



**HAL**  
open science

# Incorporating animal agency into research design could improve behavioral and neuroscience research

Cédric Sueur, Sarah Zanaz, Marie Pelé

► **To cite this version:**

Cédric Sueur, Sarah Zanaz, Marie Pelé. Incorporating animal agency into research design could improve behavioral and neuroscience research. *Journal of Comparative Psychology*, 2023, 137 (2), pp.129-143. 10.1037/com0000335 . hal-03299505v5

**HAL Id: hal-03299505**

**<https://hal.science/hal-03299505v5>**

Submitted on 14 Sep 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Incorporating animal agency into research design could improve behavioral and**  
2 **neuroscience research**

3 Cédric Sueur<sup>1,2,3</sup>, Sarah Zanaz<sup>1,4</sup>, and Marie Pelé<sup>5</sup>.

4 1 Université de Strasbourg, CNRS, IPHC UMR 7178, Strasbourg, France.

5 2 Institut Universitaire de France, Paris, France.

6 3 CEERE Centre Européen d'Enseignement et de Recherche en Ethique, Strasbourg, France.

7 4 Benemérita Universidad Autónoma de Puebla, Facultad de Filosofía y Letras, Puebla

8 5 Anthro-po-Lab, ETHICS EA7446, Université Catholique de Lille, F-59000 Lille, France.

9

10 The authors declare no competing interests.

11

12 Correspondence to Cédric Sueur: [cedric.sueur@iphc.cnrs.fr](mailto:cedric.sueur@iphc.cnrs.fr)

13

14

15 **Abstract**

16 Despite increasing numbers of publications showing that many animals possess the neural  
17 substrates involved in emotions and consciousness, and exhibit agency in their behavior,  
18 many animals are still restrained and forced to take part in applied or fundamental research.  
19 However, these restraints and procedures, because they stress animals and because they  
20 limit the expression of adaptive behavior, may result in compromised findings. Researchers  
21 should alter their research paradigms to understand mechanisms and functions of the brain  
22 and behavior so that the paradigms incorporate animals' agency. This paper discusses how  
23 animal agency can not only be the key to more wide-ranging and improved research in  
24 existing domains, but can also lead to new research questions about behavior and brain  
25 evolution.

26

27 **Keywords:** 3Rs, animal research, ethology, ethics, animal welfare, scientific advance

28

29

30 **Introduction**

31 By definition, animal research requires the involvement of animals. Although researchers  
32 have made great progress and improved experimental conditions for animals through the  
33 application of the 3R (Replace, Reduce, Refine) rules, some behavioral experiments showed  
34 that animals are still restrained through different methods, such as the use of throw nets,  
35 primate restraint chairs (specifically-designed chairs that require non-human primates to 'sit'  
36 in place for sustained periods of time (NC3Rs, [https://www.nc3rs.org.uk/our-portfolio/chair-  
37 restraint-training-non-human-primates](https://www.nc3rs.org.uk/our-portfolio/chair-restraint-training-non-human-primates))), rat restrainer, cages, or by food deprivation (Ben-Ami  
38 Bartal et al., 2011; Chang et al., 2017; He et al., 2020; McMillan et al., 2017; Prescott &  
39 Buchanan-Smith, 2003; Slater et al., 2016). According to McMillan et al. (2017), too many  
40 researchers continue to use methods that entail negative reinforcement (when the  
41 individual has to perform an action to remove a stressor), whilst procedures using restraint  
42 chairs in primates or similar restrainers in other species could comprise positive  
43 reinforcement methods (when the individual receives a reward after entering in the chair

44 and then getting its head out from the chair) (McMillan et al., 2017). These protocols are  
45 used to obtain results in behavioral or neuroscience research but are problematic for several  
46 reasons. Beyond the ethical issues of such restraints for animals, these examples of  
47 experimental setups lead us to consider which possibilities and results have yet to be  
48 investigated and more importantly, whether such compulsory protocols could lead to false  
49 negatives or false positives (Chang et al., 2017; Huttunen et al., 2017; Liu et al., 2017). False  
50 negatives or false positives mean that studies show respectively negative (not expected, H<sub>0</sub>)  
51 or positive results (expected, H<sub>1</sub>) but these results are not due to the tested condition (e.g. a  
52 drug, a gene, an environmental condition) but to uncontrolled factors (e.g. stress,  
53 personality). Indeed, stress and coercion (i.e., the animal is immobilized and restrained in an  
54 apparatus, such as a chair for primate or a box or a system of collars for rats or dogs) can not  
55 only modify some behaviors but also entirely prevent others from being displayed (Lecorps  
56 et al., 2021; Mason et al., 2019; Prescott, 2016). Some authors, such as Van Patter, Blattner,  
57 Matsuzawa, King and McMillan consider that the current 3R framework is not sufficient to  
58 ensure that animals are meaningful participants in experiments, which is crucial to  
59 guarantee that scientific results are not altered by stress or personality of animals (King,  
60 2021; Matsuzawa, 2016a; McMillan et al., 2014; Van Patter & Blattner, 2020). Studies carried  
61 out on animals under restraints offer few meaningful opportunities for them to show their  
62 full behavioral and cognitive capacities, and in this way to exercise agency with their  
63 environment and in their relationships, both with each other and with humans (*Homo*  
64 *sapiens*) (Blattner et al., 2020). Gillespie (2019) wrote that ‘there is a long tradition of  
65 studying nonhuman animals in spaces of animal use and exploitation, where researchers and  
66 teachers in effect become complicit through passive participation in violence against  
67 nonhuman animals...’ (p. 19). According to Blattner et al. (2020), who worked on animal  
68 agency in rehomed farm animals and from which this paper is inspired, ‘longstanding  
69 ideological blinders and anthropocentric bias frame animals as limited beings whose lives  
70 unfold according to fixed genetic or species-specific scripts, rather than as complex subjects  
71 who act with intention and purpose, both individually and collectively’ (p. 1).

72 Culture, ontology, political leaning, as well as university courses influence how a person  
73 considers animals as objects (Bègue & Vezirian, 2021; Furnham & Heyes, 1993; Miele et al.,  
74 1993). It would be interesting to look at the textbooks of comparative cognition to find

75 evidence that students are being taught to think of animals as objects; that is the method  
76 (Andrews, 2020b) used to defend the claim that comparative cognition eschews the study of  
77 consciousness. This view of animals as objects is not limited to research but is also found in  
78 different aspects of everyday life (food, work, clothing, etc.). In this way, the consideration of  
79 animals as agents could be extended from research to other domains: a new ontology  
80 considering non-human animals as agents can have political, ethical, and legal  
81 consequences.

82 We argue that restraint-based experiments are severely limited in terms of what researchers  
83 can learn from animals, in individual and group contexts. In contrast, letting animals express  
84 their will or intentions in behavior could bring new advances in research and human-animal  
85 cooperation. Incorporating animal agency should be considered a central feature of research  
86 and husbandry protocols, particularly when applying for funding. In this article we seek to  
87 provide researchers with arguments in favor of this practice.

## 88 **Animal agency**

89 Agency is the capacity of an individual to act in a given environment. In the broadest sense,  
90 agency is the ability to have an influence or an effect on something. However, agency is  
91 considered here as the expression or manifestation of a subjective existence; agency implies  
92 affecting the world in ways that reflect a subject's desires or will (Krause, 2013). It refers to  
93 an individual pursuing its own good in its own way (Taylor, 2011). Gergely & Jacob (2012)  
94 described that from birth on, human infants are exposed to two basic kinds of agency:  
95 instrumental action and communicative action. When researchers allow too little room for  
96 the animals' own forms of agency, the true abilities of these individuals are obscured  
97 (McFarland & Hediger, 2009).

98 Blattner et al. (2020) investigate animal agency in a sanctuary for rehomed farm animals,  
99 considering how a careful exploration of dimensions of agency in this setting might inform  
100 ideas of interspecies interactions (work, research, politics, etc.) and ethics. Their study  
101 focused on animals of many species living in this sanctuary. For the owners of the sanctuary  
102 and the researchers, the sanctuary is an 'integrated multispecies community or society  
103 whose members shape spaces and practices together, take on recognized social roles, and  
104 create and transmit social norms across species lines'. Blattner et al. (2020), De Waal (2016),

105 Le Neindre et al. (2017, 2018), and Meijer (2019) affirm that researchers need to spend time  
106 in community with animals, learn from them, and be prepared to respond and adjust  
107 scientific learning process through relationships with them. This means that animals should  
108 no longer be considered as the subjects of scientific experiments, but rather as participants –  
109 that is, as agents (Haraway, 1989). For example, when it comes to assessing cognitive  
110 abilities, the researchers' focus should encompass goals that are meaningful, useful, and of  
111 interest to animals instead of focusing on goals that are only relevant to the human scientist  
112 (Pepperberg, 2006).

113 It is also important to recognize animals as agents by forming relationship with them. As  
114 Andrews (2020) notes, it is important to treat animals as sentient research participants who  
115 exist within their own context and with whom researchers will be in a relationship. She  
116 defends a range of scientific benefits that come from forming relationships with animal  
117 research subjects and that we develop below. Interaction and communication have to go in  
118 both directions. Researchers need to make themselves understandable to animals as many  
119 species are able to understand our facial expressions and emotions (Bhattacharjee et al.,  
120 2019; Good et al., 2018; Hoffman et al., 2018; Patterson & Cohn, 1990; Pedersen, 2020;  
121 Savage-Rumbaugh & Lewin, 1994). For instance, applying the same agency and research  
122 protocols in horses (*Equus caballus*) as were applied in primates led to advances in our  
123 understanding of equine cognition (Matsuzawa, 2017). The first study with horses using  
124 computer touch panels was realized recently (Tomonaga et al., 2015). The primary  
125 motivation to study horses comes from the idea of understanding humans not just from a  
126 primate perspective, but from a broader mammalian (*Mammalia*) perspective. Tomonaga et  
127 al. (2015) used a computer-controlled touchscreen system to show differences in  
128 discrimination abilities between horses, chimpanzees (*Pan troglodytes*) and humans.

129 Animals may act in different dimensions as space and time and different situations as  
130 socializing, foraging, parenting, etc. Blattner et al. (2020) analyzed in their paper what  
131 freedoms of actions may result in the expression of agency in animals as well as how humans  
132 take up these freedoms, meaning how they use these dimensions to enhance animals'  
133 agency or the behavioral repertoire. Their observational analysis, using multispecies  
134 ethnography (i.e., the study of the interconnectedness and inseparability of humans and  
135 other life forms; Kirksey & Helmreich, 2010; Ogden et al., 2013) and directed toward a

136 number of methodological and ethical questions on animal-human and animal-animal  
137 relationships, led them to divide animal agency into four domains (Figure 1):

138 *1. Agency through space and time:*

139 Animals are mobile and explore/exploit their environments. Their exploration and  
140 exploitation can be used to better understand animals' preferences in terms of habitats,  
141 sleeping areas, and social relationships. Studies on these issues contribute to the emergence  
142 of new disciplines such as animal geographies (Buller, 2014) or animal mobilities (Hodgetts &  
143 Lorimer, 2020). Whilst this form of agency seems obvious to many researchers and the  
144 criteria are often applied to livestock and farmed animals (Bouissou et al., 2001; Scanes,  
145 2018; Sosa et al., 2019), it is less often applied in comparative psychology or neuroscience,  
146 despite well-known works on exploration and curiosity in animals published more than half a  
147 century ago (Berlyne, 1966; Glickman & Sroges, 1966). In neurophysiological studies of  
148 nonhuman primates, restraint chairs are widely used (McMillan et al., 2017) as boxes or  
149 other systems in rats (Bartal et al., 2011; Galichanin et al., 2011).

150 Modifications of the environment can be used to shape animals' decisions and can remove  
151 some of the negative reinforcement that is still applied to animals. For example, animals  
152 could experience less stress in some parts of their environment than others, and carrying out  
153 experiments in these places could increase their motivation to participate and increase the  
154 power of the study to detect experimental effects (Coe & Hoy, 2020; Matsuzawa, 2020). Of  
155 course, this statement implies that the housing of animals should be designed to take  
156 advantage of animals' preferences and adjustments to features of their environment. For  
157 example, boundaries and fences cannot be only considered as barriers and limitations of  
158 freedoms but also as security and communication touchstones as suggested by Blattner et  
159 al. (2020) or Grandin (1987, 1989). Humans should create barriers and fence placements  
160 according to the behavior of animals. Similarly, for behavioral experimental apparatus,  
161 animals should not be forcibly brought to where researchers want to test them but  
162 researchers should observe animals to determine the best position to place the devices.

163 Good urban design is adapted to human behavior in order to increase health, decrease  
164 stress, and the costs of urban refurbishment (Park & Evans, 2016; Pereira et al., 2019). A  
165 similar way of thinking could be applied to designing housing and testing spaces for

166 nonhuman animals. For example, in “modern” zoos animals of different species are housed  
167 together in larger enclosures, while retaining the possibility for each species to be isolated  
168 from the others if needed. This is a way to apply the concept of nudge (i.e. any aspect of the  
169 choice architecture that alters behavior in a predictable way without forbidding any options,  
170 Thaler, 2008) to some captive animals studies, as has already been done for species  
171 conservation (Czap et al., 2015; Eberle, 2021; Reddy et al., 2017). Kyoto University applied  
172 this concept with the WISH cages, a set of enclosures connecting habitats and equipped with  
173 a computer-controlled touch panel system for cognitive tests. This framework increases the  
174 fission-fusion dynamics of chimpanzees, i.e. their social agency, and their cognitive agency  
175 (Matsuzawa, 2020). Other labs provide similar voluntary participation testing stations  
176 associated with group-living such as the Goffin laboratory in Vienna with cockatoos (*Cacatua*  
177 *goffini*) (O’Hara et al., 2021) or the Living Links station with nonhuman primates at  
178 Edinburgh zoo (Jordan et al., 2022). This principle is not restricted to vertebrates as ants for  
179 instance showed their abilities to escape their captive nest when it was not well designed,  
180 thanks to behaviors as raft, bridge, jump or even tool use (Dussutour & Wystrach, 2022).

