. In C. Shaffer, F. Dolins, J. Hickey, N. Nibbelink, & L. Porter (Eds.), *GPS and GIS for*
1226 *primatologists: A practical guide to spatial analysis*. Cambridge: Cambridge Univ. Press.
- 1227 [132] Gaulin SJ, Fitzgerald RW. 1989. Sexual selection for spatial-learning ability. *Anim*
1228 *Beh* 37: 322-331.
- 1229 [133] Hurly TA, Healy SD. 1996. Memory for flowers in rufous hummingbirds: location or
1230 local visual cues? *Anim Behav* 51: 1149–1157.
- 1231 [134] Teichroeb J.A, Chapman CA. 2014. Sensory information and associative cues used in
1232 food detection by wild vervet monkeys. *Anim Cogn* 17(3): 517-528.
- 1233 [135] Houle A. 2004. Mécanismes de coexistence chez les primates frugivores du Parc
1234 National de Kibale en Ouganda. Ph.D. thesis, Université du Québec, Montréal, Canada, pp
1235 83–87.
- 1236 [136] Shanahan M, So S, Compton SG, Corlett R. 2001. Fig-eating by vertebrate frugivores:
1237 a global review. *Biol Rev* 76 (4): 529-572
- 1238 [137] Wheelwright NT 1985. Fruit-size, gape width, and the diets of fruit-eating birds.
1239 *Ecology* 66: 808–818.
- 1240 [138] Wrangham RW, Conklin NL, Etot G, Obua J, Hunt KD, Hauser MD, Clark AP. 1993.
1241 The value of figs to chimpanzees. *Int J Primatol* 14 (2): 243–256.
- 1242 [139] Sakai S. 2001. Phenological diversity in tropical forests. *Popul Ecol* 43: 77-86.

- 1243 [140] Kappeler PM, Watts DP. 2012. Long-term field studies of primates. Springer Science
1244 & Business Media.
- 1245 [141] Chapman CA, Wrangham RW, Chapman LJ, Kennard DK, Zanne AE. 1999. Fruit and
1246 flower phenology at two sites in Kibale National Park, Uganda. *J Trop Ecol* 15: 189e211.
- 1247 [142] Crofoot MC, Rubenstein DI, Maiya AS, Berger-Wolf TY. 2011. Aggression, grooming
1248 and group-level cooperation in white-faced capuchins (*Cebus capucinus*): insights from
1249 social networks. *Am J Primatol* 73 (8): 821-833.
- 1250 [143] Van Loon EE, Shamoun-Baranes J, Bouten W, Davis SL. 2011. Understanding soaring
1251 bird migration through interactions and decisions at the individual level. *J Theor Biol* 270 (1):
1252 112-126.
- 1253 [144] Polansky L, Kilian W, & Wittemyer G. 2015. Elucidating the significance of spatial
1254 memory on movement decisions by African savannah elephants using state–space models.
1255 *Proc. R. Soc. B* 282 (1805): 20143042.
- 1256 [145] Musgrave S, Morgan D, Lonsdorf E, Mundry R, Sanz C. 2016. Tool transfers are a
1257 form of teaching among chimpanzees. *Sci rep* 6: 34783.
- 1258 [146] Van Andel AC, Wich SA, Boesch C, Koh L. P, Robbins MM, Kelly J, Kühl HS. 2015.
1259 Locating chimpanzee nests and identifying fruiting trees with an unmanned aerial vehicle.
1260 *Am J Primatol* 77 (10): 1122-1134.
- 1261 [147] Waide RB, Thomas MO. 2012. Long-term ecological research network. In
1262 *Encyclopedia of Sustainability Science and Technology*. New York: Springer. p. 6216-6240.
- 1263 [148] Omer N, Razafimandimby D, Jeffrey JAJ, Schulz S, and Ayasse M. 2018. Fruit scent
1264 as an evolved signal to primate seed dispersal. *Science advances* 4(10): eaat4871.
- 1265 [149] Janson CH, Di Bitetti MS. 1997. Experimental analysis of food detection in capuchin
1266 monkeys: effects of distance, travel speed, and resource size. *Behav Ecol Sociobiol* 41(1): 17-
1267 24.

