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1 **Animal agency can accelerate behavioural and neuroscience research**

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9

10 **Abstract**

11 Despite increasing numbers of publications showing that many animals possess the neural
12 substrates involved in emotions and consciousness, animals are still restrained and forced to
13 take part in applied or fundamental research. However, these restraints stress animals and
14 may result in false negatives or false positives. A change is needed in researchers' work
15 paradigm with animals to progress in behavioural and neuroscience research and thus gain
16 access to hitherto inaccessible yet important scientific results. Animals interact in their own
17 ways with the world and researchers need to adopt these ways, i.e. their agency, to perform
18 better research and develop a better understanding of how the brain and behaviour evolve.
19 This paper discusses how animal agency can not only be the key to more wide-ranging and
20 improved research in existing domains, but can also lead to new research questions resulting
21 from anthropocentric view.

22 **Keywords:** 3Rs, animal research, ethology, ethics, sentience

23 Introduction

24 By definition, animal research requires the involvement of animals. Although researchers
25 have made great progress and improved experimental conditions for animals through
26 application of the 3R rules (replace, reduce, refine), some behavioural experiments showed
27 that animals are still restrained through different processes such as throw nets, restraint
28 chairs, cages or food deprivation¹⁻⁶. According to McMillan and colleagues², too many
29 researchers still continue to use methods that entail negative reinforcement, whilst
30 procedures using restraint chairs could comprise positive reinforcement methods². Beyond
31 the ethical issues of such restraints for animals, these examples of experimental set-ups lead
32 us to consider which possibilities and results have yet to be investigated and more
33 importantly, whether such invasive protocols could lead to false negatives or false positives
34 ⁷⁻¹⁰. False negatives or False positives mean that studies show respectively negative (not
35 expected, H0) or positive results (expected, H1) but these results are not due to the tested
36 condition (e.g. a drug, a gene, an environmental condition) but to uncontrolled factors (e.g.,
37 stress, personality). Indeed, stress and contention can not only modify some animal
38 behaviours but also entirely prevent others from being displayed¹¹⁻¹³. Some authors as
39 Patter, Blattner, Matsuzawa, King B.J. or McMillan¹⁴⁻¹⁷ consider that the current 3R
40 framework is not sufficient to ensure that animals are meaningful participants, which is
41 crucial to guarantee that scientific results are not altered by stress or personality of animals.
42 These studies with restraints offer few meaningful opportunities for animals to exercise
43 agency in their relationships, both between each other and with humans¹⁸. Gillespie wrote
44 that 'there is a long tradition of studying nonhuman animals in spaces of animal use and
45 exploitation, where researchers and teachers in effect become complicit through passive
46 participation in violence against nonhuman animals...' ¹⁹. According to Blattner et al. (2020)
47 ¹⁸ who worked on animal agency in rehomed farm animals and from which this paper is
48 inspired, 'longstanding ideological blinders and anthropocentric bias frame animals as
49 limited beings whose lives unfold according to fixed genetic or species-specific scripts, rather
50 than as complex subjects who act with intention and purpose, both individually and
51 collectively'. Restraint-based experiments are severely limited in terms of what researchers
52 can learn from animals, in individual and group contexts.

53 Indeed, increasing numbers of publications show that many animals (mammals, birds and
54 other creatures including octopuses) possess the neural substrates involved in emotions and
55 consciousness^{20,21}. Rats, primates and pigeons are capable of metacognition, i.e. knowing if
56 they are wrong or right in a test^{22,23}. Cetaceans and apes are conscious of their own
57 existence, and that of others²⁴. Self-awareness was also found in cleaner fishes^{25,26}. Apes
58 know what their conspecifics know²⁷ and believe²⁸. Empathy has been observed in apes²⁹
59 and in rats⁴. Finally, some apes have a sense of morality³⁰⁻³². Researchers obtained these
60 results by changing their way of thinking from an anthropocentric approach³³ to an
61 acceptance of anthropomorphism³⁴. For instance, self-awareness was not found in some
62 species when the mirror test²⁴ was used, but it was found when researchers used the senses
63 of animals, such as the sense of smell for dogs³⁵ or vocalisations in gibbons³⁶. Merleau-
64 Ponty had already noted this problem in his *Causeries* back in 1948: researchers usually do
65 not try to understand animals in their singularity, *as they are*, but rather in comparison with
66 human beings, projecting essentially human characteristics on to animals³⁷. However, this is
67 a means to measure the distance between human beings and other animals rather than a
68 tool allowing a real understanding of how animals live and express a subjective existence
69^{38,39}. Studied in the light of properly human normative references, animals always lack
70 something³⁷. For as long as animals are studied from a human perspective and are tested in
71 terms of human problems (capacity to count, to draw, to speak a human language) instead
72 of their own questions and problems, they will always respond “as they can”⁴⁰, without ever
73 being able to fully express their agency. Animals interact with the world in their own ways
74 and these ways, i.e. their agency, are precisely the view what researchers need to adopt to
75 perform better research and develop a better understanding of how the brain and behaviour
76 evolve.