## 181 *2. Agency through practice and routine:*

182 Animals have habits. Social animals collectively organize their day in order to meet their  
183 requirements and maintain the advantages of living in groups (Sueur, 2011). Allowing  
184 animals to accept or refuse to participate in a research activity according to their routine  
185 would increase the robustness and reliability of the results. For example, some studies allow  
186 an animal to use a digital tablet or workstation or to open boxes to obtain food inside (Aplin  
187 et al., 2015, Whiten et al., 1996). In domains such as visual cognition testing could be  
188 conducted in a naturalistic environment with an integrated touchscreen workstation,  
189 favoring animal exploration (Jacob et al., 2021). Specific protocols for individuals in a group  
190 can be based on technologies like RFID (Radio Frequency IDentification) (Claidière et al.  
191 2017; Matsuzawa, 2013); these tools allow individuals to participate in the testing at the  
192 time and for the duration of their choosing. Health checks or medical procedures that  
193 require restraints, should also be based on these routines in order to decrease animal stress  
194 and injuries, as already shown in their use by zoos (e.g., the Great Ape Heart Project,  
195 Murphy et al., 2018). Knowing routines of animals or observing why the routine of an animal  
196 is different from others or for a day allows us to better understand their behavior without



197 the need to disturb them by subjecting them to experiments or health checks. Moreover,  
198 modifying the routines of animals is a way to measure their behavioral flexibility,  
199 personality, and group cohesiveness.

200 Whilst many researchers working with captive nonhuman primates already invoke a form of  
201 consent to work with animals (Fenton, 2014), this protocol could be applied to many other  
202 orders and classes, such as rodents. To our knowledge, there are no testing devices that can  
203 be used in the cages of rats with which they can play when they want and for the duration  
204 they want (although some housing includes different kinds of objects and surfaces for  
205 voluntary activity; Bailoo et al., 2018; Crawford et al., 2020). This kind of system should be  
206 extended to all species involved in research.

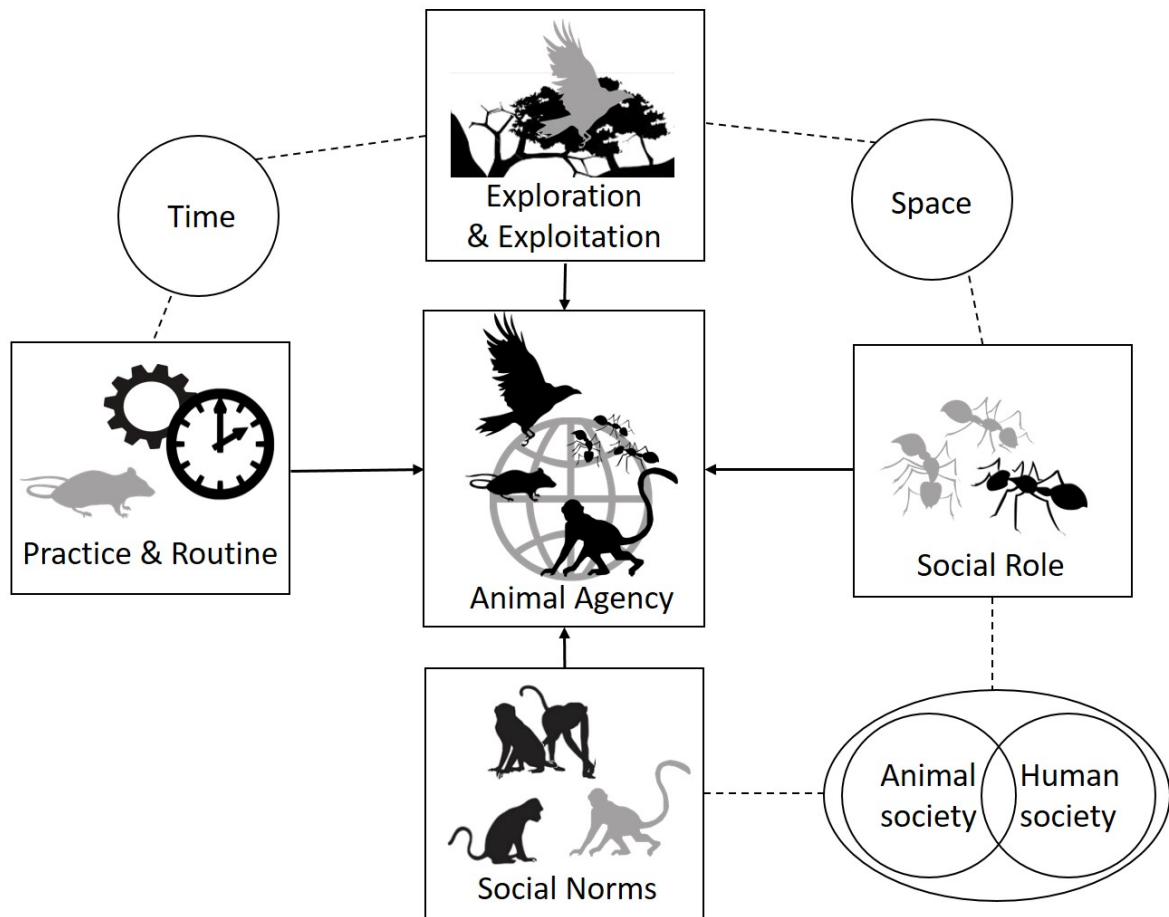
### 207 *3. Agency in the social environment:*

208 A social role is the behavior expected of an individual who occupies a given social position or  
209 status. Individuals understand the place that conspecifics hold in their society (Borgeaud et  
210 al., 2016; Bret et al., 2013; Levé et al., 2016). The adoption of roles that are recognized and  
211 acknowledged by others, and indeed mutually constructed with conspecifics, is an important  
212 dimension of relational agency and a means by which researchers can effectively affirm their  
213 subjective existence within a community. This role can be intraspecific or interspecific. Roles  
214 of individuals inside their group have been amply described in terms of dominance (policing  
215 behaviors, protecting groups), kinship, and maternal relationships (Krause & Ruxton, 2002).  
216 Individuals also develop strong relationships when they share similar attributes, such as sex  
217 or age (Abeyesinghe et al., 2013; Massen & Koski, 2014; Rault, 2012; Silk, 2002; Tsuji et al.,  
218 2007). These affiliative but interspecific relationships are used in the case of animal  
219 mediation and zootherapy where dogs, cats, and horses respond to the pain of patients, not  
220 only passively but also proactively by initiating for instance play sessions (Chouinard, 2021;  
221 Muschel, 1984). With time, these mediation animals developed strong relationships with  
222 certain patients. When doing tests, researchers also know which pairs of individuals can  
223 easily be tested together or not. Group members influence each other (Duboscq et al., 2016)  
224 and can transmit important information to others (Grampp et al., 2019). Social learning can  
225 aid animals learning to use experimental apparatus or spaces (Biro et al., 2006; Whiten,  
226 2011). This works in many vertebrate species and even in invertebrates: fruitflies (*Drosophila*  
227 *sp.*) are able to learn from their conspecifics where to lay eggs and bumblebees (*Bombus*

228 *terrestris*) learn to pull a string to obtain food when interacting with another bumblebee that  
229 does so (Alem et al., 2016; Battesti et al., 2015; Pasquaretta et al., 2016). Biased attention of  
230 group members towards dominant or older individuals in some species (Grampp et al., 2019)  
231 might be used by researchers to make animals more rapidly or more efficiently learn a new  
232 behavior. By influencing the leaders, researchers can manage the movements of an entire  
233 group (Ramos et al., 2018, 2021).

#### 234 4. Agency through social norms:

235 Social norms are the customary rules that govern behavior in groups and societies (Bicchieri  
236 & Muldoon, 2011). Behavioral rules and social systems are partly genetic in animals but are  
237 also transmitted through learning (Brent et al., 2013; Krause & Ruxton, 2002; Sinha, 2005;  
238 Sueur, 2015; Ward & Webster, 2016). There is a debate as to whether animals have social  
239 norms, but all theorists agree that social norms require a social maintenance constraint,  
240 such that other group members care whether an individual follows the pattern or not  
241 (Andrews, 2020a; Fitzpatrick, 2020). This might be the case in animal collective decisions  
242 (Sueur et al., 2021). Although collective decision processes are species-specific, variations  
243 are observed between groups and individuals of the same species. The roles played by  
244 individuals can lead to a strong leadership or the development of a more democratic  
245 process, such as voting (King & Sueur, 2011). Voting systems (Pennisi & Giallongo, 2018) are  
246 described in many species, reinforcing the idea of agency. A sense of community (Blattner et  
247 al., 2020) seems to exist in chimpanzees and cetaceans (*Cetacea*), and indeed animals of  
248 many species know exactly who belongs or does not belong to their group.



249

250 Figure 1: The four schemes of animal agency (squares) and the environmental factors  
 251 affecting them (circles).

252

253 These different instances show that animals have agency over their spatial, temporal, and  
 254 social environment. Animals can therefore be viewed as *agents*; their choice to act has direct  
 255 consequences on their environment, or they can also resist conditions that do not please  
 256 them and act accordingly to change them (Carter & Charles, 2013). The behavior that  
 257 animals show, the facial expressions they display, and the places they occupy are cues to  
 258 indicate their intentions as well as their stress. By observing these intentions and/or stress,  
 259 researchers could use animals' agency to improve their welfare and to obtain more robust  
 260 experimental results whilst extending the scope of behavioral and neuroscience research to  
 261 more natural conditions. Indeed, a major challenge facing behavioral neuroscientists today is  
 262 to measure the behaviors and the neuronal activities of sentient animals in natural  
 263 conditions. We have to keep in mind that in the research process, some of the limitations

264 shown by the animals are actually the limitations of the scientific methods, rather than the  
265 animals themselves (Savage-Rumbaugh et al., 2006). This is particularly the case with visual  
266 cognition (Hopper et al., 2021; Jacob et al., 2021) and auditory cognition (Calapai et al.,  
267 2022) with new systems allowing significant advances in testing animals. Similarly, De Waal  
268 (2006) argues, about studies with apes (*Hominidae*) aiming to examine their theory of mind:  
269 'All that most experiments have done thus far is test the ape's theory of the human mind.  
270 We would do better to focus on the ape's theory of the ape mind', (p. 70). Following the  
271 concept of animal agency, this paper proposes a future research framework to work with  
272 animals and progress in research.

273

#### 274 **Evidence that animals have agency**

275 Many animals (mammals, birds, and other classes) possess the neural substrates involved in  
276 emotions and consciousness (Ben-Haim et al., 2021; Low et al., 2012). Authors have argued  
277 that nonhuman animals may evidence several aspects of cognition that until recently were  
278 attributed to humans but not other animals. For example, rats, apes, macaques (*Macaca*  
279 *sp.*), and pigeons (*Columba livia*) may be capable of metacognition, i.e., knowing if they are  
280 wrong or right in a test (Le Neindre et al., 2017, 2018). Cetaceans and apes may be conscious  
281 of their own existence, and that of others (Gallup et al., 2002). Cleaner fish may have some  
282 elements of self-awareness (Kohda et al., 2019). Apes may know what their conspecifics  
283 know (Kaminski, Call, & Tomasello, 2008) and believe (Krupenye et al., 2016). Apes (De Waal,  
284 2012) and rats (Ben-Ami Bartal et al., 2011) may experience empathy. Finally, some apes  
285 may have a sense of morality (De Waal, 2006; Jensen et al., 2007; Tomasello & Vaish, 2013).

286 Of course, there remains debate on how to interpret behavioral studies when it comes to  
287 the cognitive capacities we listed above (Bekoff & Allen, 1997; Buckner, 2011; Sober, 2009),  
288 and we need to be careful about how to interpret these results (Janson & Byrne, 2007;  
289 Péron, 2012). Whilst some individuals show the particular capacities in some experiments,  
290 other members of the same species fail in other studies or replications (Boyle, 2021; Voelkl  
291 et al., 2020, 2021), thus proving the importance of comparative methods to investigate  
292 these phenomena (Krasheninnikova et al., 2019; Schmitt et al., 2012). Moreover, there is no  
293 need to have these specific cognitive capacities to be an agent according to some views of

294 agency (Carter & Charles, 2013). Methods used by ants to find resources are used as an  
295 algorithm for the traveling salesman problem (Dorigo & Gambardella, 1997a, 1997b). In both  
296 illustrations, the organisms are not only an inspiration for researchers to resolve a problem,  
297 they resolved it with their own capacities in their own world. In that sense, both can be  
298 considered as co-creators of the new knowledge, even if they are not aware of it. Accepting  
299 this paradigm of co-creation of knowledge can create new research questions that are  
300 different from those made under an anthropocentric view.

301 More and more, researchers showed that animals may have previously unrecognized  
302 cognitive capacities by changing their way of thinking from an anthropocentric approach,  
303 looking for human-like cognition to hypothesizing that animals can think in a way different  
304 from how humans do (Andrews, 2020b; Birch et al., 2020; De Waal, 2016). For instance,  
305 some species do not respond to mark on themselves when looking in a mirror (Gallup et al.,  
306 2002) but do respond in a self-directed manner, suggesting a sense of self, when researchers  
307 presented stimuli in a sensory modality relied upon by the particular animal, such as the  
308 sense of smell for dogs (Cazzolla Gatti, 2016) or hearing in gibbons (*Nomascus leucogenys*)  
309 (D'Agostino et al., 2017). As the same way for mirror and face recognition, researchers  
310 presented to gibbons and dogs respectively vocalizations and odors of themselves and  
311 observed how they reacted compared to vocalizations and odors of conspecifics. Merleau-  
312 Ponty had already noted this problem in his *Causeries* back in 1948: researchers usually do  
313 not try to understand animals in their singularity, *as they are*, but rather in comparison with  
314 human beings, projecting what are essentially human characteristics onto animals (Merleau-  
315 Ponty, 2017). However, this is a means to measure the distance between human beings and  
316 other animals rather than a tool allowing a real understanding of how animals live and  
317 express a subjective existence (Sueur et al., 2020; Sueur & Pelé, 2017; Tokuyama et al.,  
318 2012). Studied in the light of human normative references, animals always lack something  
319 (Merleau-Ponty, 2017). For as long as animals are studied from a human perspective and are  
320 tested in terms of human problems (capacity to count, to draw, to speak a human language)  
321 instead of their own questions and problems, they will always respond 'as they can'  
322 (Canguilhem, 1992), without ever being able to fully express their agency. However, there  
323 have been philosophical and anthropological attempts to blur the boundaries between  
324 humans and other animals (Andrews, 2020b; Böhnert & Hilbert, 2018; Daly Bezerra de Melo,

325 2012, 2018; De Waal, 2016; Langlitz, 2020; Wendler, 2020). As Jacques Derrida wrote in *The*  
326 *Animal That Therefore I Am* (2008), the traditional scientific and philosophical discourse on  
327 animals observes and speaks of non-human animals but never really engages with,  
328 experiments *with*, or gains experience with the latter (Derrida, 2008): this type of discourse  
329 can therefore only position animals as mere passive objects of the theoretical knowledge  
330 these disciplines build. Such methods are completely blind to the animals' own processes of  
331 interacting with their world (Derrida, 2008), and are completely blind to their agency.  
332 Animals interact with the world in their own ways and these ways, i.e. their agency, are  
333 precisely the view that researchers need to adopt to perform better research and develop a  
334 better understanding of how the brain and behavior evolve.