- 1268 [150] Laska M, Liesen A, Teuber P. 1999. Enantioselectivity of odor perception in squirrel
1269 monkeys and humans. *Am J Phys* 277: 1098-1103.
- 1270 [151] Laska M, Hernandez Salazar LT, Luna ER. 2003. Successful acquisition of an olfactory
1271 discrimination paradigm by spider monkeys, *Ateles geoffroyi*. *Physiol Behav* 78: 321-329.
- 1272 [152] Matsui A, Go Y, Niimura Y. 2010. Degeneration of olfactory receptor gene repertoires
1273 in primates: no direct link to full trichromatic vision. *Mol Biol Evol* 27(5): 1192-1200.
- 1274 [153] Cavonius CR, Robbins DO. 1973. Relationships between luminance and visual acuity
1275 in the rhesus monkey. *J Psych* 232: 239-246.
- 1276 [154] Golla H, Ignashchenkova A, Haarmeier T, Thrier P. 2004. Improvement of visual
1277 acuity by spatial cueing: a comparative study in human and non-human primates. *Vis Res* 44:
1278 1589-1600.
- 1279 [155] Janson CH. 1998. Experimental evidence for spatial memory in foraging wild capuchin
1280 monkeys, *Cebus apella*. *Anim Behav* 55(5): 1229-1243.
- 1281 [156] Cunningham EP, Janson CH. 2013. Effect of fruit scarcity on use of spatial memory in
1282 a seed predator, white-faced saki (*Pithecia pithecia*). *Intern J Primatol* 34(4): 808-822.
- 1283 [157] Rakoczy H, Clüver A, Saucke L, Stoffregen N, Gräbener A, Migura J, Call J. 2014.
1284 Apes are intuitive statisticians. *Cognition* 131 (1): 60-68.
- 1285 [158] Eckert J, Rakoczy H, Call J. 2017. Are great apes able to reason from multi-item
1286 samples to populations of food items? *Am J Primatol* 79(10): e22693.
- 1287 [159] Pochron S. 2001. Can concurrent speed and directness of travel indicate purposeful
1288 encounter in the yellow baboons (*Papio hamadryas cynocephalus*) of Ruaha National Park,
1289 Tanzania? *Int J Primatol* 22 (5): 773-785.
- 1290 [160] Normand E, Boesch C. 2009. Sophisticated Euclidean maps in forest chimpanzees.
1291 *Anim Behav* 77:1195–1201.
- 1292 [161] Byrne RW, Noser R, Bates LA, Jupp PE. 2009. How did they get here from there?
1293 Detecting changes of direction in terrestrial ranging. *Anim Behav* 77(3): 619-631.

- 1294 [162] Ban SD, Boesch C, N'Guessan A, N' Goran EK, Tako A, Janmaat KRL. 2016. Tai
1295 chimpanzees change their travel direction for rare feeding trees providing fatty fruits. *Anim*
1296 *Behav* 118: 135-147.
- 1297 [163] Normand E, Ban DS, Boesch C. 2009. Forest chimpanzees (*Pan troglodytes verus*)
1298 remember the location of numerous fruit trees. *Anim Cogn*12: 797e807.
- 1299 [164] Manly BFL, McDonald L, Thomas D, McDonald TL, Erickson WP. 2007. Resource
1300 selection by animals: statistical design and analysis for field studies. Springer Science &
1301 Business Media.
- 1302 [165] Schlesselman J. 1982. Case-control studies: design, conduct, analysis. Oxford: Oxford
1303 University Press.
- 1304 [166] Boesch C, Boesch-Achermann H. 2000. The Chimpanzees of the Tai Forest:
1305 Behavioural Ecology and Evolution. Oxford: Oxford University Press.
- 1306 [167] Mielke A, Samuni L, Preis A, Gogarten JF, Crockford C, Wittig RM. 2017. Bystanders
1307 intervene to impede grooming in Western chimpanzees and sooty mangabeys. *Royal Society*
1308 *Open Science* 4 (11): 171296.
- 1309 [168] Myowa-Yamakoshi M, Matsuzawa T. 1999. Factors influencing imitation of
1310 manipulatory actions in chimpanzees. *J Comp Psychol* 113: 128-136.
- 1311 [169] Baayen RH. 2008. Analyzing linguistic data. Cambridge, U.K.: Cambridge University
1312 Press.
- 1313 [170] Bolker BM, Brooks, ME Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White
1314 JSS. 2008. Generalized linear mixed models: a practical guide for ecology and evolution.
1315 *Trends Ecol Evol* 24: 127-135.
- 1316 [171] Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models
1317 and extensions in ecology with R. New York: Springer.
- 1318 [172] Bates B, Maechler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models
1319 Using lme4. *J Stat Softw* 67: 1-48.