77 **Animal agency**

78 Agency is the capacity of an actor to act in a given environment. In the broadest sense,
79 agency is the ability to have an influence or an effect on something. In this sense, the agency
80 is owned by all humans and animals, but also by viruses, stones or tornadoes as explained by
81 Blattner et al. (2020)¹⁸. However, its focus might be narrower when agency is considered as
82 the expression or manifestation of a subjective existence; agency implies affecting the world
83 in ways that reflect a subject’s desires or will⁴¹. It refers to an individual pursuing its own

84 good in its own way⁴². Blattner et al.¹⁸ investigate animal agency in a sanctuary for formerly
85 farmed animals, considering how a careful exploration of dimensions of agency in this
86 setting might inform ideas of interspecies interactions (work, research, politics, etc.) and
87 ethics. Their study focused on multispecific animals living in a sanctuary. For the owners of
88 the sanctuary and for the study researchers, the sanctuary is an ‘integrated multispecies
89 community or society whose members shape spaces and practices together, take on
90 recognised social roles, and create and transmit social norms across species lines’. Blattner
91 et al.¹⁸ as Frans de Waal⁴³, Le Leindre et al.^{22,23}, Meijer⁴⁴ affirm that researchers need to
92 spend time in community with animals, to learn from them, and to be prepared to respond
93 and adjust scientific learning process through relationships with them. This means that
94 animals should no longer be considered as the subjects of scientific experiments, but rather
95 as participants. For example, when it comes to assessing animal intelligence, the
96 researchers’ focus should encompass goals that are meaningful, useful and of interest to
97 animals instead of focusing on goals that are only relevant to the human scientist⁴⁵. Animals
98 should no longer be seen as objects of knowledge, or mere matter for the act of the human
99 knower, but should rather be granted a status as an *agent* in the production of knowledge⁴⁶.
100 Interaction and communication have to go in both directions. Researchers need to make
101 themselves understandable to animals as many species are able to understand our facial
102 expressions and emotions^{47–52}. Of course, this communication would only be possible for
103 some species, such as apes and some monkeys, cetaceans, certain birds including parrots or
104 corvids, social carnivores and cephalopods. However, researchers need to extend this circle
105 as some other species are surely able to understand their intentions as behavioural or even
106 neuroscientific experiments, particularly in rats and mice being the most used animals in
107 laboratories but having sense of empathy^{4,53,54} and feeling human intention (i.e. Pygmalion
108 effect⁴⁸). When researchers allow too little room for the animals’ own forms of agency, the
109 true abilities of these individuals are obscured⁵⁵.

110 The study of agencies in animals can be divided into four schemes according to Blattner et al.
111 (2020)¹⁸ (Figure 1):

- 112 1. Agency through space and time: animals are mobile and explore/exploit their
113 environments. This exploration and exploitation can be used to better understand
114 the behaviours of animals but also their preferences in terms of habitats, sleeping

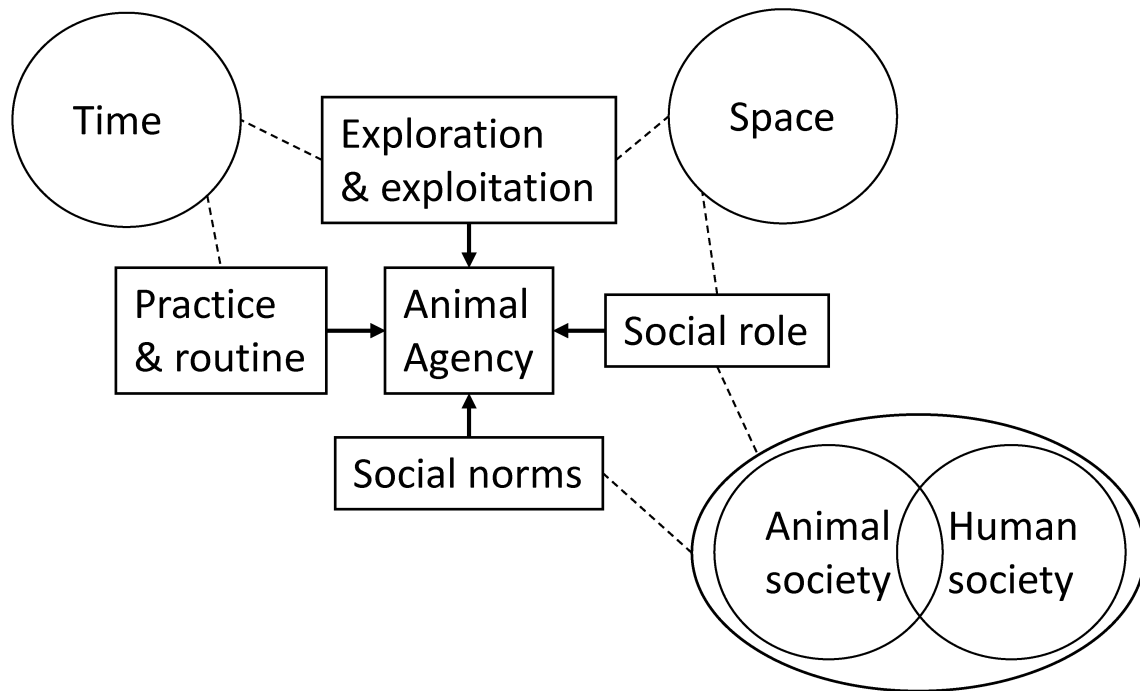
115 areas and social relationships and conduct to new disciplines as animal geographies⁵⁶
116 or animal mobilities⁵⁷. Whilst this agency seems obvious for many researchers and is
117 often applied for livestock and farmed animals ⁵⁸⁻⁶⁰, it is rarely applied in
118 comparative psychology or neuroscience. Specifically, modifications of the
119 environment can be used to shape animal decisions and can remove some of the
120 negative reinforcement that is still applied to animals. Animals could experience less
121 stress in some parts of their environment than others, and carrying out experiments
122 in these places could increase their motivation to participate and decrease the risk of
123 false negatives ^{61,62}.