335

## 336 **Future research framework**

337

### 338 1. *Testing agency from the laboratory*

339 Some studies, especially in the biomedical or physiological/cellular domains, cannot be  
340 performed outside the laboratory. It is important for these experiments to respect the 3Rs  
341 (Replace, Reduce, Refine) but also to think about the Bateson cube (Bout et al., 2014),  
342 meaning that scientists need to evaluate the ethical acceptability of their research for  
343 society as a whole, including animals. Bateson's cube is a model of the cost–benefit analysis  
344 for animal research in which research protocols are evaluated through three criteria: the  
345 degree of animal suffering, the quality of the research and the potential applied or  
346 fundamental benefit. The principles can be extended by testing animals in correct  
347 conditions, meaning in conditions not leading to strong false negatives or strong false  
348 positives. Overly standardized laboratory conditions, for instance, decrease the replicability  
349 of studies by decreasing behavioral variability; this is commonly known as the  
350 standardization fallacy (Voelkl et al., 2021; Würbel, 2000).

351 Indeed, laboratory conditions for nonhuman primates and rodents were standardized for  
352 many years in terms of husbandry and diet, in order to support comparisons across  
353 experiments and laboratories. However, this way of conducting research is criticized today  
354 because the conditions in which animals live have a strong effect on them, and thus on the

355 scientific results, so studies of animals in narrow conditions provide results relevant only to  
356 those narrow conditions. Moreover, it is difficult to replicate conditions across laboratories,  
357 specifically in studies about comparative cognition because of a large variance of  
358 physiological, behavioral or cognitive traits between individuals (Boyle, 2021). Indeed, it is  
359 first difficult to replicate same group living conditions in terms of animal density, group  
360 composition, conditions which have an impact on cognitive capabilities (Meguerditchian et  
361 al., 2021), but even when it is possible, animals that are genetically similar and live in similar  
362 environments develop different personalities (Bierbach et al., 2017). Lastly, poor husbandry  
363 conditions stress individuals (Cait et al., 2022; Pomerantz et al., 2022) and do not allow them  
364 to express their full agency. Indeed, sociality has an important impact on the health of  
365 animals, and a large number of publications highlight the link between sociality and health  
366 aging (Boyer et al., 2019; Lacreuse et al., 2020; Rosati et al., 2020). Enabling animals' social  
367 agency can even reverse cognitive decline and extend longevity (Baker et al., 2012;  
368 Richardson et al., 2020; Wild et al., 2021). Sociality is an important part of animal agency and  
369 social life of animals has to be respected even in laboratory conditions, for their welfare as  
370 well as for the robustness of scientific results.

## 371 2. ... To the wild or at least in more natural conditions

372 Traditional approaches to studying for instance visual cognition or decision-making involve  
373 bringing animals into a laboratory and restraining them while they perform tasks in order to  
374 ensure accurate measurements, for example, of gaze-tracking and neural activity (see for  
375 instance D'Souza et al., 2021; Honda et al., 2021). However, this unnatural setting does not  
376 permit the study of brain activity during natural, social, and complex behaviors (Testard et  
377 al., 2021). Many discoveries about ants' behavior could not be made if not in natural  
378 conditions (Dussutour & Wystrach, 2022) as the one showing that the termite-hunting ant  
379 (*Megaponera analis*) is capable of saving injured individuals by taking them back to the nest  
380 (Frank et al., 2017). Ideally, experimental settings will permit animals to move normally and  
381 to engage in natural activities, such as foraging and in social interactions, but this requires  
382 that animals accept to wear some devices, not tear off some cables or even just come at the  
383 right place at the right time. Culture of animals also have to be considered and for instance,  
384 study of percussive tools by nonhuman primates, known from field observations, has been  
385 difficult to achieve in the laboratory. Laboratory studies of this phenomenon (e.g., Bril et al.,

386 2009) have been less numerous than field experiments, that have been very productive (e.g.,  
387 Biro et al., 2006; Leca et al., 2007; Visalberghi et al., 2009). In the same way, field  
388 experiments or experiments close to natural conditions led to important results in  
389 understanding foraging strategies in bees (*Apidae*) (Pasquaretta et al., 2017) and  
390 hummingbirds (*Trochilidae*) (Bateson et al., 2002). Several authors highlight that studying  
391 animals in nature instead of in the laboratory provides more easily interpretable findings  
392 (Cauchoix et al., 2017; Kumpan et al., 2020; Verhaeghen et al., 2012). Specific ethical  
393 guidelines exist now for behavioral or psychological research in the wild (Costello et al.,  
394 2016; Soulsbury et al., 2020). The likely benefits and possible negative effects of researchers'  
395 presence and field methods on study subjects, their environment, and the local human  
396 community should, of course, be considered (MacKinnon & Riley, 2010).

397 Progress has to be made first to avoid restraining animals in a captive environment and  
398 second, to conduct tests on animals in more natural conditions. Such processes are applied  
399 today to not only different primate species (Huebner et al., 2018; Schofield et al., 2019; Van  
400 de Waal et al., 2013) but also to horses (Maeda et al., 2021; Matsuzawa, 2017), birds (Aplin  
401 et al., 2015; Shaw, 2017), and even bees (Muth et al., 2018). These studies, conducted on  
402 different species all showed that testing in the wild is more productive than testing in the  
403 labs in terms of ecological and social cognition (Pritchard et al., 2016). An intermediate  
404 method would be research in zoos. Zoos provide more adequate living conditions than many  
405 laboratories. This seems to allow animals to express their agency (McEwen et al., 2022).  
406 Testing these same species in more natural and more complex captive habitats or even in  
407 natural settings could enhance the possibility of them expressing their agency.

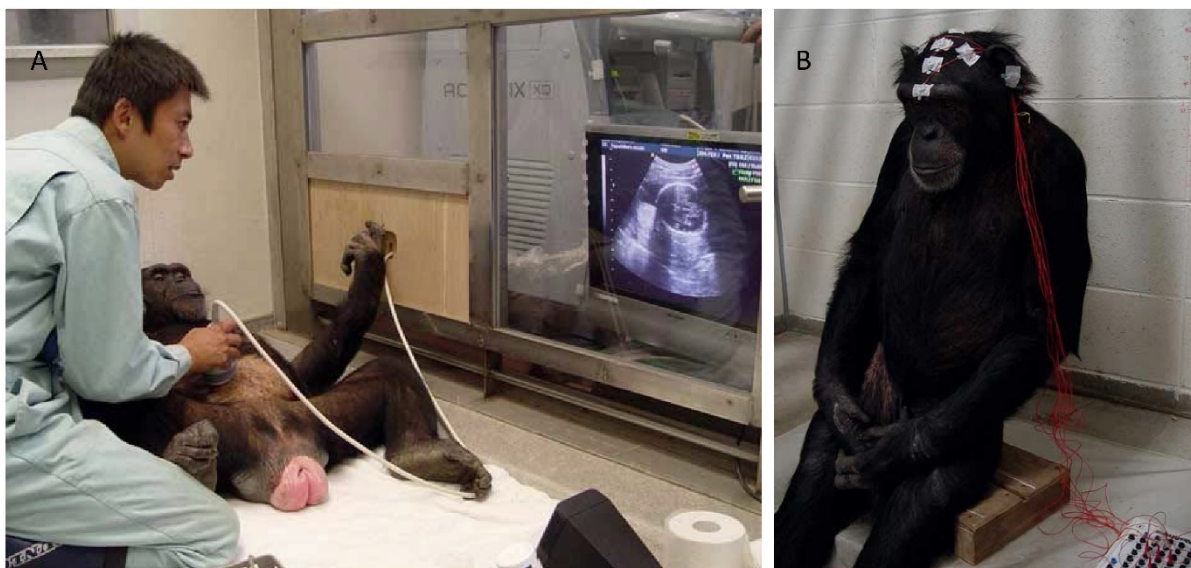
### 408 *3. Agency promotes the use of new technologies and vice-versa*

409 Researchers need to change their way of thinking to a perspective of working *with* animals  
410 rather than *on* animals. Researchers need to trust their capabilities (Nielsen, 2018; Nielsen,  
411 2020) in order to increase research possibilities. Experimental setups, such as restraint chairs  
412 or food privation, cause stress to animals and prevent them (both physically and mentally)  
413 from fully expressing their agency. This challenge of giving animals more freedoms may  
414 certainly takes time but would be hugely beneficial. Van Patter and Blattner (2020) suggest  
415 core principles to follow with animals: non-maleficence, beneficence, and voluntary  
416 participation (Webb et al., 2019). Positive methods exist and have proved to be efficient



417 (Laule et al., 2003; Prescott et al., 2010; Prescott, 2016; Prescott & Buchanan-Smith, 2003;  
418 Prescott & Buchanan-Smith, 2007; Schapiro et al., 2003). Use of cooperation handling in  
419 macaques instead of chair restraint leads to a diminution of stress, decreases the use of  
420 sedation and increases behavioral acquisition (Graham et al., 2012). The readiness of  
421 chimpanzees (which are no longer used for invasive experiments – Matsuzawa, 2016b) to  
422 voluntarily participate in interactions or allow humans to observe them can facilitate the  
423 measurement of embryo development and brain activities in unanesthetized and  
424 unrestrained individuals (Figure 2 - Matsuzawa, 2013; Sakai et al., 2011, 2012; Ueno et al.,  
425 2010). Unrestrained or minimally restrained and voluntary animals can be trained to put  
426 their head in a mask voluntarily (Slater et al., 2016) and be tested whilst receiving fruit juice.  
427 This allows the measurement of different metrics with eye tracking (apes: Kano &  
428 Tomonaga, 2009; Krupenye et al., 2016; monkeys: Machado & Nelson, 2011; Ryan et al.,  
429 2019) and non-invasive neuroimaging (Basso et al., 2021) (Figure 3.A). Magnetic resonance  
430 imaging (MRI) requires the subject to remain still during the scan. Dogs can be trained to  
431 remain still during fMRIs without any restriction (Berns & Cook, 2016). Surely, this  
432 cooperation can be achieved with other species, allowing testing emotions and cognitive  
433 capacities as done with humans (Cheng et al., 2010; Eisenberger et al., 2003; Yang et al.,  
434 2022; Yates et al., 2021).

435



436  
437 Figure 2: (A) Developmental neuroscience. Fetal brain development in chimpanzees was  
438 measured by a non-invasive ultrasound technique. (B) EEG recordings in a chimpanzee. The

439 chimpanzee quietly sat on the chair and allowed the experimenter to put electrode patches  
440 on the skin of her forehead and the top of her head. Photos provided courtesy of Satoshi  
441 Hirata.

442

443 Touchscreens are useful tools that demonstrate agency in nonhuman animals. Individuals  
444 have to learn by themselves how to solve visual problems. Software running the displays and  
445 data collection systems are easy to adapt to individuals' cognitive capacities and perception.  
446 Researchers can measure different parameters (time of answering the test, success, type of  
447 answers) for each individual and species. The possibility of more freedoms of action can  
448 produce individual and group specificity. For instance, Claidière et al. (2014) gave a task to  
449 baboons (*Papio papio*) where they have to click on red squares on a 4\*4 squares matrix.  
450 Instead of forcing animals to answer specific patterns, the authors took into account how  
451 baboons succeed to click on some patterns to transmit these patterns to other baboons and  
452 showed evidence of cultural transmission in baboons as in humans. Some years ago,  
453 applying the use of touchscreens with nonhuman animals, or studying mouse personality  
454 was almost unimaginable in neuroscience. Yet today, these projects have become reality. For  
455 instance, the use of a touchscreen was initially difficult but eventually, use of this testing  
456 method led to tests of new concepts more quickly than tests without touchscreens in  
457 chimpanzees (Gao et al., 2018; Inoue & Matsuzawa, 2007; Martinet et al., 2021) and  
458 macaques (Ballesta et al., 2021; Ferrucci et al., 2019; Huskisson et al., 2021). In the same  
459 vein, it took time for naïve capuchins (*Sapajus sp.*), macaques (*Macaca sp.*), and apes (*Pan*  
460 *troglydytes*, *Pongo pygmaeus abelii*) to understand a food – for - food exchange task (Dufour  
461 et al., 2007; Pelé et al., 2009; Pelé et al., 2010; Ramseyer et al., 2006), but once the behavior  
462 was acquired, it was easily transmitted from adults to their young (Pelé, personal  
463 observation). Touchscreens or joysticks are now used to understand cognition (Kaneko &  
464 Tomonaga, 2011) in a wide range of species (pigs – *Sus scrofa*, macaques, baboons – *Papio*  
465 *papio*, marmosets - *Callithrix jacchus*, goats, horses, rats, mice – *mus musculus*, etc.) (Belsey  
466 et al., 2020; Calapai et al., 2022; Claidière et al., 2017; Croney & Boysen (2021); Jacobson et  
467 al., 2019; Tomonaga et al., 2015; Washburn et al., 2004; Yang et al. 2022; Zeagler et al.,  
468 2014). Researchers trained archerfish (*Toxotes chatareus*) to spit on a touchscreen and  
469 showed that they are able to differentiate human faces (Newport et al., 2016). However,

470 touchscreen technology is still limited despite its potential and even if more and more  
471 neuroscience studies have been using it in mice or rats (Bussey et al., 1997, 2008; Delotterie  
472 et al., 2015; Slutzky et al., 2010). So, touchscreens and joystick apparatuses promote animal  
473 agency, even though it is in a limited artificial environment. However, these devices can be  
474 extended to the wild and the principle of touchscreen (touching for a visual choice) should  
475 be extended to other senses as it was done for testing auditory capabilities in common  
476 marmosets (Calapai et al., 2022).