- 1320 [173] Janmaat KRL, Chancellor R. 2010. Exploring new areas: How important is long-term
1321 spatial memory for mangabey (*Lophocebus albigena johnstonii*) foraging efficiency? Int J
1322 Primatol 31 (5): 863-886.
- 1323 [174] Siegel S, Castellan NJ. 1988. Nonparametric Statistics for the Behavioral Sciences.
1324 New York: McGraw-Hill Book Company.
- 1325 [175] Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 49
1326 (3): 227-266.
- 1327 [176] Janmaat K, Byrne RW, Zuberbühler K. 2006. Primates take weather into account when
1328 searching for fruits. Cur Biol, 16(12): 1232-1237.
- 1329 [177] Levinson SC. 2012. The original sin of cognitive science. Top Cogn Sci 4(3): 396-403.
- 1330 [178] Leggio MG, Mandolesi L, Federico F, Spirito F, Ricci B, Gelfo F, Petrosinia L. 2005.
1331 Environmental enrichment promotes improved spatial abilities and enhanced dendritic
1332 growth in the rat. Behav Brain Res 163: 78-90.
- 1333 [179] Salvanes AGV, Moberg O, Ebbesson LOE, Nilsen TO, Jensen KH, Braithwaite VA.
1334 2013. Environmental enrichment promotes neural plasticity and cognitive ability in fish. Proc
1335 Roy Soc B: Biol Sci 280: 20131331.
- 1336 [180] Wessling EG, Kühl HS, Mundry R, Deschner T, Pruetz JD. 2018. The costs of living at
1337 the edge: Seasonal stress in wild savanna-dwelling chimpanzees. J Hum Evol. 121: 1-11.
- 1338 [181] Henkel S, Lambides AR, Berger A, Thomsen R, Widdig A. 2015. Rhesus macaques
1339 (*Macaca mulatta*) recognize group membership via olfactory cues alone. Behav Ecol
1340 Sociobiol 69(12): 2019-2034.
- 1341 [182] Melin AD, Chiou K, Walco E, Bergstrom M, Kawamura S, Fedigan L. Trichromacy
1342 increases fruit intake rates of wild capuchins (*Cebus capucinus imitator*). Proc Natl Acad Sci
1343 USA 114:10402-10407.

- 1344 [183] Boogert NJ, Hofstede FE, Aguilar Monge I. 2006. The use of food source scent marks
1345 by the stingless bee *Trigona corvina* (*Hymenoptera: Apidae*): the importance of the
1346 depositor's identity. *Apidologie*, 37(3), 366-375.
- 1347 [184] Garber PA, Paciulli LM. 1997. Experimental field study of spatial memory and
1348 learning in wild capuchin monkeys (*Cebus capucinus*). *Folia primatol* 68(3-5): 236-253.
- 1349 [185] Noser R, Byrne RW. 2015. Wild chacma baboons (*Papio ursinus*) remember single
1350 foraging episodes. *Anim Cogn* 18(4): 921-929.
- 1351 [186] Janmaat KRL, Chapman CA, Meijer R, Zuberbühler K. 2012. The use of fruiting
1352 synchrony by foraging mangabey monkeys: A 'simple tool' to find fruit. *Anim Cogn* 15 (1):
1353 83-96.
- 1354 [187] Menzel CR. 1991. Cognitive aspects of foraging in Japanese monkeys. *Anim Behav* 41:
1355 397-402.
- 1356 [188] Bijleveld AI, Egas M, van Gils JA, Piersma T. 2010. Beyond the information centre
1357 hypothesis: Communal roosting for information on food, predators, travel companions and
1358 mates? *Oikos* 119(2):277-285.
- 1359 [189] Garber PA, Bicca-Marques JC, Azevedo-Lopes Mado. 2009. Primate cognition:
1360 integrating social and ecological information in decision-making. In: Garber PA, Estrada A,
1361 Bicca-Marques JC, Heymann EW, Strier KB, editors. *South American Primates*. New York:
1362 Springer. p. 365-385.
- 1363 [190] Glabischnig M. 2018. The Value of Lab and Field Studies for Learning about the
1364 Evolution of Human Cognition MSc thesis. University of Amsterdam.
1365 <https://doi.org/10.13140/RG.2.2.17120.74248>
1366