124 2. Agency through practice and routine: Animals have habits, even in the wild. Social
125 animals collectively organise their day in order to meet their requirements and
126 maintain the advantages of living in groups ⁶³. Rather than forcing animals to
127 participate in experiments, accepting that animals can accept or refuse to participate
128 according to their routine would increase the robustness and viability of results. Any
129 animals that want to be tested seek to use tablets or other interactive apparatus
130 such as artificial fruits⁶⁴ or opening boxes⁶⁵ with food inside that are based on
131 technologies such as RFID^{66,67}; these tools respect their habits and routines. Medical
132 aspects such as health checks or medical procedures that require restraints should
133 also be based on these routines to decrease animal stress and injuries, as already
134 shown in their use by zoos.

135 3. Agency through social roles: A social role is the behaviour expected of an individual
136 who occupies a given social position or status. Individuals understand the place that
137 conspecifics hold in their society. The adoption of roles that are recognised and
138 acknowledged by others, and indeed mutually constructed with conspecifics, is an
139 important dimension of relational agency and a means by which researchers can
140 effectively affirm their subjective existence within a community. This role can be
141 intraspecific or interspecific. Roles of individuals inside their group 'have been amply
142 described in terms of dominance (policing behaviours, protecting groups), kinship
143 and maternal relationships ⁶⁸. Individuals also develop strong relationships when they
144 share similar attributes as sex or age⁶⁹⁻⁷³. Group members influence each other, and
145 particularly share knowledge ⁷⁴. Dominant or old individuals can transmit important
146 information to others, and this social transmission can be used to make animals learn

147 how to use experimental apparatus or spaces. These individuals can consequently
148 become leaders. Multispecific and positive interactions or associations are also found
149 naturally in the wild in situations such as multispecies group protection, interspecies
150 grooming and predator alerts, even if negative interactions (cheating, predating,
151 competition) are also observed. Blattner et al.¹⁸ described multispecies interactions
152 in the sanctuary for formerly farmed animals. Individuals of specific species adopt
153 different roles with geese, cows or dogs acting as guardians and policers, cows
154 teaching sheep and multispecies friendship and parenting. Multispecific leadership is
155 also described in different reports with geese leading ducks and chickens, and goats
156 leading sheep ⁷⁵⁻⁷⁷.

157 4. Agency through social norms: Social norms are the customary rules that govern
158 behaviour in groups and societies ⁷⁸. The previous example of learners and teachers
159 brings us to the subject of social norms. Behavioural rules and social systems are
160 partly genetic in animals but are also transmitted by cultures ^{68,79-82}. Many traditions
161 of tool use and social habits have been described in chimpanzees or macaques ⁸³.
162 Although collective decision processes are species-specific, variations are observed
163 between groups of the same species. The roles played by individuals can lead to a
164 strong leadership or the development of a more democratic process such as votes ⁸⁴.
165 Voting systems ⁸⁵ are described in many species, with intentional behaviours and
166 perceptions of the mental states of conspecifics indicating some theory of mind and
167 reinforcing the idea of agency. A sense of community ¹⁸ seems to exist in
168 chimpanzees and in cetaceans, and indeed many other animals know exactly who
169 belongs or does not belong to their group by recognising the faces or voices of group
170 members.



171

172 Figure 1: The four schemes of animal agency (squares) and the environmental factors
 173 affecting them (circles)

174

175 These different instances show that animals have agency over their spatial, temporal and
 176 social environment. Animals can therefore be viewed as *agents*; their choice to act has direct
 177 consequences on their environment, or they can also resist conditions that do not please
 178 them, and act accordingly to change them⁸⁶. The behaviours animal show, facial expressions
 179 they display, the places they occupy are cues to indicate their willingness. Researchers could
 180 use this agency to increase animal welfare and obtain more viable and robust results, whilst
 181 extending the scope of behavioural and neuroscience research. Indeed, the great difficulty
 182 today is to measure the behaviours or the neuronal activities of aware animals whilst
 183 seeking to do so in natural conditions: the results of many experiments have been criticised,
 184 as the associated captivity, animal microbiota, genetic or behavioural variance of animals
 185 made it impossible to allow to reproduce or generalise any results that were unaffected by
 186 false negatives or false positives⁸⁷⁻⁸⁹. Often, in the research process, many of the limitations
 187 shown by the animals to date are actually the limitations of the scientific methods, rather
 188 than the animals themselves⁹⁰. Similarly, Frans De Waal argues: 'All that most experiments
 189 have done thus far is testing the ape's theory of the human mind. We would do better to

190 focus on the ape's theory of the ape mind' ³⁰. Following the concept of animal agency, this
191 paper proposes a future research framework to work with animals and progress in research.