477 Other new technologies allow us to bring devices into natural settings to test unrestrained  
478 animals in their natural (including social) environment, thus removing experimental sources  
479 of stress and allowing them agency and expression of their entire behavioral repertoire.  
480 Field experiments of this type are possible in many species including rodents (Evans et al.  
481 2020; Lopes & König, 2020; Raulo et al., 2021). The animals can be identified individually by  
482 observation or by using RFID techniques (Fehlmann & King, 2016) or via artificial intelligence  
483 with the recognition of individuals by video tracking (Charpentier et al., 2020; Ferreira et al.,  
484 2020; Schofield et al., 2019). The latter removes the need to capture animals. RFID  
485 techniques allowed demonstration, for example, that bats (*Myotis bechsteinii*) form long-  
486 term social relationships (Kerth et al., 2011) and that tits (*Parus major*) learned according to  
487 their social networks (Aplin et al., 2015). Face and behavioral recognition using artificial  
488 intelligence gave some indices about social networks in chimpanzees (Schofield et al., 2019)  
489 and signaling kinship in mandrills (*Mandrillus sphinx*) (Charpentier et al., 2020). It could also  
490 be extended to theory of mind and intentionality as gaze-following (Horschler et al., 2020) or  
491 false belief attribution (Krupenye et al., 2016).

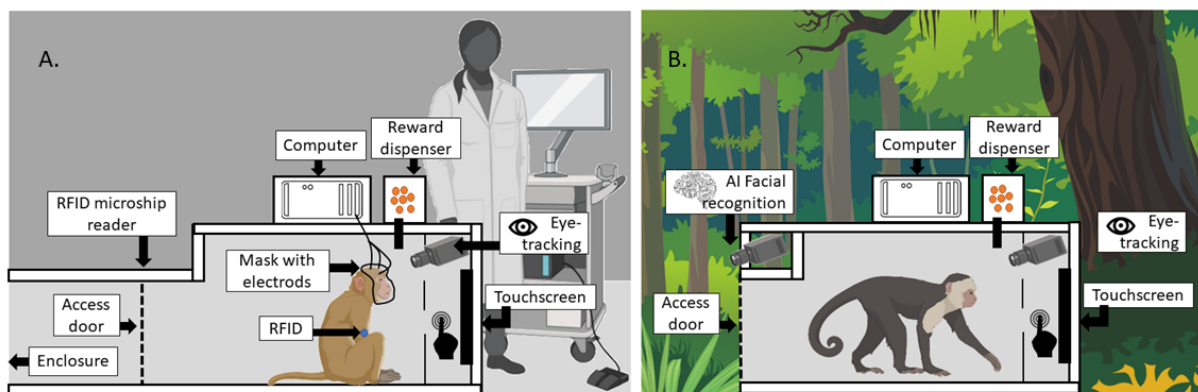
492 A general idea of how a laboratory- bound experimental method could be adapted for use  
493 in a field experiment is given in Figure 3.B. A location is defined where different operable  
494 devices can be installed, such as touchscreens, to deliver food or another valuable  
495 commodity, with activation only for certain species and individuals. Researchers can imagine  
496 implementing eye tracking and other apparatus in the wild when technology permits. This  
497 could open up new research avenues in species that cannot be maintained in captivity.

498 Some automatic devices already exist to make some playback experiments as BoomBox: An  
499 Automated Behavioral Response (ABR) camera trap module for wildlife experiments (Palmer  
500 et al., 2022). Food containers of various kinds, have been used in field experiments (De la

501 Fuente et al., 2022; Van de Waal et al., 2013) and robots are increasingly used with wild  
502 animals (Grémillet et al., 2012; Le Maho et al., 2014). Research possibilities in this domain  
503 are huge.

504 Although there are logistical challenges attendant on any new methodology, we should  
505 consider how to take advantage of technological advances to bring our science to animals in  
506 natural settings, while ensuring the health and security of the animal participants. As  
507 Schaefer and Claridge-Chang (2012) wrote, ‘the new automation is not just faster: it is also  
508 allowing new kinds of experiments, many of which erase the boundaries of the traditional  
509 neuroscience disciplines (psychology, ethology, and physiology) while producing insight into  
510 problems that were otherwise opaque’ (p. 170). Figure 3 illustrates a hypothetical system for  
511 conducting eye tracking while an individual voluntarily operates a touchscreen apparatus, in  
512 the laboratory and in field settings.

513



514

515 Figure 3: (A) Hypothetical non-invasive neuroimaging and eye-tracking system with  
516 touchscreen interactive component and voluntary participation in the laboratory. (B)  
517 Hypothetical touchscreen system with voluntary engagement and individual identification in  
518 the field. In setup A, the subject would show better agency than if it was restrained in a  
519 chair. However, the same subject in setup B would show greater agency than in setup A, as it  
520 is free to express its entire behavioral repertoire in natural conditions. The box is needed to  
521 assure the isolation of the tested individual and the resistance of the materials to outside  
522 conditions. This figure was realized using FAVPNG.com and Biorender.

523

## 524 **Conclusion**

525 Great efforts have been made toward enabling the agency of animals in behavioral research  
526 but there is still much progress to be made to obtain a more compassionate, less stressful,  
527 and more robust animal research model. This requires training and teaching researchers to  
528 adopt new methods including animal agency and to change their view of the role animals  
529 play in research (see for instance the book “Handbook of Primate Behavioral Management”  
530 Schapiro, 2017, for methods to achieve voluntary participation of primates in various health-  
531 related and husbandry procedures). Animals are agents in scientific research. They are active  
532 in the research process and agency may promote the use of new technologies. This  
533 recognition of animals as agents rather than objects is not approved by some researchers,  
534 who consider that this position is tantamount to committing over-anthropomorphism, and  
535 overstepping the will of animals to cooperate. However, acknowledging animal agency could  
536 facilitate broader social acceptance of research with nonhuman animals (Webb et al., 2019)  
537 and be of benefit to the animals concerned (supporting well-being through learning,  
538 creating, and participating – Franks et al., 2020).

539 Considering the agency of the animals we work with is clearly a time investment that  
540 ultimately pays off for more time-efficient data collection in the long term. This time  
541 investment in animal agency should be highlighted and recognized as promoting animal  
542 welfare (in the same way as plans for adoption research animals, for instance) when  
543 readying a proposal for financial support. This new way of viewing animal agency can  
544 therefore raise critical ethical questions in regard to the treatment of animals in research  
545 and to the place humans grant them in the human social world.

546

## 547 **Author Contributions Statement**

548 Conceptualization: CS and MP; Project administration: CS and MP; Writing original draft: CS;  
549 Review and editions: all authors.

550

## 551 **Acknowledgments**

552 We thank the three anonymous reviewers who accepted to revise our manuscript and the  
553 editor Dorothy Fragaszy for their helpful comments.

554

## 555 **References**

556 Abeyesinghe, S. M., Drewe, J. A., Asher, L., Wathes, C. M., & Collins, L. M. (2013). Do hens have  
557 friends? *Applied Animal Behaviour Science*, *143*(1), 61-66.

558 <https://doi.org/10.1016/j.applanim.2012.12.003>

559 Alem, S., Perry, C. J., Zhu, X., Loukola, O. J., Ingraham, T., Sjøvik, E., & Chittka, L. (2016). Associative  
560 Mechanisms Allow for Social Learning and Cultural Transmission of String Pulling in an Insect.

561 *PLOS Biology*, *14*(10), e1002564. <https://doi.org/10.1371/journal.pbio.1002564>

562 Andrews, K. (2020a). Naïve Normativity : The Social Foundation of Moral Cognition. *Journal of the*  
563 *American Philosophical Association*, *6*(1), 36-56. <https://doi.org/10.1017/apa.2019.30>

564 Andrews, K. (2020b). *How to Study Animal Minds*. Cambridge University Press.

565 <https://www.cambridge.org/core/elements/how-to-study-animal->

566 [minds/FC90846C50ED2E992CA2AC51D7C249AC](https://www.cambridge.org/core/elements/how-to-study-animal-minds/FC90846C50ED2E992CA2AC51D7C249AC)

567 Aplin, L. M., Farine, D., Morand-Ferron, J., & Sheldon, B. (2012). Social networks predict patch  
568 discovery in a wild population of songbirds. *Proceedings of the Royal Society of London B:*  
569 *Biological Sciences*, rspb20121591.

570 Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015).  
571 Experimentally induced innovations lead to persistent culture via conformity in wild birds.

572 *Nature*, *518*(7540), 538.

573 Bailoo, J. D., Murphy, E., Boada-Saña, M., Varholick, J. A., Hintze, S., Baussière, C., Hahn, K. C.,

574 Göpfert, C., Palme, R., Voelkl, B., & Würbel, H. (2018). Effects of Cage Enrichment on  
575 Behavior, Welfare and Outcome Variability in Female Mice. *Frontiers in Behavioral*

576 *Neuroscience*, *12*. <https://www.frontiersin.org/article/10.3389/fnbeh.2018.00232>

577 Baker, N., Wolschin, F., & Amdam, G. V. (2012). Age-related learning deficits can be reversible in  
578 honeybees *Apis mellifera*. *Experimental Gerontology*, 47(10), 764-772.  
579 <https://doi.org/10.1016/j.exger.2012.05.011>

580 Ballesta, S., Sadoughi, B., Miss, F., Whitehouse, J., Aguenounon, G., & Meunier, H. (2021). Assessing  
581 the reliability of an automated method for measuring dominance hierarchy in non-human  
582 primates. *Primates*, 62(4), 595-607. <https://doi.org/10.1007/s10329-021-00909-7>

583 Bartal, I. B.-A., Decety, J., & Mason, P. (2011). Empathy and pro-social behavior in rats. *Science*,  
584 334(6061), 1427-1430.

585 Basso, M. A., Frey, S., Guerriero, K. A., Jarraya, B., Kastner, S., Koyano, K. W., Leopold, D. A., Murphy,  
586 K., Poirier, C., Pope, W., Silva, A. C., Tansey, G., & Uhrig, L. (2021). Using non-invasive  
587 neuroimaging to enhance the care, well-being and experimental outcomes of laboratory non-  
588 human primates (monkeys). *NeuroImage*, 228, 117667.  
589 <https://doi.org/10.1016/j.neuroimage.2020.117667>

590 Bateson, M., Healy, S. D., & Hurly, T. A. (2002). Irrational choices in hummingbird foraging behaviour.  
591 *Animal Behaviour*, 63(3), 587-596. <https://doi.org/10.1006/anbe.2001.1925>

592 Battesti, M., Pasquaretta, C., Moreno, C., Teseo, S., Joly, D., Klensch, E., Petit, O., Sueur, C., & Mery, F.  
593 (2015). Ecology of information : Social transmission dynamics within groups of non-social  
594 insects. *Proceedings of the Royal Society of London B: Biological Sciences*, 282(1801),  
595 20142480. <https://doi.org/10.1098/rspb.2014.2480>

596 Bègue, L., & Vezirian, K. (2021). Sacrificing Animals in the Name of Scientific Authority : The  
597 Relationship Between Pro-Scientific Mindset and the Lethal Use of Animals in Biomedical  
598 Experimentation. *Personality & Social Psychology Bulletin*, 1461672211039413.  
599 <https://doi.org/10.1177/01461672211039413>

600 Bekoff, M., & Allen, C. (1997). Cognitive Ethology : Slayers, Skeptics, and Proponents. In R. Mitchell,  
601 N. S. Thompson, & H. L. Miles (Éds.), *Anthropomorphism, Anecdotes, and Animals* (p.  
602 313-334). Suny Press.

603 Belsey, P. P., Nicholas, M. A., & Yttri, E. A. (2020). Open-Source Joystick Manipulandum for Decision-  
604 Making, Reaching, and Motor Control Studies in Mice. *eNeuro*, 7(2), ENEURO.0523-19.2020.  
605 <https://doi.org/10.1523/ENEURO.0523-19.2020>

606 Ben-Haim, M. S., Monte, O. D., Fagan, N. A., Dunham, Y., Hassin, R. R., Chang, S. W. C., & Santos, L. R.  
607 (2021). Disentangling perceptual awareness from nonconscious processing in rhesus  
608 monkeys (*Macaca mulatta*). *Proceedings of the National Academy of Sciences*, 118(15).  
609 <https://doi.org/10.1073/pnas.2017543118>

610 Berlyne, D. E. (1966). Curiosity and Exploration : Animals spend much of their time seeking stimuli  
611 whose significance raises problems for psychology. *Science*, 153(3731), 25-33.

612 Berns, G. S., & Cook, P. F. (2016). Why Did the Dog Walk Into the MRI? *Current Directions in*  
613 *Psychological Science*, 25(5), 363-369. <https://doi.org/10.1177/0963721416665006>

614 Bhattacharjee, D., Mandal, S., Shit, P., Varghese, M. G., Vishnoi, A., & Bhadra, A. (2020). Free-Ranging  
615 Dogs Are Capable of Utilizing Complex Human Pointing Cues. *Frontiers in Psychology*, 10.  
616 <https://doi.org/10.3389/fpsyg.2019.02818>

617 Bicchieri, C., & Muldoon, R. (2011). *Social norms*.

618 Bierbach, D., Laskowski, K. L., & Wolf, M. (2017). Behavioural individuality in clonal fish arises despite  
619 near-identical rearing conditions. *Nature Communications*, 8, 15361.  
620 <https://doi.org/10.1038/ncomms15361>

621 Birch, J., Schnell, A. K., & Clayton, N. S. (2020). Dimensions of animal consciousness. *Trends in*  
622 *Cognitive Sciences*.

623 Biro, D., Sousa, C., & Matsuzawa, T. (2006). Ontogeny and cultural propagation of tool use by wild  
624 chimpanzees at Bossou, Guinea : Case studies in nut cracking and leaf folding. In *Cognitive*  
625 *development in chimpanzees* (p. 476-508). Springer.