An Observational Approach to Study Cognition in the Wild**A PRIORI DESIGN:****Step 1 : Selecting study species**

- Choose a reliable, observable and well-studied species

Step 2 : Identifying Crucial Situations

- Determine when animals will likely benefit from using cognitive skills

Step 3: Identifying alternative explanations and Observational control

- Record variables or behaviors that can exclude alternative explanations (e.g., record informative failing)

Step 4: Enlarging detection probability of the ability of interest

- Record a suite of behaviors that can exhibit the same cognitive skill
- Record non-events (conduct quasi-experiments)
- Record variables that allow for testing of conditional decision-making (interactive effects)

A POSTERIORI DESIGN:**Step 5: Statistical Control**

- Combine recorded data with long-term contextual data
- Apply hierarchical modelling techniques

Table 1. Example situations in which one can expect an animal to employ several cognitive mechanisms

Cognitive Mechanisms	Potential Crucial Situations
Physical Cognition	
Intuitive statistics/Categorization	When the proportion of food-bearing trees differs substantially between species
What where and when memory	When there are differences in ripening or degradation rates of food
Euclidean map use	When having entered areas, where shortcuts between food sources will decrease travel time
Causal understanding/Insight	When being young and needing to learn how to reach food by using a tool
Social Cognition	
Cooperation	When catching a prey on your own is too difficult
Intentionality/Information sharing	When having seen a predator and others, who are related to you, have not
Theory of mind	When wanting to get food that others want as well
Social learning	When having migrated to a new group and need to know who has the highest rank

Table 2. Examples of which Generalized Linear (Mixed) Model types can be best applied for varying types of observational data

RESPONSE TYPE	MODEL TYPE
Normal (e.g., departure time)	Gaussian
Binary (e.g., approach or no approach)	Logistic
Count (e.g., number of visits)	Poisson or Negative binomial
Count with many zero's (e.g., number of visits when visits are rare)	Zero inflated Poisson or Negative binomial
Count with upper and lower bound (e.g., number of trials correct out of fixed number of trials)	Logistic (only after translating into proportions by use of R)
Continuous with upper and lower bound (e.g., angle deviation)	Beta



Fig. 2. The author collecting data on chimpanzee behavior using a voice recorder and GPS

1286x965mm (72 x 72 DPI)

Supplementary materials

Table S1: Overall distribution of unique citations (excluding multiple citations) across the 16 target papers. “lab” = study in captive environment; “field” = study in natural environment; “exp” = experimental; “obs” = observational

Studies in captive environments			Studies in natural environments		
lab - exp	384	84.58%	field - exp	46	20.63%
lab - obs	64	14.10%	field - obs	160	71.75%
lab - exp & lab - obs	6	1.32%	field - exp & field - obs	17	7.62%
Total	454	67.06%	Total	223	32.94%
Studies in captive + natural environments					
lab - obs & field - obs	2				
lab - exp & lab - obs & field - exp + field - obs	2				

Manuscript selection method

To obtain eight papers from each type of primatologist, four review papers on the topic of foraging cognition, known by the author were selected (top two for each type in Table 1). The remaining 12 papers were obtained by online search with Google Scholar, using the search terms “*social cognition*”, “*ecological cognition*”, “*physical cognition*”, “*foraging*”, “*cooperation*”, “*communication*”, “*information sharing*” and “*prospective thinking*” in combination with the term “*primate*”. Papers that explicitly stated that they focus on wild non-human primates were excluded from the search. No papers in the search results explicitly stated to focus on captive non-human primates. The search was conducted by MSc. Biology student Martin Glabischnig on his personal laptop computer. Glabischnig had neither a background nor knowledge in the field of primatology, minimizing potential biased search by Google Scholar. In a first step, Glabischnig used the top 30 listings of the respective online searches to select relevant review papers. Unfortunately, this resulted into an overrepresentation of review or theoretical papers from captive-based scientists. Thus, in order to reach a balanced selection he started to add the surnames of field-based primatologists known by the author to the search string until he found eight review or theoretical papers in each field. Field and captive-oriented primatologists were defined as those mainly orientated towards research in the natural versus captive environment, respectively. Captive environments were defined as any kind of artificial enclosure in which the study animals live and/or are tested. This category includes laboratories, zoos, sanctuaries and enclosed field stations. Natural environments were defined as the non-enclosed wild habitat of study animals.