192 **Future research framework**

193 Some years ago, applying the use of touchscreens in macaques, or studying mouse
194 personality was almost unimaginable in neuroscience. Yet today, these projects have
195 become reality. Touchscreens or joysticks are used to understand cognition and self-agency
196 ⁹¹ in a wide range of species (pigs, macaques, baboons, goats, horses, rats, mice, etc.^{67,92-97}).
197 However, this use is still limited given its potential even if more and more neuroscience
198 studies use it in mice or rats ⁹⁸⁻¹⁰¹. There is a huge amount of literature describing how
199 animal personality and microbiota can influence results. This success demonstrates the
200 importance of not limiting scientific imagination about how researchers could work with
201 animals to obtain new results in biological sciences.

202 First researchers need to change their way of thinking to a perspective of working *with*
203 animals rather than *on* animals. Animals are agents endowed with intentions which
204 transcend traditional subject-object relations. Researchers need to trust their
205 capabilities^{102,103} in order to increase research possibilities. Experimental set-ups such as
206 restraint chairs or food privation, stress animals and prevent them both physically and
207 mentally from fully expressing their agency. This challenge may certainly take time, but
208 would be hugely beneficial. Patter and Blattner ¹⁴ suggest core principles to follow with
209 animals: non-maleficence, beneficence and voluntary participation ¹⁰⁴. Positive methods
210 exist and have proved to be efficient ^{6,11,105-108}. The readiness of chimpanzees (not used
211 anymore for invasive experiments but present in primate research centers¹⁰⁹) to voluntarily
212 participate in interactions or allow humans to observe them can facilitate the measurement
213 of embryo development and brain activities in unanesthetized and unrestrained individuals
214 (Figure 2⁶⁶). Unrestrained and voluntary animals can be trained to put their head in a mask ⁵
215 and be tested whilst receiving fruit juice. This allows the measurement of different metrics
216 with eye tracking ^{28,110,111} and non-invasive neuroimaging ¹¹² (Figure 3.A).

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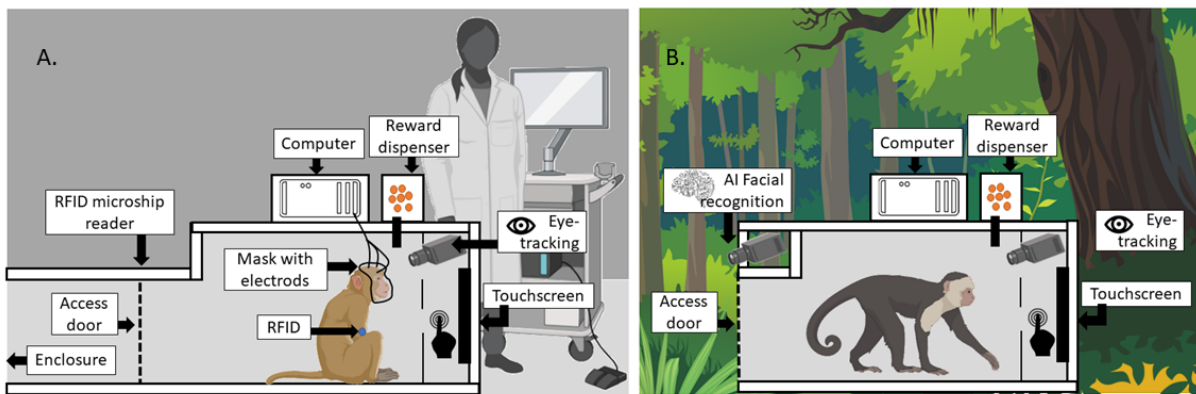


218
219 Figure 2: (A) Developmental neuroscience. Fetal brain development in chimpanzees was
220 measured by a non-invasive ultrasound technique. (B) EEG recordings in a chimpanzee. The
221 chimpanzee quietly sat on the chair and allowed the experimenter to put electrode patches
222 on the skin of her forehead and the top of her head. Photos provided with the courtesy of
223 Satoshi Hirata.