626 Blattner, C. E., Donaldson, S., & Wilcox, R. (2020). Animal Agency in Community. *Politics and Animals*,  
627 6, 1-22.



628 Böhnert, M., & Hilbert, C. (2018). ?Other Minds Than Ours? : A Controversial Discussion on the Limits  
629 and Possibilities of Comparative Psychology in the Light of C. Lloyd Morgan?s Work. *History*  
630 *and Philosophy of the Life Sciences*, 40(3), 44. <https://doi.org/10.1007/s40656-018-0211-4>

631 Borgeaud, C., Sosa, S., Bshary, R., Sueur, C., & van de Waal, E. (2016). Intergroup Variation of Social  
632 Relationships in Wild Vervet Monkeys : A Dynamic Network Approach. *Frontiers in*  
633 *Psychology*, 7, 915. <https://doi.org/10.3389/fpsyg.2016.00915>

634 Bouissou, M.-F., Boissy, A., Le Neindre, P., & Veissier, I. (2001). The social behaviour of cattle. *Social*  
635 *behaviour in farm animals*, 113-145.

636 Bout, H. J., van Vlissingen, J. M. F., & Karssing, E. D. (2014). Evaluating the ethical acceptability of  
637 animal research. *Lab Animal*, 43(11), 411-414. <https://doi.org/10.1038/lablan.572>

638 Boyer, F., Jaouen, F., & El Chérif Ibrahim, E. G. (2019). Deficits in social behavior precede cognitive  
639 decline in middle-aged mice. *Frontiers in behavioral neuroscience*, 13.

640 Boyle, A. (2021). Replication, Uncertainty and Progress in Comparative Cognition. *Animal Behaviour*  
641 *and Cognition*, 8(2), 296-304.

642 Brent, L. J. N., Heilbronner, S. R., Horvath, J. E., Gonzalez-Martinez, J., Ruiz-Lambides, A., Robinson, A.  
643 G., Skene, J. H. P., & Platt, M. L. (2013). Genetic origins of social networks in rhesus  
644 macaques. *Scientific Reports*, 3. <https://doi.org/10.1038/srep01042>

645 Bret, C., Sueur, C., Ngoubangoye, B., Verrier, D., Deneubourg, J.-L., & Petit, O. (2013). Social Structure  
646 of a Semi-Free Ranging Group of Mandrills (*Mandrillus sphinx*) : A Social Network Analysis.  
647 *PLoS ONE*, 8(12), e83015. <https://doi.org/10.1371/journal.pone.0083015>

648 Bril, B., Dietrich, G., Foucart, J., Fuwa, K., & Hirata, S. (2009). Tool use as a way to assess cognition :  
649 How do captive chimpanzees handle the weight of the hammer when cracking a nut? *Animal*  
650 *cognition*, 12(2), 217-235.

651 Buckner, C. (2011). Two Approaches to the Distinction Between Cognition and « Mere Association ».  
652 *International Journal for Comparative Psychology*, 24(1), 1-35.

653 Buller, H. (2014). Animal geographies I. *Progress in Human Geography*, 38(2), 308-318.

654 Bussey, T. J., Muir, J. L., Everitt, B. J., & Robbins, T. W. (1997). Triple dissociation of anterior cingulate,  
655 posterior cingulate, and medial frontal cortices on visual discrimination tasks using a  
656 touchscreen testing procedure for the rat. *Behavioral Neuroscience*, *111*(5), 920-936.  
657 <https://doi.org/10.1037/0735-7044.111.5.920>

658 Bussey, T. J., Padain, T. L., Skillings, E. A., Winters, B. D., Morton, A. J., & Saksida, L. M. (2008). The  
659 touchscreen cognitive testing method for rodents : How to get the best out of your rat.  
660 *Learning & Memory*, *15*(7), 516-523. <https://doi.org/10.1101/lm.987808>

661 Cait, J., Cait, A., Scott, R. W., Winder, C. B., & Mason, G. J. (2022). Conventional laboratory housing  
662 increases morbidity and mortality in research rodents : Results of a meta-analysis. *BMC*  
663 *Biology*, *20*(1), 15. <https://doi.org/10.1186/s12915-021-01184-0>

664 Calapai, A., Cabrera-Moreno, J., Moser, T., & Jeschke, M. (2022). Flexible auditory training,  
665 psychophysics, and enrichment of common marmosets with an automated, touchscreen-  
666 based system. *Nature Communications*, *13*(1), 1648. [https://doi.org/10.1038/s41467-022-](https://doi.org/10.1038/s41467-022-29185-9)  
667 [29185-9](https://doi.org/10.1038/s41467-022-29185-9)

668 Canguilhem, G. (1992). *La connaissance de la vie*. Vrin.

669 Carter, B., & Charles, N. (2013). Animals, Agency and Resistance. *Journal for the Theory of Social*  
670 *Behaviour*, *43*(3), 322-340. <https://doi.org/10.1111/jtsb.12019>

671 Cauchoix, M., Hermer, E., Chaine, A. S., & Morand-Ferron, J. (2017). Cognition in the field :  
672 Comparison of reversal learning performance in captive and wild passerines. *Scientific*  
673 *Reports*, *7*(1), 12945. <https://doi.org/10.1038/s41598-017-13179-5>

674 Cazzolla Gatti, R. (2016). Self-consciousness : Beyond the looking-glass and what dogs found there.  
675 *Ethology Ecology & Evolution*, *28*(2), 232-240.

676 Chang, L., Fang, Q., Zhang, S., Poo, M., & Gong, N. (s. d.). Mirror-Induced Self-Directed Behaviors in  
677 Rhesus Monkeys after Visual-Somatosensory Training. *Current Biology*, *0*(0).  
678 <https://doi.org/10.1016/j.cub.2014.11.016>

679 Chang, L., Zhang, S., Poo, M., & Gong, N. (2017). Spontaneous expression of mirror self-recognition in  
680 monkeys after learning precise visual-proprioceptive association for mirror images.  
681 *Proceedings of the National Academy of Sciences*, *114*(12), 3258-3263.

682 Charpentier, M. J. E., Harté, M., Poirotte, C., Bellefon, J. M. de, Laubi, B., Kappeler, P. M., & Renoult,  
683 J. P. (2020). Same father, same face : Deep learning reveals selection for signaling kinship in a  
684 wild primate. *Science Advances*, *6*(22), eaba3274. <https://doi.org/10.1126/sciadv.aba3274>

685 Cheng, Y., Chen, C., Lin, C.-P., Chou, K.-H., & Decety, J. (2010). Love hurts : An fMRI study.  
686 *NeuroImage*, *51*(2), 923-929. <https://doi.org/10.1016/j.neuroimage.2010.02.047>

687 Chouinard, E. F. (2021). Humanimal Model of Animal Mediation Practice (Zootherapy). Or putting our  
688 footsteps in their paw prints to open up new possibilities. *Sociographe*, *14*(4), 87-118.

689 Claidière, N., Gullstrand, J., Latouche, A., & Fagot, J. (2017). Using Automated Learning Devices for  
690 Monkeys (ALDM) to study social networks. *Behavior Research Methods*, *49*(1), 24-34.  
691 <https://doi.org/10.3758/s13428-015-0686-9>

692 Claidière, N., Smith, K., Kirby, S., & Fagot, J. (2014). Cultural evolution of systematically structured  
693 behaviour in a non-human primate. *Proceedings of the Royal Society B: Biological Sciences*,  
694 *281*(1797), 20141541. <https://doi.org/10.1098/rspb.2014.1541>

695 Coe, J., & Hoy, J. (2020). Choice, control and computers : Empowering wildlife in human care.  
696 *Multimodal Technologies and Interaction*, *4*(4), 92.

697 Costello, M., Beard, K. H., Corlett, R. T., Cumming, G. S., Devictor, V., Loyola, R., Maas, B., Miller-  
698 Rushing, A. J., Pakeman, R., & Primack, R. B. (2016). *Field work ethics in biological research*.

699 Crawford, L. E., Knouse, L. E., Kent, M., Vavra, D., Harding, O., LeServe, D., Fox, N., Hu, X., Li, P., Glory,  
700 C., & Lambert, K. G. (2020). Enriched environment exposure accelerates rodent driving skills.  
701 *Behavioural Brain Research*, *378*, 112309. <https://doi.org/10.1016/j.bbr.2019.112309>

702 Croney, C. C., & Boysen, S. T. (2021). Acquisition of a Joystick-Operated Video Task by Pigs (*Sus*  
703 *scrofa*). *Frontiers in Psychology*, *12*. <https://doi.org/10.3389/fpsyg.2021.631755>

704 Czap, N. V., Czap, H. J., Lynne, G. D., & Burbach, M. E. (2015). Walk in my shoes : Nudging for  
705 empathy conservation. *Ecological Economics*, 118, 147-158.  
706 <https://doi.org/10.1016/j.ecolecon.2015.07.010>

707 D'Agostino, J., Pasetta, C., & Reichard, U. (2017). *Preliminary results of a vocal self-recognition test in*  
708 *northern white-cheeked gibbons (Nomascus leucogenys)*. 162, 157-157.

709 Daly Bezerra de Melo, G. (2012). Nature and culture intertwined or redefined? On the challenges of  
710 cultural primatology and sociocultural anthropology. *Revue de Primatologie*, 4, Article 4.  
711 <https://doi.org/10.4000/primatologie.1020>

712 Daly, G. B. de M. (2018). *Drawing and blurring boundaries between species : An etho-ethnography of*  
713 *human-chimpanzee social relations at the Primate research institute of Kyoto university*  
714 [Phdthesis, Université Paris sciences et lettres]. <https://tel.archives-ouvertes.fr/tel-02171263>

715 David, G., William, P., Véronique, G., Thierry, B., & Yvon Le, M. (2012). Robots in Ecology : Welcome  
716 to the machine. *Open Journal of Ecology*, 2012. <https://doi.org/10.4236/oje.2012.22006>

717 De la Fuente, M. F., Sueur, C., Garber, P. A., Bicca-Marques, J. C., Souto, A., & Schiel, N. (2022).  
718 Foraging networks and social tolerance in a cooperatively breeding primate (*Callithrix*  
719 *jacchus*). *Journal of Animal Ecology*, 91(1), 138-153.

720 De Waal, F. (2006). „Morally Evolved.“. *Primates and philosophers: How morality evolved*, 1-80.

721 De Waal, F. (2016). *Are we smart enough to know how smart animals are?* WW Norton & Company.

722 De Waal, F. B. (2012). The antiquity of empathy. *Science*, 336(6083), 874-876.

723 Delotterie, D. F., Mathis, C., Cassel, J.-C., Rosenbrock, H., Dorner-Ciossek, C., & Marti, A. (2015).  
724 Touchscreen tasks in mice to demonstrate differences between hippocampal and striatal  
725 functions. *Neurobiology of Learning and Memory*, 120, 16-27.  
726 <https://doi.org/10.1016/j.nlm.2015.02.007>

727 Derrida, J. (2008). *The animal that therefore I am*. Fordham Univ Press.

728 Dorigo, M., & Gambardella, L. M. (1997a). Ant colony system : A cooperative learning approach to  
729 the traveling salesman problem. *IEEE Transactions on Evolutionary Computation*, 1(1), 53-66.  
730 <https://doi.org/10.1109/4235.585892>

731 Dorigo, M., & Gambardella, L. M. (1997b). Ant colonies for the travelling salesman problem.  
732 *Biosystems*, 43(2), 73-81. [https://doi.org/10.1016/S0303-2647\(97\)01708-5](https://doi.org/10.1016/S0303-2647(97)01708-5)

733 D'Souza, J. F., Price, N. S. C., & Hagan, M. A. (2021). Marmosets : A promising model for probing the  
734 neural mechanisms underlying complex visual networks such as the frontal–parietal network.  
735 *Brain Structure and Function*, 226(9), 3007-3022. [https://doi.org/10.1007/s00429-021-](https://doi.org/10.1007/s00429-021-02367-9)  
736 [02367-9](https://doi.org/10.1007/s00429-021-02367-9)

737 Duboscq, J., Romano, V., MacIntosh, A., & Sueur, C. (2016). Social Information Transmission in  
738 Animals : Lessons from Studies of Diffusion. *Frontiers in Psychology*, 7.

739 Dussutour, A., & Wystrach, A. (2022). *L'Odyssée des fourmis* (Grasset).  
740 <https://www.grasset.fr/livres/lodysee-des-fourmis-9782246817192>

741 Eberle, U. (2021). Nudging nature. *New Scientist*, 250(3340), 42-45. [https://doi.org/10.1016/S0262-](https://doi.org/10.1016/S0262-4079(21)01109-X)  
742 [4079\(21\)01109-X](https://doi.org/10.1016/S0262-4079(21)01109-X)

743 Eisenberger, N. I., Lieberman, M. D., & Williams, K. D. (2003). Does Rejection Hurt? An fMRI Study of  
744 Social Exclusion. *Science*, 302(5643), 290-292. <https://doi.org/10.1126/science.1089134>

745 Evans, J. C., Liechti, J. I., Boatman, B., & König, B. (2020). A natural catastrophic turnover event :  
746 Individual sociality matters despite community resilience in wild house mice. *Proceedings of*  
747 *the Royal Society B: Biological Sciences*, 287(1926), 20192880.  
748 <https://doi.org/10.1098/rspb.2019.2880>

749 Fehlmann, G., & King, A. J. (2016). Bio-logging. *Current Biology*, 26(18), R830-R831.

750 Fenton, A. (2014). Can a chimp say “no”? : Reenvisioning chimpanzee dissent in harmful research.  
751 *Cambridge Quarterly of Healthcare Ethics*, 23(2), 130-139.

752 Ferreira, A. C., Silva, L. R., Renna, F., Brandl, H. B., Renoult, J. P., Farine, D. R., Covas, R., & Doutrelant,  
753 C. (2020). Deep learning-based methods for individual recognition in small birds. *Methods in*  
754 *Ecology and Evolution*, 11(9), 1072-1085. <https://doi.org/10.1111/2041-210X.13436>

755 Ferrucci, L., Nougaret, S., & Genovesio, A. (2019). Macaque monkeys learn by observation in the  
756 ghost display condition in the object-in-place task with differential reward to the observer.  
757 *Scientific Reports*, 9(1), 401. <https://doi.org/10.1038/s41598-018-36803-4>

758 Fitzpatrick, S. (2020). Chimpanzee normativity : Evidence and objections. *Biology & Philosophy*, 35(4),  
759 45. <https://doi.org/10.1007/s10539-020-09763-1>

760 Frank, E. T., Schmitt, T., Hovestadt, T., Mitesser, O., Stiegler, J., & Linsenmair, K. E. (2017). Saving the  
761 injured : Rescue behavior in the termite-hunting ant *Megaponera analis*. *Science Advances*,  
762 3(4), e1602187.