Table S2: Distribution of lab- and field-based studies that are cited in review and theoretical papers from “captive-oriented-primatologists” and “field- oriented primatologists”. Captive-study = captive environments; Field-study = natural environment

Primatologists who are mainly oriented towards research in captive environments			
Captive studies	Field studies	Ratio Captive/Field	Papers (Author names and Manuscript title)
88	7	12.57	Beran, M. J., Menzel, C. R., Parrish, A. E., Perdue, B. M., Sayers, K., Smith, J. D., & Washburn, D. A. (2016). Primate cognition: attention, episodic memory, prospective memory, self-control, and metacognition as examples of cognitive control in nonhuman primates.
33	6	5.50	Rosati, A. G. (2017). Foraging Cognition: Reviving the Ecological Intelligence Hypothesis.
46	6	7.67	Leavens, D. A., & Bard, K. A. (2011). Environmental Influences on Joint Attention in Great Apes: Implications for Human Cognition.
43	7	6.14	Leavens, D. A., Bard, K. A., & Hopkins, W. D. (2017). The mismeasure of ape social cognition.
12	4	3.00	Osvath, M., & Martin-Ordas, G. (2014). The future of future-oriented cognition in non-humans: theory and the empirical case of the great apes.
28	10	2.80	Tomasello, M., & Call, J. (2018). Thirty years of great ape gestures.
25	1	25	Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition.
42	12	3.50	Hall, K., & Brosnan, S. F. (2017). Cooperation and deception in primates.
317	53	8.27	Total
Primatologists who are mainly oriented towards research in natural environments			
Captive studies	Field studies	Ratio Captive/Field	Papers (Author names and Manuscript title)
20	49	0.41	Tujague, M & Janson, C. (2017). Foraging cognition in Neotropical primates: integrating studies from the wild and from captivity
7	36	0.19	Zuberbühler, K., & Janmaat, K. (2010). Foraging Cognition in Nonhuman Primates.
14	29	0.48	Seyfarth, R. M. & Cheney, D. L. (2016). Social Cognition in Animals.
16	32	0.50	Cunningham, E., & Janson, C. (2007). A socioecological perspective on primate cognition, past and present.
41	29	1.41	Fischer, J. (2017). Information Transmission in Nonhuman Primates: From Communication to Social Learning.
9	10	0.90	Townsend, S. W., Koski, S. E., Byrne, R. W., Slocombe, K. E., Bickel, B., Boeckle, M., ... Manser, M. B. (2017). Exorcising Grice's ghost: an empirical approach to studying intentional communication in animals.
101	22	4.59	Burkart, J. M., & Schaik, C. P. van. (2010). Cognitive consequences of cooperative breeding in primates?
58	33	1.76	Byrne, R. W., & Bates, L. A. (2010). Primate Social Cognition: Uniquely Primate, Uniquely Social, or Just Unique?
266	240	1.28	Total

Table S3: Distribution of absolute citations between captive- and field-oriented primatologists (including absolute count of citations that were referenced in multiple papers)

Primatologists mainly oriented towards research in CAPTIVE environments					
Studies in captive environments			Studies in natural environments		
lab - exp	276	87.07%	field - exp	2	4.17%
lab - obs	38	11.99%	field - obs	44	91.67%
lab - exp & lab - obs	3	0.95%	field - exp & field - obs	2	4.17%
Total	317	83.14%		48	13.15%
Studies in captive + natural environments					
lab + field - obs	2				
Primatologists mainly oriented towards research in NATURAL environments					
Studies in captive environments			Studies in natural environments		
lab - exp	219	82.33%	field - exp	57	23.75%
lab - obs	42	15.79%	field - obs	165	68.75%
lab - exp & lab - obs	5	1.88%	field - exp & field - obs	18	7.50%
Total	266	52.57%	Total	240	47.43%
Studies in captive + natural environments					
lab - obs & field - obs	1				
lab - exp & lab - obs & field - exp & field - obs	4				