224

225 Some traditional approaches involve bringing animals into a lab and restraining them while
226 they perform tasks in order to ensure stable gaze-tracking and neural recordings. However,
227 this unnatural setting does not permit the study of brain activity during natural, social and
228 complex behaviours. Specific ethical guidelines exist now for research in the wild ^{113,114}. The
229 likely benefits and possible negative effects of researchers' presence and field methods on
230 study subjects, their environment and the local human community should, of course, be
231 considered ¹¹⁵. New technologies allow us to bring science into the wild and test animals in a
232 free condition in their natural environment, thus removing any experimental source of stress
233 (as they would come by themselves to be tested) and measuring their entire behavioural
234 repertoire. This allows to study behavioural responses and the brain activity during natural,
235 social and complex behaviours. This field works are possible in many species including
236 rodents^{116–118}. The animals studied can be identified using RFID techniques ¹¹⁹ but also via
237 artificial intelligence with the recognition of individuals by videotracking ^{120–122}. The latter
238 removes the need to catch animals. A location can then be defined where different
239 touchscreens deliver food, with activation only for certain species and individuals.

240 Researchers can imagine going beyond the use of touchscreens with the implementation of
241 eye-tracking and neuroimaging apparatus in the wild (Figure 3.B). This could open up new
242 research avenues in species that are in danger of extinction or cannot be easily maintained
243 in captivity. As Schaefer and Claridge-Chang wrote, ‘the new automation is not just faster: it
244 is also allowing new kinds of experiments, many of which erase the boundaries of the
245 traditional neuroscience disciplines (psychology, ethology and physiology) while producing
246 insight into problems that were otherwise opaque’¹²³.



247
248 Figure 3: (A) Non-invasive neuroimaging and eye-tracking system with voluntary experience
249 in the lab. (B) Non-invasive touchscreen system with voluntary engagement and individual
250 identification in the wild. This figure was realized using FAVPNG.com and Biorender.

251
252 Some studies, and especially the biomedical or physiological/cellular domains, cannot be
253 performed outside the laboratory. It is important for these experiments to respect the 3Rs
254 but also to think about the Bateson cube ¹²⁴, meaning that scientists need to evaluate the
255 ethical acceptability of their research for society as a whole, including animals. The 3Rs can
256 be extended by testing animals in viable conditions. These too standardized lab conditions
257 for instance decrease the replicability of studies by decreasing the behavioural variability
258 (issue called standardization fallacy^{125,126}). Indeed, lab conditions were standardised for
259 many years in terms of animal genetics, husbandry, food for study comparison and
260 repeatability. However, this way of doing research is criticised today as animals are agents
261 interacting with their world, and the lab conditions in which they live have a strong effect on
262 them and thus on scientific results. Moreover, it is difficult to replicate similar conditions in
263 the laboratory, as even animals that are genetically similar and live in similar environments

264 develop different personalities ¹²⁷. Moreover, even if animals are living in similar conditions,
265 similar food and litter sources affect their microbiota ¹²⁸⁻¹³⁰ and their behaviours differently
266 ¹³¹. Animal sociality was long forgotten in neuroscience or biomedical research, but it is an
267 important part of animal agency ¹⁸. Indeed, sociality has an important impact on the health
268 of animals, and a great number of publications highlight the link between sociality and
269 health ageing ¹³²⁻¹³⁴. Making use of the sociality of animals, i.e. their agency, can even
270 reverse cognitive decline and extend longevity ¹³⁵⁻¹³⁷.

271 **Conclusion**

272 Great efforts are made towards animal but there is still much progress to be made to attain
273 a more compassionate, less stressful and more robust animal research model. This requires
274 training and teaching researchers, through MOOC ^{138,139}, books^{17,43,102,140} or workshops, to
275 adopt new methods including animal agency and change their view of the role animals play
276 in research. As Jacques Derrida wrote in *The Animal That Therefore I Am*, the traditional
277 scientific and philosophical discourse on animals observes and speaks of non-human animals
278 but never really engages with, experiments *with* or gains experience with the latter ¹⁴¹: this
279 type of discourse can therefore only position animals as mere passive objects of the
280 theoretical knowledge these disciplines build. Such methods are completely blind to the
281 animals' own processes of interacting with their world ¹⁴¹, and are completely blind to their
282 agency. This view of animals as objects is not limited to research but is also found in
283 different aspects of everyday life (food, work, clothing, etc.). Researchers worldwide must
284 have the conviction that ethical animal research must consider individuals as subjects of
285 their own life and of their own world, and as co-creators of knowledge. Accepting this co-
286 creation of knowledge can create new research questions from anthropocentric view, as
287 animal cognition dimensions are different from ours³³. Animals are agents in scientific
288 research. They are active in the research process and some researchers have even gone so
289 far as to add them in the acknowledgments or even list them as co-authors ^{14,142}. This
290 recognition of animals as agents rather than objects is not approved of by some researchers,
291 who consider that this is tantamount to removing animal agency, committing over-
292 anthropomorphism and overstepping the will of animals to cooperate. Acknowledging
293 animal agency could facilitate social acceptance of animal research ¹⁰⁴ and be of benefit to
294 the animals concerned (well-being through learning, creating and participating¹⁴³). The

295 consideration of animals as agents could be extended from research to other domains: a
296 new ontology considering non-human animals as agents can have political, ethical and legal
297 consequences. The concept of capital applied to animals needs to be extended to social
298 capital, ecological capital and cultural capital ¹⁴⁴: citizens but not only researchers can learn
299 from animals and they can be part of human societies ¹⁴⁵. This new way of viewing animal
300 agency can therefore raise critical ethical questions in regard to the treatment of animals in
301 research and to the place humans grant them politically in human social world.