763 Franks, B., Webb, C., Gagliano, M., & Smuts, B. (2020). Conventional science will not do justice to  
764 nonhuman interests : A fresh approach is required. *Animal Sentience*, 4(27), 17.

765 Furnham, A., & Heyes, C. (1993). Psychology students' beliefs about animals and animal  
766 experimentation. *Personality and Individual Differences*, 15(1), 1-10.  
767 [https://doi.org/10.1016/0191-8869\(93\)90036-3](https://doi.org/10.1016/0191-8869(93)90036-3)

768 Galichanin, K., Wang, J., Löfgren, S., & Söderberg, P. (2011). A new universal rat restrainer for  
769 ophthalmic research. *Acta Ophthalmologica*, 89(1), e67-e71. [https://doi.org/10.1111/j.1755-](https://doi.org/10.1111/j.1755-3768.2010.01874.x)  
770 [3768.2010.01874.x](https://doi.org/10.1111/j.1755-3768.2010.01874.x)

771 Gallup Jr, G. G., Anderson, J. R., & Shillito, D. J. (2002). The mirror test. *The cognitive animal:*  
772 *Empirical and theoretical perspectives on animal cognition*, 325-333.

773 Gao, J., Su, Y., Tomonaga, M., & Matsuzawa, T. (2018). Learning the rules of the rock–paper–scissors  
774 game : Chimpanzees versus children. *Primates*, 59(1), 7-17. [https://doi.org/10.1007/s10329-](https://doi.org/10.1007/s10329-017-0620-0)  
775 [017-0620-0](https://doi.org/10.1007/s10329-017-0620-0)

776 Gergely, G., & Jacob, P. (2012). Reasoning about instrumental and communicative agency in human  
777 infancy. *Advances in child development and behavior*, 43, 59-94.

778 Gillespie, K. A. (2019). For a politicized multispecies ethnography. *Politics and Animals*, 5, 17-32.

779 Glickman, S. E., & Sroges, R. W. (1966). Curiosity in zoo animals. *Behaviour*, 26(1-2), 151-187.

780 Good, T. L., Sterzinger, N., & Lavigne, A. (2018). Expectation effects : Pygmalion and the initial 20  
781 years of research. *Educational Research and Evaluation*, 24(3-5), 99-123.  
782 <https://doi.org/10.1080/13803611.2018.1548817>

783 Graham, M. L., Rieke, E. F., Mutch, L. A., Zolondek, E. K., Faig, A. W., DuFour, T. A., Munson, J. W.,  
784 Kittredge, J. A., & Schuurman, H.-J. (2012). Successful implementation of cooperative  
785 handling eliminates the need for restraint in a complex non-human primate disease model.  
786 *Journal of Medical Primatology*, 41(2), 89-106. [https://doi.org/10.1111/j.1600-](https://doi.org/10.1111/j.1600-0684.2011.00525.x)  
787 [0684.2011.00525.x](https://doi.org/10.1111/j.1600-0684.2011.00525.x)

788 Grampp, M., Sueur, C., van de Waal, E., & Botting, J. (2019). Social attention biases in juvenile wild  
789 vervet monkeys : Implications for socialisation and social learning processes. *Primates*, 60(3),  
790 261-275.

791 Grandin, T. (1987). Animal Handling. *Veterinary Clinics of North America: Food Animal Practice*, 3(2),  
792 323-338. [https://doi.org/10.1016/S0749-0720\(15\)31155-5](https://doi.org/10.1016/S0749-0720(15)31155-5)

793 Grandin, T. (1989). Behavioral Principles of Livestock Handling. *The Professional Animal Scientist*,  
794 5(2), 1-11. [https://doi.org/10.15232/S1080-7446\(15\)32304-4](https://doi.org/10.15232/S1080-7446(15)32304-4)

795 Haraway, D. J. (1989). *Primate visions : Gender, race, and nature in the world of modern science*.  
796 Psychology Press.

797 He, L.-W., Zeng, L., Tian, N., Li, Y., He, T., Tan, D.-M., Zhang, Q., & Tan, Y. (2020). Optimization of food  
798 deprivation and sucrose preference test in SD rat model undergoing chronic unpredictable  
799 mild stress. *Animal Models and Experimental Medicine*, 3(1), 69-78.  
800 <https://doi.org/10.1002/ame2.12107>

801 Hodgetts, T., & Lorimer, J. (2020). Animals' mobilities. *Progress in Human Geography*, 44(1), 4-26.  
802 <https://doi.org/10.1177/0309132518817829>

803 Hoffman, J. M., Creevy, K. E., Franks, A., O'Neill, D. G., & Promislow, D. E. L. (2018). The companion  
804 dog as a model for human aging and mortality. *Aging Cell*, 17(3), e12737.  
805 <https://doi.org/10.1111/ace1.12737>

806 Honda, Y., Nakamura, S., Ogawa, K., Yoshino, R., Tobler, P. N., Nishimura, Y., & Tsutsui, K.-I. (2021).  
807 Changes in beta and high-gamma power in resting-state electrocorticogram induced by  
808 repetitive transcranial magnetic stimulation of primary motor cortex in unanesthetized  
809 macaque monkeys. *Neuroscience Research*, 171, 41-48.  
810 <https://doi.org/10.1016/j.neures.2021.02.002>

811 Hopper, L. M., Gulli, R. A., Howard, L. H., Kano, F., Krupenye, C., Ryan, A. M., & Paukner, A. (2021).  
812 The application of noninvasive, restraint-free eye-tracking methods for use with nonhuman  
813 primates. *Behavior Research Methods*, 53(3), 1003-1030. [https://doi.org/10.3758/s13428-](https://doi.org/10.3758/s13428-020-01465-6)  
814 [020-01465-6](https://doi.org/10.3758/s13428-020-01465-6)

815 Horschler, D. J., MacLean, E. L., & Santos, L. R. (2020). Advancing Gaze-Based Research on Primate  
816 Theory of Mind. *Trends in Cognitive Sciences*, 24(10), 778-779.  
817 <https://doi.org/10.1016/j.tics.2020.07.008>

818 Huebner, F., Fichtel, C., & Kappeler, P. M. (2018). Linking cognition with fitness in a wild primate :  
819 Fitness correlates of problem-solving performance and spatial learning ability. *Philosophical*  
820 *Transactions of the Royal Society B: Biological Sciences*, 373(1756), 20170295.  
821 <https://doi.org/10.1098/rstb.2017.0295>

822 Huskisson, S. M., Doelling, C. R., Ross, S. R., & Hopper, L. M. (2021). Assessing the potential impact of  
823 zoo visitors on the welfare and cognitive performance of Japanese macaques. *Applied Animal*  
824 *Behaviour Science*, 243, 105453. <https://doi.org/10.1016/j.applanim.2021.105453>

825 Huttunen, A. W., Adams, G. K., & Platt, M. L. (2017). Can self-awareness be taught ? Monkeys pass  
826 the mirror test—Again. *Proceedings of the National Academy of Sciences*, 114(13),  
827 3281-3283.



828 Inoue, S., & Matsuzawa, T. (2007). Working memory of numerals in chimpanzees. *Current Biology*,  
829 17(23), R1004-R1005. <https://doi.org/10.1016/j.cub.2007.10.027>

830 Jacob, G., Katti, H., Cherian, T., Das, J., Zhivago, K., & Arun, S. (2021). A naturalistic environment to  
831 study visual cognition in unrestrained monkeys. *eLife*, 10, e63816.  
832 <https://doi.org/10.7554/eLife.63816>

833 Jacobson, S. L., Kwiatt, A. C., Ross, S. R., & Cronin, K. A. (2019). The effects of cognitive testing on the  
834 welfare of zoo-housed Japanese macaques (*Macaca fuscata*). *Applied Animal Behaviour*  
835 *Science*, 212, 90-97. <https://doi.org/10.1016/j.applanim.2018.12.014>

836 Janson, C., & Byrne, R. (2007). What wild primates know about resources : Opening up the black box.  
837 *Animal Cognition*, 10(3), 357-367. <https://doi.org/10.1007/s10071-007-0080-9>

838 Jensen, K., Call, J., & Tomasello, M. (2007). Chimpanzees are vengeful but not spiteful. *Proceedings of*  
839 *the National Academy of Sciences*, 104(32), 13046-13050.

840 Jordan, E. J., Völter, C. J., & Seed, A. M. (2022). Do capuchin monkeys (*Sapajus apella*) use exploration  
841 to form intuitions about physical properties? *Cognitive Neuropsychology*, 1-13.

842 Kaminski, J., Call, J., & Tomasello, M. (2008). Chimpanzees know what others know, but not what  
843 they believe. *Cognition*, 109(2), 224-234.

844 Kaneko, T., & Tomonaga, M. (2011). The perception of self-agency in chimpanzees (*Pan troglodytes*).  
845 *Proceedings of the Royal Society B: Biological Sciences*, 278(1725), 3694-3702.  
846 <https://doi.org/10.1098/rspb.2011.0611>

847 Kano, F., & Tomonaga, M. (2009). How chimpanzees look at pictures : A comparative eye-tracking  
848 study. *Proceedings of the Royal Society B: Biological Sciences*, 276(1664), 1949-1955.  
849 <https://doi.org/10.1098/rspb.2008.1811>

850 Kerth, G., Perony, N., & Schweitzer, F. (2011). Bats are able to maintain long-term social relationships  
851 despite the high fission–fusion dynamics of their groups. *Proceedings of the Royal Society B:*  
852 *Biological Sciences*, 278(1719), 2761-2767. <https://doi.org/10.1098/rspb.2010.2718>

853 King, A. J., & Sueur, C. (2011). Where Next? Group Coordination and Collective Decision Making by  
854 Primates. *International Journal of Primatology*, 32(6), 1245-1267.  
855 <https://doi.org/10.1007/s10764-011-9526-7>

856 King, B. J. (2021). *Animals' Best Friends : Putting Compassion to Work for Animals in Captivity and in*  
857 *the Wild*. University of Chicago Press.  
858 <https://press.uchicago.edu/ucp/books/book/chicago/A/bo33375440.html>

859 Kirksey, S. E., & Helmreich, S. (2010). The Emergence of Multispecies Ethnography. *Cultural*  
860 *Anthropology*, 25(4), 545-576. <https://doi.org/10.1111/j.1548-1360.2010.01069.x>

861 Kohda, M., Hotta, T., Takeyama, T., Awata, S., Tanaka, H., Asai, J., & Jordan, A. L. (2019). If a fish can  
862 pass the mark test, what are the implications for consciousness and self-awareness testing in  
863 animals? *PLoS biology*, 17(2), e3000021.

864 Krasheninnikova, A., Berardi, R., Lind, M.-A., O'Neill, L., & von Bayern, A. M. (2019). Primate cognition  
865 test battery in parrots. *Behaviour*, 156(5-8), 721-761.

866 Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford University Press.

867 Krause, S. R. (2013). Beyond non-domination : Agency, inequality and the meaning of freedom.  
868 *Philosophy & social criticism*, 39(2), 187-208.

869 Krupenye, C., Kano, F., Hirata, S., Call, J., & Tomasello, M. (2016). Great apes anticipate that other  
870 individuals will act according to false beliefs. *Science*, 354(6308), 110-114.

871 Kumpan, L. T., Smeltzer, E. A., & Teichroeb, J. A. (2020). Animal cognition in the field : Performance of  
872 wild vervet monkeys (*Chlorocebus pygerythrus*) on a reversal learning task. *Animal Cognition*,  
873 23(3), 523-534. <https://doi.org/10.1007/s10071-020-01356-5>

874 Lacreuse, A., Raz, N., Schmidtke, D., Hopkins, W. D., & Herndon, J. G. (2020). Age-related decline in  
875 executive function as a hallmark of cognitive ageing in primates : An overview of cognitive  
876 and neurobiological studies. *Philosophical Transactions of the Royal Society B: Biological*  
877 *Sciences*, 375(1811), 20190618. <https://doi.org/10.1098/rstb.2019.0618>

878 Langlitz, N. (2020). Chimpanzee Culture Wars : Rethinking Human Nature alongside Japanese,  
879 European, and American Cultural Primatologists. In *Chimpanzee Culture Wars*. Princeton  
880 University Press. <https://doi.org/10.1515/9780691204260>

881 Laule, G. E., Bloomsmith, M. A., & Schapiro, S. J. (2003). The Use of Positive Reinforcement Training  
882 Techniques to Enhance the Care, Management, and Welfare of Primates in the Laboratory.  
883 *Journal of Applied Animal Welfare Science*, 6(3), 163.  
884 [https://doi.org/10.1207/S15327604JAWS0603\\_02](https://doi.org/10.1207/S15327604JAWS0603_02)

885 Le Maho, Y., Whittington, J. D., Hanuise, N., Pereira, L., Boureau, M., Brucker, M., Chatelain, N.,  
886 Courtecuisse, J., Crenner, F., Friess, B., Grosbellet, E., Kernaléguen, L., Olivier, F., Saraux, C.,  
887 Vetter, N., Viblanc, V. A., Thierry, B., Tremblay, P., Groscolas, R., & Le Bohec, C. (2014).  
888 Rovers minimize human disturbance in research on wild animals. *Nature Methods*, 11(12),  
889 1242-1244. <https://doi.org/10.1038/nmeth.3173>

890 Le Neindre, P., Bernard, E., Boissy, A., Boivin, X., Calandreau, L., Delon, N., Deputte, B., Desmoulin-  
891 canselier, S., Dunier, M., & Faivre, N. (2017). *Animal consciousness. Summary of the*  
892 *multidisciplinary assesment*.