Generalized Linear Mixed Models

Generalized Linear Mixed models encompass all statistical models that enable scientists to test the effects of categorical as well as quantitative predictor (independent) variables on a response (dependent) variable that can have various distributions (e.g., Binomial, Gaussian, Poisson etc. (Baayen 2008); Table 2). These models are called Mixed because they include both familiar 'fixed' effects (ones in which the level of the predictor variable is held fixed to a specific value) as well as 'random' effects (whose effects are assumed to be constant but unknown for each value of the variable). Random effects can be “individual identity” or other factors such as “species”, “research group” or experimental stimulus (such as “play-back call identity”) that have been observed or were used repeatedly. Including such effects enables scientists to control for “random” aspects of each level of these factors that can influence the response in unpredictable ways. For example, when one aims to study the effect of variables that influence travel speed (as a proxy for spatial knowledge) we know that not all observed individuals walk with exactly the same average speed (Fig. S1). The reasons why individuals differ cannot always be captured by the value of a predictor variable, such as time of day, and may concern for instance the physiological state or habit, or other unidentifiable “random” aspects of each particular individual. The inclusion of random effect enables scientists to avoid pseudo-

replication by explicitly modeling (as random effects) the contribution of sources of potential non-independence caused by repeated observations of, for instance, the same individual. Mixed models make specific assumptions to allow us to include such repeated observations on individuals (or other categories such as "species").

Generalized Linear Mixed Models are far from new, and encompass, for example, repeated measures ANOVA (Huck & McLean 1975; Bar et al., 2013), but they are continuously under development (Bates et al., 2015). Hence, using them requires a certain level of caution. The increasing familiarization of scientists with the software R and the freedom it provides to design statistical models exactly as we like brings increased responsibility. One important concept to consider in mixed model designs, for which its importance only recently became apparent, are *random slopes* (Bar et al., 2013). Random slopes take into account that the same predictor variable can differentially affect a response variable, depending on the level of a random effect (e.g., the individual). For example, if the response variable is travel speed, individuals may for "random" reasons differ in their ability to travel fast (represented by the random intercept; Fig.S1); however, individuals may also differ in the way their travel speed is affected by a predictor variable, such as their hunger level (estimated by the time since their last feeding event) at the travel goal (a predictor variable). This can cause the duration since the last feeding to increase speed more steeply in some individuals than in others (represented by a random slope; Fig.S1). Not including random slopes that control for this possibility as terms in the model equation can dramatically increase type I error rates and can lead to ridiculously significant predictor variables and spurious results (Bar et al., 2013). Earlier studies (including my own) should, therefore, be interpreted with care and the focus should always be on the strength and direction of the effects (the estimates) and the visualization of distribution of the response with regard to the predictor(s) and the fitted model (the predicted values of the model) and not on P-values only. To be able to include random slopes in a model equation requires sufficient variation in the predictor variable for all or most levels of the random effect. Hence, prior to the start of data collection, a choice needs to be made between collecting a larger number of observations per individual (enabling one to include random slopes) or fewer observations per individual (enabling one to better account for variation among individuals).

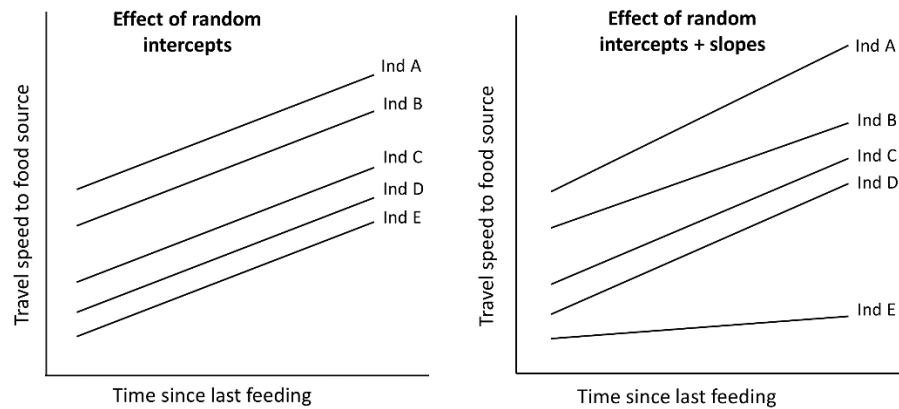


Fig. S1. Schematic illustration of the predicted effect of the time duration since last feeding on travel speed towards a food source for different individuals, illustrating the importance of the inclusion of random intercepts and slopes in Generalized Linear Mixed Models.