302

303

304 **References**

- 305 1. Chang, L., Fang, Q., Zhang, S., Poo, M. & Gong, N. Mirror-Induced Self-Directed Behaviors in
306 Rhesus Monkeys after Visual-Somatosensory Training. *Curr. Biol.* **0**,
- 307 2. McMillan, J. L., Bloomsmith, M. A. & Prescott, M. J. An International Survey of Approaches to
308 Chair Restraint of Nonhuman Primates. *Comp. Med.* **67**, 442–451 (2017).
- 309 3. He, L.-W. *et al.* Optimization of food deprivation and sucrose preference test in SD rat model
310 undergoing chronic unpredictable mild stress. *Anim. Models Exp. Med.* **3**, 69–78 (2020).
- 311 4. Bartal, I. B.-A., Decety, J. & Mason, P. Empathy and pro-social behavior in rats. *Science* **334**,
312 1427–1430 (2011).
- 313 5. Slater, H. *et al.* Individually customisable non-invasive head immobilisation system for non-
314 human primates with an option for voluntary engagement. *J. Neurosci. Methods* **269**, 46–60
315 (2016).
- 316 6. Prescott, M. J. & Buchanan-Smith, H. M. Training nonhuman primates using positive
317 reinforcement techniques. *J. Appl. Anim. Welf. Sci.* **6**, 157–161 (2003).
- 318 7. Chang, L., Zhang, S., Poo, M. & Gong, N. Spontaneous expression of mirror self-recognition in
319 monkeys after learning precise visual-proprioceptive association for mirror images. *Proc. Natl.*
320 *Acad. Sci.* **114**, 3258–3263 (2017).

- 321 8. Huttunen, A. W., Adams, G. K. & Platt, M. L. Can self-awareness be taught? Monkeys pass the
322 mirror test—again. *Proc. Natl. Acad. Sci.* **114**, 3281–3283 (2017).
- 323 9. Liu, X., Liu, T. & Huang, X. Commentary: Spontaneous expression of mirror self-recognition in
324 monkeys after learning precise visual-proprioceptive association for mirror images. *Front.*
325 *Psychol.* **8**, 1151 (2017).
- 326 10. Ueno, H. *et al.* Behavioural Changes in Mice after Getting Accustomed to the Mirror. *Behav.*
327 *Neurol.* **2020**, (2020).
- 328 11. Prescott, M. J. Online resources for improving the care and use of non-human primates in
329 research. *Primate Biol.* **3**, 33 (2016).
- 330 12. Mason, S. *et al.* Effective chair training methods for neuroscience research involving rhesus
331 macaques (*Macaca mulatta*). *J. Neurosci. Methods* **317**, 82–93 (2019).
- 332 13. Lecorps, B., Weary, D. M. & von Keyserlingk, M. A. G. Captivity-Induced Depression in Animals.
333 *Trends Cogn. Sci.* (2021) doi:10.1016/j.tics.2021.03.010.
- 334 14. Patter, L. E. V. & Blattner, C. Advancing Ethical Principles for Non-Invasive, Respectful Research
335 with Nonhuman Animal Participants. *Soc. Anim.* **28**, 171–190 (2020).
- 336 15. Matsuzawa, T. Euthanasia is not an option: 10 years' care of a chimpanzee with acute
337 tetraparesis. (2016).
- 338 16. McMillan, J. L., Perlman, J. E., Galvan, A., Wichmann, T. & Bloomsmith, M. A. Refining the pole-
339 and-collar method of restraint: emphasizing the use of positive training techniques with rhesus
340 macaques (*Macaca mulatta*). *J. Am. Assoc. Lab. Anim. Sci.* **53**, 61–68 (2014).
- 341 17. King, B. J. *Animals' Best Friends: Putting Compassion to Work for Animals in Captivity and in the*
342 *Wild.* (University of Chicago Press, 2021).
- 343 18. Blattner, C. E., Donaldson, S. & Wilcox, R. Animal Agency in Community. *Polit. Anim.* **6**, 1–22
344 (2020).
- 345 19. Gillespie, K. A. For a politicized multispecies ethnography. *Polit. Anim.* **5**, 17–32 (2019).
- 346 20. Low, P. *et al.* The Cambridge declaration on consciousness. in 1–2 (2012).