893 Le Neindre, P., Dunier, M., Larrère, R., & Prunet, P. (2018). *La conscience des animaux* (Éditions  
894 Quæ). Quæ. [https://www.quae.com/produit/1520/9782759228713/la-conscience-des-](https://www.quae.com/produit/1520/9782759228713/la-conscience-des-animaux)  
895 [animaux](https://www.quae.com/produit/1520/9782759228713/la-conscience-des-animaux)

896 Leca, J.-B., Gunst, N., & Huffman, M. A. (2007). Japanese macaque cultures : Inter-and intra-troop  
897 behavioural variability of stone handling patterns across 10 troops. *Behaviour*, 144(3),  
898 251-281.

899 Lecorps, B., Weary, D. M., & von Keyserlingk, M. A. G. (2021). Captivity-Induced Depression in  
900 Animals. *Trends in Cognitive Sciences*. <https://doi.org/10.1016/j.tics.2021.03.010>

901 Levé, M., Sueur, C., Petit, O., Matsuzawa, T., & Hirata, S. (2016). Social grooming network in captive  
902 chimpanzees : Does the wild or captive origin of group members affect sociality? *Primates;*  
903 *Journal of Primatology*, 57(1), 73-82. <https://doi.org/10.1007/s10329-015-0494-y>

904 Liu, X., Liu, T., & Huang, X. (2017). Commentary : Spontaneous expression of mirror self-recognition  
905 in monkeys after learning precise visual-proprioceptive association for mirror images.  
906 *Frontiers in psychology, 8*, 1151.

907 Lopes, P. C., & König, B. (2020). Wild mice with different social network sizes vary in brain gene  
908 expression. *BMC Genomics, 21*(1), 506. <https://doi.org/10.1186/s12864-020-06911-5>

909 Low, P., Panksepp, J., Reiss, D., Edelman, D., Van Swinderen, B., & Koch, C. (2012). *The Cambridge*  
910 *declaration on consciousness*. 1-2.

911 Machado, C. J., & Nelson, E. E. (2011). Eye-tracking with nonhuman primates is now more accessible  
912 than ever before. *American Journal of Primatology, 73*(6), 562-569.  
913 <https://doi.org/10.1002/ajp.20928>

914 MacKinnon, K. C., & Riley, E. P. (2010). *Field primatology of today : Current ethical issues*.

915 Maeda, T., Ochi, S., Ringhofer, M., Sosa, S., Sueur, C., Hirata, S., & Yamamoto, S. (2021). Aerial drone  
916 observations identified a multilevel society in feral horses. *Scientific Reports, 11*(1), 71.  
917 <https://doi.org/10.1038/s41598-020-79790-1>

918 Maeda, T., Sueur, C., Hirata, S., & Yamamoto, S. (2021). Behavioural synchronization in a multilevel  
919 society of feral horses. *PLOS ONE, 16*(10), e0258944.  
920 <https://doi.org/10.1371/journal.pone.0258944>

921 Martinet, L., Sueur, C., Hirata, S., Hosselet, J., Matsuzawa, T., & Pelé, M. (2021). New indices to  
922 characterize drawing behavior in humans ( Homo sapiens ) and chimpanzees ( Pan  
923 troglodytes ). *Scientific Reports, 11*(1), 3860. <https://doi.org/10.1038/s41598-021-83043-0>

924 Mason, S., Premereur, E., Pelekanos, V., Emberton, A., Honess, P., & Mitchell, A. S. (2019). Effective  
925 chair training methods for neuroscience research involving rhesus macaques (Macaca  
926 mulatta). *Journal of Neuroscience Methods, 317*, 82-93.  
927 <https://doi.org/10.1016/j.jneumeth.2019.02.001>

928 Massen, J. J., & Koski, S. E. (2014). Chimps of a feather sit together : Chimpanzee friendships are  
929 based on homophily in personality. *Evolution and Human Behavior, 35*(1), 1-8.

930 Matsuzawa, T. (2013). Evolution of the brain and social behavior in chimpanzees. *Current opinion in*  
931 *neurobiology*, 23(3), 443-449.

932 Matsuzawa, T. (2016a). *Euthanasia is not an option : 10 years' care of a chimpanzee with acute*  
933 *tetraparesis*.

934 Matsuzawa, T. (2016b). *SAGA and GAIN for great apes*.

935 Matsuzawa, T. (2017). Horse cognition and behavior from the perspective of primatology. *Primates*,  
936 58(4), 473-477. <https://doi.org/10.1007/s10329-017-0632-9>

937 Matsuzawa, T. (2020). WISH cages : Constructing multiple habitats for captive chimpanzees.  
938 *Primates*, 61(2), 139-148. <https://doi.org/10.1007/s10329-020-00806-5>

939 McEwen, E. S., Warren, E., Tenpas, S., Jones, B., Durdevic, K., Rapport Munro, E., & Call, J. (2022).  
940 Primate cognition in zoos : Reviewing the impact of zoo-based research over 15 years.  
941 *American Journal of Primatology*, n/a(n/a), e23369. <https://doi.org/10.1002/ajp.23369>

942 McFarland, S. E., & Hediger, R. (2009). *Animals and agency : An interdisciplinary exploration* (Vol. 8).  
943 Brill.

944 McMillan, J. L., Bloomsmith, M. A., & Prescott, M. J. (2017). An International Survey of Approaches to  
945 Chair Restraint of Nonhuman Primates. *Comparative medicine*, 67(5), 442-451.

946 McMillan, J. L., Perlman, J. E., Galvan, A., Wichmann, T., & Bloomsmith, M. A. (2014). Refining the  
947 pole-and-collar method of restraint : Emphasizing the use of positive training techniques with  
948 rhesus macaques (*Macaca mulatta*). *Journal of the American Association for Laboratory*  
949 *Animal Science*, 53(1), 61-68.

950 Meguerditchian, A., Marie, D., Margiotoudi, K., Roth, M., Nazarian, B., Anton, J.-L., & Claidière, N.  
951 (2021). Baboons (*Papio anubis*) living in larger social groups have bigger brains. *Evolution and*  
952 *Human Behavior*, 42(1), 30-34. <https://doi.org/10.1016/j.evolhumbehav.2020.06.010>

953 Meijer, E. (2019). *When Animals Speak : Toward an Interspecies Democracy*. NYU Press.

954 Merleau-Ponty, M. (2017). *Causeries 1948*. Média Diffusion.

955 Miele, J., Tingley, L., Kimball, R., & Broida, J. (1993). Personality Differences between Pro- and  
956 Antivivisectionists. *Society & Animals*, 1(2), 129-144.  
957 <https://doi.org/10.1163/156853093X00037>

958 Murphy, H. W., Danforth, M. D., & Clyde, V. L. (2018). The Great Ape Heart Project. *International Zoo*  
959 *Yearbook*, 52(1), 103-112. <https://doi.org/10.1111/izy.12180>

960 Muschel, I. J. (1984). Pet Therapy with Terminal Cancer Patients. *Social Casework*, 65(8), 451-458.  
961 <https://doi.org/10.1177/104438948406500801>

962 Muth, F., Cooper, T. R., Bonilla, R. F., & Leonard, A. S. (2018). A novel protocol for studying bee  
963 cognition in the wild. *Methods in Ecology and Evolution*, 9(1), 78-87.  
964 <https://doi.org/10.1111/2041-210X.12852>

965 Newport, C., Wallis, G., Reshitnyk, Y., & Siebeck, U. E. (2016). Discrimination of human faces by  
966 archerfish (*Toxotes chatareus*). *Scientific reports*, 6(1), 1-7.

967 Nielsen, B. (2020). *Asking Animals : An Introduction to Animal Behaviour Testing*. CABI.

968 Nielsen, B. L. (2018). Making sense of it all : The importance of taking into account the sensory  
969 abilities of animals in their housing and management. *Applied Animal Behaviour Science*, 205,  
970 175-180. <https://doi.org/10.1016/j.applanim.2018.04.013>

971 Ogden, L. A., Hall, B., & Tanita, K. (2013). Animals, Plants, People, and Things : A Review of  
972 Multispecies Ethnography. *Environment and Society*, 4(1), 5-24.  
973 <https://doi.org/10.3167/ares.2013.040102>

974 O'Hara, M., Mioduszewska, B., Mundry, R., Yohanna, Haryoko, T., Rachmatika, R., Prawiradilaga, D.  
975 M., Huber, L., & Auersperg, A. M. I. (2021). Wild Goffin's cockatoos flexibly manufacture and  
976 use tool sets. *Current Biology*, 31(20), 4512-4520.e6.  
977 <https://doi.org/10.1016/j.cub.2021.08.009>

978 Park, G., & Evans, G. W. (2016). Environmental stressors, urban design and planning : Implications for  
979 human behaviour and health. *Journal of Urban Design*, 21(4), 453-470.  
980 <https://doi.org/10.1080/13574809.2016.1194189>

981 Pasquaretta, C., Battesti, M., Klenschi, E., Bousquet, C. A. H., Sueur, C., & Mery, F. (2016). How social  
982 network structure affects decision-making in *Drosophila melanogaster*. *Proc. R. Soc. B*,  
983 283(1826), 20152954. <https://doi.org/10.1098/rspb.2015.2954>

984 Pasquaretta, C., Jeanson, R., Andalo, C., Chittka, L., & Lihoreau, M. (2017). Analysing plant–pollinator  
985 interactions with spatial movement networks. *Ecological Entomology*, 42, 4-17.  
986 <https://doi.org/10.1111/een.12446>

987 Patter, L. E. V., & Blattner, C. (2020). Advancing Ethical Principles for Non-Invasive, Respectful  
988 Research with Nonhuman Animal Participants. *Society & Animals*, 28(2), 171-190.  
989 <https://doi.org/10.1163/15685306-00001810>

990 Patterson, F. G. P., & Cohn, R. H. (1990). Language acquisition by a lowland gorilla : Koko’s first ten  
991 years of vocabulary development. *WORD*, 41(2), 97-143.  
992 <https://doi.org/10.1080/00437956.1990.11435816>

993 Pedersen, J. (2020). Nonhuman Primates and Language : Primates Raised by Humans. In *The*  
994 *International Encyclopedia of Linguistic Anthropology* (p. 1-9). John Wiley & Sons, Ltd.  
995 <https://doi.org/10.1002/9781118786093.iela0289>

996 Pennisi, A., & Giallongo, L. (2018). Animal Biopolitics : How Animals Vote. *International Journal for*  
997 *the Semiotics of Law-Revue internationale de Sémiotique juridique*, 31(3), 491-499.

998 Pepperberg, I. M. (2006). *Intelligence and rationality in parrots*.

999 Pereira, M., Nogueira, H., & Padez, C. (2019). The role of urban design in childhood obesity : A case  
1000 study in Lisbon, Portugal. *American Journal of Human Biology*, 31(3), e23220.  
1001 <https://doi.org/10.1002/ajhb.23220>

1002 Péron, F. (2012). Language-trained animals : A window to the « black box ». *International Journal of*  
1003 *Intelligence Science*, 2(4A), 149-159. <https://doi.org/10.4236/ijis.2012.224020>

1004 Pomerantz, O., Baker, K. C., Bellanca, R. U., Bloomsmith, M. A., Coleman, K., Hutchinson, E. K., Pierre,  
1005 P. J., Weed, J. L., & Consortium, N. P. R. C. B. M. (2022). Improving transparency—A call to  
1006 include social housing information in biomedical research articles involving nonhuman

1007 primates. *American Journal of Primatology*, n/a(n/a), e23378.

1008 <https://doi.org/10.1002/ajp.23378>

1009 Prescott, M., & Buchanan-Smith, H. (2007). Training laboratory-housed non-human primates, part I: a  
1010 UK survey. *ANIMAL WELFARE-POTTERS BAR THEN WHEATHAMPSTEAD-*, 16(1), 21.

1011 Prescott, M. J. (2016). Online resources for improving the care and use of non-human primates in  
1012 research. *Primate Biology*, 3(2), 33.

1013 Prescott, M. J., Brown, V. J., Flecknell, P. A., Gaffan, D., Garrod, K., Lemon, R. N., Parker, A. J., Ryder,  
1014 K., Schultz, W., & Scott, L. (2010). Refinement of the use of food and fluid control as  
1015 motivational tools for macaques used in behavioural neuroscience research : Report of a  
1016 Working Group of the NC3Rs. *Journal of neuroscience methods*, 193(2), 167-188.

1017 Prescott, M. J., & Buchanan-Smith, H. M. (2003). Training nonhuman primates using positive  
1018 reinforcement techniques. *Journal of Applied Animal Welfare Science*, 6(3), 157-161.

1019 Pritchard, D. J., Hurly, T. A., Tello-Ramos, M. C., & Healy, S. D. (2016). Why study cognition in the wild  
1020 (and how to test it)? *Journal of the Experimental Analysis of Behavior*, 105(1), 41-55.

1021 <https://doi.org/10.1002/jeab.195>

1022 Ramos, A., Bousquet, C. A. H., & Sueur, C. (2021). How leadership could be used to manage domestic  
1023 and wild ungulate herds. *Applied Animal Behaviour Science*, 239, 105326.

1024 <https://doi.org/10.1016/j.applanim.2021.105326>

1025 Ramos, A., Manizan, L., Rodriguez, E., Kemp, Y. J. M., & Sueur, C. (2018). How can leadership  
1026 processes in European bison be used to improve the management of free-roaming herds.  
1027 *European Journal of Wildlife Research*, 64(2). <https://doi.org/10.1007/s10344-018-1175-0>

1028 Raulo, A., Allen, B. E., Troitsky, T., Husby, A., Firth, J. A., Coulson, T., & Knowles, S. C. L. (2021). Social  
1029 networks strongly predict the gut microbiota of wild mice. *The ISME Journal*, 15(9),  
1030 2601-2613. <https://doi.org/10.1038/s41396-021-00949-3>

1031 Rault, J.-L. (2012). Friends with benefits : Social support and its relevance for farm animal welfare.  
1032 *Applied Animal Behaviour Science*, 136(1), 1-14.