References:

- Baayen RH. 2008. Analyzing linguistic data. Cambridge, U.K.: Cambridge University Press.
- Barr DJ, Levy R, Scheepers C, Tily HJ. 2013. Random effects structure for confirmatory hypothesis testing: Keep it maximal. *J Memory Lang* 68: 255–278.
- Garber PA. 1988. Foraging Decisions During Nectar Feeding by Tamarin Monkeys (*Saguinus mystax* and *Saguinus fuscicollis*, Callitrichidae, Primates) in Amazonian Peru. *Biotropica* 20: 100-106.
- Bates B, Maechler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *J Stat Softw* 67: 1-48.
- Beran, M. J., Menzel, C. R., Parrish, A. E., Perdue, B. M., Sayers, K., Smith, J. D., & Washburn, D. A. (2016). Primate cognition: attention, episodic memory, prospective memory, self-control, and metacognition as examples of cognitive control in nonhuman primates. *Wiley Interdisciplinary Reviews: Cognitive Science*, 7(5), 294–316.
- Burkart, J. M., & Schaik, C. P. van. (2010). Cognitive consequences of cooperative breeding in primates? *Animal Cognition*, 13(1), 1–19.
- Byrne, R. W., & Bates, L. A. (2010). Primate Social Cognition: Uniquely Primate, Uniquely Social, or Just Unique? *Neuron*, 65(6), 815–830.
- Cunningham, E., & Janson, C. (2007). A socioecological perspective on primate cognition, past and present. *Animal Cognition*, 10(3), 273–281.
- Fischer, J. (2017). Information Transmission in Nonhuman Primates: From Communication to Social Learning. In *Learning and Memory: A Comprehensive Reference* (pp. 171–188). Elsevier.
- Hall, K., & Brosnan, S. F. (2017). Cooperation and deception in primates. *Infant Behavior and Development*, 48, 38–44.

- Huck SW, McLean RA. 1975. Using a repeated measures ANOVA to analyze the data from a pretest-posttest design: A potentially confusing task. *Psychol Bull* 82(4): 511.
- Leavens, D. A., & Bard, K. A. (2011). Environmental Influences on Joint Attention in Great Apes: Implications for Human Cognition. *Journal of Cognitive Education and Psychology*, 10(1), 9–31.
- Leavens, D. A., Bard, K. A., & Hopkins, W. D. (2017). The mismeasure of ape social cognition. *Animal Cognition*, 1-18.
- Osvath, M., & Martin-Ordas, G. (2014). The future of future-oriented cognition in non-humans: theory and the empirical case of the great apes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1655).
- Rosati, A. G. (2017). Foraging Cognition: Reviving the Ecological Intelligence Hypothesis. *Trends in Cognitive Sciences*, 21(9), 691–702.
- Seyfarth, R. M. & Cheney, D. L. (2016). Social Cognition in Animals. In Sommerville, J. A. & Decety, J. *Social Cognition: development across the lifespan* (pp.46-68). New York, NY, USA: Routledge.
- Tomasello, M., & Call, J. (2018). Thirty years of great ape gestures. *Animal Cognition*, 1–9.
- Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*, 28(5), 675–691.
- Townsend, S. W., Koski, S. E., Byrne, R. W., Slocombe, K. E., Bickel, B., Boeckle, M., ... Manser, M. B. (2017). Exorcising Grice's ghost: an empirical approach to studying intentional communication in animals. *Biological Reviews*, 92(3), 1427–1433.
- Tujague, M & Janson, C. (2017). Foraging cognition in Neotropical primates: integrating studies from the wild and from captivity. In Kowalewski, M.M. & Oklander, I.L. (eds.), *Primate Neuroethology in Argentina* (Chapter 9). Buenos Aires: Argentina
- Zuberbühler, K., & Janmaat, K. (2010). Foraging Cognition in Nonhuman Primates. In M. Platt & A. Ghazanfar (Eds.), *Primate Neuroethology* (pp. 64–83). Oxford University Press.