- 347 21. Ben-Haim, M. S. *et al.* Disentangling perceptual awareness from nonconscious processing in
348 rhesus monkeys (*Macaca mulatta*). *Proc. Natl. Acad. Sci.* **118**, (2021).
- 349 22. Le Neindre, P. *et al.* Animal consciousness. Summary of the multidisciplinary assesment. (2017).
- 350 23. Le Neindre, P., Dunier, M., Larrère, R. & Prunet, P. *La conscience des animaux*. (Quae, 2018).
- 351 24. Gallup Jr, G. G., Anderson, J. R. & Shillito, D. J. The mirror test. *Cogn. Anim. Empir. Theor.*
352 *Perspect. Anim. Cogn.* 325–333 (2002).
- 353 25. de Waal, F. B. Fish, mirrors, and a gradualist perspective on self-awareness. *PLoS Biol.* **17**,
354 e3000112 (2019).
- 355 26. Kohda, M. *et al.* If a fish can pass the mark test, what are the implications for consciousness and
356 self-awareness testing in animals? *PLoS Biol.* **17**, e3000021 (2019).
- 357 27. Kaminski, J., Call, J. & Tomasello, M. Chimpanzees know what others know, but not what they
358 believe. *Cognition* **109**, 224–234 (2008).
- 359 28. Krupenye, C., Kano, F., Hirata, S., Call, J. & Tomasello, M. Great apes anticipate that other
360 individuals will act according to false beliefs. *Science* **354**, 110–114 (2016).
- 361 29. De Waal, F. B. The antiquity of empathy. *Science* **336**, 874–876 (2012).
- 362 30. De Waal, F. „Morally Evolved.“. *Primates Philos. Moral. Evolved* 1–80 (2006).
- 363 31. Jensen, K., Call, J. & Tomasello, M. Chimpanzees are vengeful but not spiteful. *Proc. Natl. Acad.*
364 *Sci.* **104**, 13046–13050 (2007).
- 365 32. Tomasello, M. & Vaish, A. Origins of human cooperation and morality. *Annu. Rev. Psychol.* **64**,
366 231–255 (2013).
- 367 33. Birch, J., Schnell, A. K. & Clayton, N. S. Dimensions of animal consciousness. *Trends Cogn. Sci.*
368 (2020).
- 369 34. Griffin, D. R. *Animal minds: Beyond cognition to consciousness*. (University of Chicago Press,
370 2013).
- 371 35. Cazzolla Gatti, R. Self-consciousness: Beyond the looking-glass and what dogs found there.
372 *Ethol. Ecol. Evol.* **28**, 232–240 (2016).

- 373 36. D'Agostino, J., Pasetta, C. & Reichard, U. Preliminary results of a vocal self-recognition test in
374 northern white-cheeked gibbons (*Nomascus leucogenys*). in vol. 162 157–157 (WILEY 111
375 RIVER ST, HOBOKEN 07030-5774, NJ USA, 2017).
- 376 37. Merleau-Ponty, M. *Causeries 1948*. (Média Diffusion, 2017).
- 377 38. Sueur, C. & Pelé, M. Editorial: Anthropomorphism, between merits and demerits. *Lett. CEERE*
378 *Cent. Eur. Enseign. Rech. En Ethique* **107**, 1 (2017).
- 379 39. Sueur, C., Forin-Wiart, M.-A. & Pelé, M. Do They Really Try to Save Their Buddy?
380 Anthropomorphism about Animal Epimeletic Behaviours. (2020)
381 doi:10.20944/preprints202008.0711.v1.
- 382 40. Canguilhem, G. *La connaissance de la vie*. (Vrin, 1992).
- 383 41. Krause, S. R. Beyond non-domination: Agency, inequality and the meaning of freedom. *Philos.*
384 *Soc. Crit.* **39**, 187–208 (2013).
- 385 42. Taylor, P. W. *Respect for nature: A theory of environmental ethics*. (Princeton University Press,
386 2011).
- 387 43. De Waal, F. *Are we smart enough to know how smart animals are?* (WW Norton & Company,
388 2016).
- 389 44. Meijer, E. *When Animals Speak: Toward an Interspecies Democracy*. (NYU Press, 2019).
- 390 45. Pepperberg, I. M. Intelligence and rationality in parrots. (2006).
- 391 46. Haraway, D. J. *Primate visions: Gender, race, and nature in the world of modern science*.
392 (Psychology Press, 1989).
- 393 47. Hoffman, J. M., Creevy, K. E., Franks, A., O'Neill, D. G. & Promislow, D. E. L. The companion dog
394 as a model for human aging and mortality. *Aging Cell* **17**, e12737 (2018).
- 395 48. Good, T. L., Sterzinger, N. & Lavigne, A. Expectation effects: Pygmalion and the initial 20 years
396 of research. *Educ. Res. Eval.* **24**, 99–123 (2018).
- 397 49. Bhattacharjee, D. *et al.* Free-Ranging Dogs Are Capable of Utilizing Complex Human Pointing
398 Cues. *Front. Psychol.* **10**, (2020).