1033 Reddy, S. M. W., Montambault, J., Masuda, Y. J., Keenan, E., Butler, W., Fisher, J. R. B., Asah, S. T., &  
1034 Gneezy, A. (2017). Advancing Conservation by Understanding and Influencing Human  
1035 Behavior. *Conservation Letters*, *10*(2), 248-256. <https://doi.org/10.1111/conl.12252>

1036 Richardson, T. O., Kay, T., Braunschweig, R., Journeau, O., Ruegg, M., McGregor, S., De Los Rios, P., &  
1037 Keller, L. (2020). Ant Behavioral Maturation Is Mediated by a Stochastic Transition between  
1038 Two Fundamental States. *Current Biology*, *30*, 1-8.  
1039 <https://doi.org/10.1016/j.cub.2020.05.038>

1040 Rosati, A. G., Hagberg, L., Enigk, D. K., Otali, E., Thompson, M. E., Muller, M. N., Wrangham, R. W., &  
1041 Machanda, Z. P. (2020). Social selectivity in aging wild chimpanzees. *Science*, *370*(6515),  
1042 473-476. <https://doi.org/10.1126/science.aaz9129>

1043 Ryan, A. M., Freeman, S. M., Murai, T., Lau, A. R., Palumbo, M. C., Hogrefe, C. E., Bales, K. L., &  
1044 Bauman, M. D. (2019). Non-invasive Eye Tracking Methods for New World and Old World  
1045 Monkeys. *Frontiers in Behavioral Neuroscience*, *13*.  
1046 <https://doi.org/10.3389/fnbeh.2019.00039>

1047 Sakai, T., Hirata, S., Fuwa, K., Sugama, K., Kusunoki, K., Makishima, H., Eguchi, T., Yamada, S., Ogihara,  
1048 N., & Takeshita, H. (2012). Fetal brain development in chimpanzees versus humans. *Current*  
1049 *Biology*, *22*(18), R791-R792.

1050 Sakai, T., Mikami, A., Tomonaga, M., Matsui, M., Suzuki, J., Hamada, Y., Tanaka, M., Miyabe-  
1051 Nishiwaki, T., Makishima, H., & Nakatsukasa, M. (2011). Differential prefrontal white matter  
1052 development in chimpanzees and humans. *Current Biology*, *21*(16), 1397-1402.

1053 Savage-Rumbaugh, E. S., & Lewin, R. (1994). *Kanzi : The ape at the brink of the human mind*. Wiley.

1054 Savage-Rumbaugh, E. S., Rumbaugh, D. M., & Fields, W. M. (2006). *Language as a window on*  
1055 *rationality*.

1056 Scanes, C. G. (2018). Animal Agriculture : Livestock, Poultry, and Fish Aquaculture. In *Animals and*  
1057 *Human Society* (p. 179). Elsevier Inc. <https://doi.org/10.1016/b978-0-12-805247-1.00007-1>

1058 Schapiro, S. J. (2017). Introduction to the handbook of primate behavioral management. In *Handbook*  
1059 *of primate behavioral management* (p. 3-8). CRC Press.

1060 Schapiro, S. J., Bloomsmith, M. A., & Laule, G. E. (2003). Positive Reinforcement Training As a  
1061 Technique to Alter Nonhuman Primate Behavior : Quantitative Assessments of Effectiveness.  
1062 *Journal of Applied Animal Welfare Science*, 6(3), 175.  
1063 [https://doi.org/10.1207/S15327604JAWS0603\\_03](https://doi.org/10.1207/S15327604JAWS0603_03)

1064 Schmitt, V., Pankau, B., & Fischer, J. (2012). Old World Monkeys Compare to Apes in the Primate  
1065 Cognition Test Battery. *PLOS ONE*, 7(4), e32024.  
1066 <https://doi.org/10.1371/journal.pone.0032024>

1067 Schofield, D., Nagrani, A., Zisserman, A., Hayashi, M., Matsuzawa, T., Biro, D., & Carvalho, S. (2019).  
1068 Chimpanzee face recognition from videos in the wild using deep learning. *Science Advances*,  
1069 5(9), eaaw0736. <https://doi.org/10.1126/sciadv.aaw0736>

1070 Shaw, R. C. (2017). Testing cognition in the wild : Factors affecting performance and individual  
1071 consistency in two measures of avian cognition. *Behavioural Processes*, 134, 31-36.  
1072 <https://doi.org/10.1016/j.beproc.2016.06.004>

1073 Silk, J. B. (2002). Females, food, family, and friendship. *Evolutionary Anthropology: Issues, News, and*  
1074 *Reviews*, 11(3), 85-87. <https://doi.org/10.1002/evan.10011>

1075 Sinha, A. (2005). Not in their genes : Phenotypic flexibility, behavioural traditions and cultural  
1076 evolution in wild bonnet macaques. *Journal of Biosciences*, 30(1), 51-64.  
1077 <https://doi.org/10.1007/BF02705150>

1078 Slater, H., Milne, A. E., Wilson, B., Muers, R. S., Balezeau, F., Hunter, D., Thiele, A., Griffiths, T. D., &  
1079 Petkov, C. I. (2016). Individually customisable non-invasive head immobilisation system for  
1080 non-human primates with an option for voluntary engagement. *Journal of Neuroscience*  
1081 *Methods*, 269, 46-60. <https://doi.org/10.1016/j.jneumeth.2016.05.009>

- 1082 Slutzky, M. W., Jordan, L. R., Bauman, M. J., & Miller, L. E. (2010). A new rodent behavioral paradigm  
1083 for studying forelimb movement. *Journal of Neuroscience Methods*, *192*(2), 228-232.  
1084 <https://doi.org/10.1016/j.jneumeth.2010.07.040>
- 1085 Sober, E. (2009). Parsimony and Models of Animal Minds. In R. W. Lurz (Éd.), *The Philosophy of*  
1086 *Animal Minds* (p. 237). Cambridge University Press.
- 1087 Sosa, S. O., Pelé, M., Debergue, É., Kuntz, C., Keller, B., Robic, F., Siegwalt-Baudin, F., Richer, C.,  
1088 Ramos, A., & Sueur, C. (2019). Impact of Group Management and Transfer on Individual  
1089 Sociality in Highland Cattle (*Bos taurus*). *Frontiers in Veterinary Science*, *6*, 183.  
1090 <https://doi.org/10.3389/fvets.2019.00183>
- 1091 Soulsbury, C. D., Gray, H. E., Smith, L. M., Braithwaite, V., Cotter, S. C., Elwood, R. W., Wilkinson, A., &  
1092 Collins, L. M. (2020). The welfare and ethics of research involving wild animals : A primer.  
1093 *Methods in Ecology and Evolution*, *11*(10), 1164-1181.
- 1094 Sueur, C. (2011). A Non-Lévy Random Walk in Chacma Baboons : What Does It Mean? *PLoS ONE*, *6*(1),  
1095 e16131. <https://doi.org/10.1371/journal.pone.0016131>
- 1096 SUEUR, C. (2015). *Analyse des réseaux sociaux appliquée à l'éthologie et l'écologie*. Editions  
1097 Matériologiques. <https://doi.org/10.13140/RG.2.1.4100.5601>
- 1098 Sueur, C., Bousquet, C., Espinosa, R., & Deneubourg, J.-L. (2021). *Improving human collective*  
1099 *decision-making through animal and artificial intelligence*. [https://hal.archives-](https://hal.archives-ouvertes.fr/hal-03299087)  
1100 [ouvertes.fr/hal-03299087](https://hal.archives-ouvertes.fr/hal-03299087)
- 1101 Sueur, C., Forin-Wiart, M.-A., & Pelé, M. (2020). *Do They Really Try to Save Their Buddy?*  
1102 *Anthropomorphism about Animal Epimeletic Behaviours*.  
1103 <https://doi.org/10.20944/preprints202008.0711.v1>
- 1104 Sueur, C., & Pelé, M. (2017). Editorial : Anthropomorphism, between merits and demerits. *Lettre du*  
1105 *CEERE, Centre Européen d'Enseignement et de Recherche en Ethique*, *107*, 1.
- 1106 Taylor, P. W. (2011). *Respect for nature : A theory of environmental ethics*. Princeton University Press.

1107 Testard, C., Tremblay, S., & Platt, M. (2021). From the field to the lab and back : Neuroethology of  
1108 primate social behavior. *Current Opinion in Neurobiology*, 68, 76-83.  
1109 <https://doi.org/10.1016/j.conb.2021.01.005>

1110 Thaler, R. H. (2008). *Nudge : Improving decisions about health, wealth, and happiness*. Yale University  
1111 Press New Haven & London.

1112 Tokuyama, N., Emikey, B., Bafike, B., Isolumbo, B., Iyokango, B., Mulavwa, M. N., & Furuichi, T.  
1113 (2012). Bonobos apparently search for a lost member injured by a snare. *Primates*, 53(3),  
1114 215-219. <https://doi.org/10.1007/s10329-012-0298-2>

1115 Tomasello, M., & Vaish, A. (2013). Origins of human cooperation and morality. *Annual review of*  
1116 *psychology*, 64, 231-255.

1117 Tomonaga, M., Kumazaki, K., Camus, F., Nicod, S., Pereira, C., & Matsuzawa, T. (2015). A horse's eye  
1118 view : Size and shape discrimination compared with other mammals. *Biology Letters*, 11(11),  
1119 20150701. <https://doi.org/10.1098/rsbl.2015.0701>

1120 Tsuji, Y., Shimoda-Ishiguro, M., Ohnishi, N., & Takatsuki, S. (2007). A friend in need is a friend indeed :  
1121 Feeding association between Japanese macaques and sika deer. *Acta Theriologica*, 52(4),  
1122 427-434.

1123 Ueno, A., Hirata, S., Fuwa, K., Sugama, K., Kusunoki, K., Matsuda, G., Fukushima, H., Hiraki, K.,  
1124 Tomonaga, M., & Hasegawa, T. (2010). Brain activity in an awake chimpanzee in response to  
1125 the sound of her own name. *Biology letters*, 6(3), 311-313.

1126 van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a  
1127 wild primate's foraging decisions. *Science*, 340(6131), 483-485.

1128 Verhaeghen, P., Martin, M., & Sędek, G. (2012). Reconnecting cognition in the lab and cognition in  
1129 real life : The role of compensatory social and motivational factors in explaining how  
1130 cognition ages in the wild. *Aging, Neuropsychology, and Cognition*, 19(1-2), 1-12.  
1131 <https://doi.org/10.1080/13825585.2011.645009>

- 1132 Visalberghi, E., Addessi, E., Truppa, V., Spagnoletti, N., Ottoni, E., Izar, P., & Frigaszy, D. (2009).  
1133 Selection of effective stone tools by wild bearded capuchin monkeys. *Current Biology*, *19*(3),  
1134 213-217.
- 1135 Voelkl, B., Altman, N. S., Forsman, A., Forstmeier, W., Gurevitch, J., Jaric, I., Karp, N. A., Kas, M. J.,  
1136 Schielzeth, H., Van de Castele, T., & Würbel, H. (2020). Reproducibility of animal research in  
1137 light of biological variation. *Nature Reviews Neuroscience*, *21*(7), 384-393.  
1138 <https://doi.org/10.1038/s41583-020-0313-3>
- 1139 Voelkl, B., Würbel, H., Krzywinski, M., & Altman, N. (2021). The standardization fallacy. *Nature*  
1140 *Methods*, *18*(1), 5-7. <https://doi.org/10.1038/s41592-020-01036-9>
- 1141 Ward, A. J. W., & Webster, M. (2016). *Sociality : The behaviour of group-living animals*. Springer.
- 1142 Washburn, D. A., Rulon, M. J., & Gullledge, J. P. (2004). A new breed of computer users : Rats control  
1143 a cursor via joystick manipulation. *Behavior Research Methods, Instruments, & Computers*,  
1144 *36*(2), 173-179. <https://doi.org/10.3758/BF03195562>
- 1145 Webb, C. E., Woodford, P., & Huchard, E. (2019). Animal ethics and behavioral science : An overdue  
1146 discussion. *BioScience*, *69*(10), 778-788.
- 1147 Wendler, H. (2020). Philosophical Primatology : Reflections on Theses of Anthropological Difference,  
1148 the Logic of Anthropomorphism and Anthropodenial, and the Self-Other Category Mistake  
1149 Within the Scope of Cognitive Primate Research. *Biological Theory*, *15*(2), 61-82.  
1150 <https://doi.org/10.1007/s13752-019-00337-3>
- 1151 Whiten, A. (2011). The scope of culture in chimpanzees, humans and ancestral apes. *Philosophical*  
1152 *Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 997-1007.
- 1153 Whiten, A., Custance, D. M., Gomez, J.-C., Teixidor, P., & Bard, K. A. (1996). Imitative learning of  
1154 artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*).  
1155 *Journal of Comparative Psychology*, *110*(1), 3-14. <https://doi.org/10.1037/0735-7036.110.1.3>

1156 Wild, B., Dormagen, D. M., Zachariae, A., Smith, M. L., Traynor, K. S., Brockmann, D., Couzin, I. D., &  
1157 Landgraf, T. (2021). Social networks predict the life and death of honey bees. *Nature*  
1158 *Communications*, 12(1), 1110. <https://doi.org/10.1038/s41467-021-21212-5>

1159 Würbel, H. (2000). Behaviour and the standardization fallacy. *Nature Genetics*, 26(3), 263-263.  
1160 <https://doi.org/10.1038/81541>

1161 Yang, J., Huber, L., Yu, Y., & Bandettini, P. A. (2021). Linking cortical circuit models to human  
1162 cognition with laminar fMRI. *Neuroscience & Biobehavioral Reviews*, 128, 467-478.  
1163 <https://doi.org/10.1016/j.neubiorev.2021.07.005>

1164 Yang, Q., Lin, Z., Zhang, W., Li, J., Chen, X., Zhang, J., & Yang, T. (2022). Monkey plays Pac-Man with  
1165 compositional strategies and hierarchical decision-making. *eLife*, 11, e74500.  
1166 <https://doi.org/10.7554/eLife.74500>

1167 Yates, T. S., Ellis, C. T., & Turk-Browne, N. B. (2021). The promise of awake behaving infant fMRI as a  
1168 deep measure of cognition. *Current Opinion in Behavioral Sciences*, 40, 5-11.  
1169 <https://doi.org/10.1016/j.cobeha.2020.11.007>

1170 Zeagler, C., Gilliland, S., Freil, L., Starner, T., & Jackson, M. (2014). *Going to the dogs : Towards an*  
1171 *interactive touchscreen interface for working dogs*. 497-507.

1172