- 399 50. Patterson, F. G. P. & Cohn, R. H. Language acquisition by a lowland gorilla: Koko's first ten years
400 of vocabulary development. *WORD* **41**, 97–143 (1990).
- 401 51. Savage-Rumbaugh, E. S. & Lewin, R. *Kanzi: the ape at the brink of the human mind*. (Wiley,
402 1994).
- 403 52. Pedersen, J. Nonhuman Primates and Language: Primates Raised by Humans. in *The*
404 *International Encyclopedia of Linguistic Anthropology* 1–9 (John Wiley & Sons, Ltd, 2020).
405 doi:10.1002/9781118786093.iela0289.
- 406 53. Venniuro, M. & Golden, S. A. Taking action: empathy and social interaction in rats.
407 *Neuropsychopharmacology* **45**, 1081–1082 (2020).
- 408 54. Klein, A. S. & Gogolla, N. How mice feel each other's pain or fear. *Science* **371**, 122–123 (2021).
- 409 55. McFarland, S. E. & Hediger, R. *Animals and agency: An interdisciplinary exploration*. vol. 8 (Brill,
410 2009).
- 411 56. Buller, H. Animal geographies I. *Prog. Hum. Geogr.* **38**, 308–318 (2014).
- 412 57. Hodgetts, T. & Lorimer, J. Animals' mobilities. *Prog. Hum. Geogr.* **44**, 4–26 (2020).
- 413 58. Bouissou, M.-F., Boissy, A., Le Neindre, P. & Veissier, I. The social behaviour of cattle. *Soc.*
414 *Behav. Farm Anim.* 113–145 (2001).
- 415 59. Scanes, C. G. *Animal Agriculture: Livestock, Poultry, and Fish Aquaculture*. *Animals and Human*
416 *Society* 179 (Elsevier Inc., 2018). doi:10.1016/b978-0-12-805247-1.00007-1.
- 417 60. Sosa, S. O. *et al.* Impact of Group Management and Transfer on Individual Sociality in Highland
418 Cattle (*Bos taurus*). *Front. Vet. Sci.* **6**, 183 (2019).
- 419 61. Coe, J. & Hoy, J. Choice, control and computers: Empowering wildlife in human care.
420 *Multimodal Technol. Interact.* **4**, 92 (2020).
- 421 62. Matsuzawa, T. WISH cages: constructing multiple habitats for captive chimpanzees. (2020).
- 422 63. Sueur, C. A Non-Lévy Random Walk in Chacma Baboons: What Does It Mean? *PLoS ONE* **6**,
423 e16131 (2011).

- 424 64. Whiten, A., Custance, D. M., Gomez, J.-C., Teixidor, P. & Bard, K. A. Imitative learning of artificial
425 fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *J. Comp.*
426 *Psychol.* **110**, 3–14 (1996).
- 427 65. Aplin, L. M. *et al.* Experimentally induced innovations lead to persistent culture via conformity
428 in wild birds. *Nature* **518**, 538 (2015).
- 429 66. Matsuzawa, T. Evolution of the brain and social behavior in chimpanzees. *Curr. Opin. Neurobiol.*
430 **23**, 443–449 (2013).
- 431 67. Claidière, N., Gullstrand, J., Latouche, A. & Fagot, J. Using Automated Learning Devices for
432 Monkeys (ALDM) to study social networks. *Behav. Res. Methods* **49**, 24–34 (2017).
- 433 68. Krause, J. & Ruxton, G. D. *Living in groups*. (Oxford University Press, 2002).
- 434 69. Abeyesinghe, S. M., Drewe, J. A., Asher, L., Wathes, C. M. & Collins, L. M. Do hens have friends?
435 *Appl. Anim. Behav. Sci.* **143**, 61–66 (2013).
- 436 70. Massen, J. J. & Koski, S. E. Chimps of a feather sit together: chimpanzee friendships are based
437 on homophily in personality. *Evol. Hum. Behav.* **35**, 1–8 (2014).
- 438 71. Rault, J.-L. Friends with benefits: social support and its relevance for farm animal welfare. *Appl.*
439 *Anim. Behav. Sci.* **136**, 1–14 (2012).
- 440 72. Silk, J. B. Females, food, family, and friendship. *Evol. Anthropol. Issues News Rev.* **11**, 85–87
441 (2002).
- 442 73. Tsuji, Y., Shimoda-Ishiguro, M., Ohnishi, N. & Takatsuki, S. A friend in need is a friend indeed:
443 feeding association between Japanese macaques and sika deer. *Acta Theriol. (Warsz.)* **52**, 427–
444 434 (2007).
- 445 74. Duboscq, J., Romano, V., MacIntosh, A. & Sueur, C. Social Information Transmission in Animals:
446 Lessons from Studies of Diffusion. *Front. Psychol.* **7**, (2016).
- 447 75. Baratay, E. *Bêtes de somme-Des animaux au service des hommes*. (Points, 2011).
- 448 76. Baratay, É. Pour une histoire éthologique et une éthologie historique. *Etudes Rural.* **189**, 91–
449 106 (2012).

- 450 77. Baratay, E. *Biographies animales. Des vies retrouvées*. (Le Seuil, 2017).
- 451 78. Bicchieri, C. & Muldoon, R. Social norms. (2011).
- 452 79. Ward, A. & Webster, M. *Sociality: the behaviour of group-living animals*. (Springer, 2016).
- 453 80. SUEUR, C. *Analyse des réseaux sociaux appliquée à l'éthologie et l'écologie*. (Editions
454 Matériologiques, 2015). doi:10.13140/RG.2.1.4100.5601.
- 455 81. Sinha, A. Not in their genes: Phenotypic flexibility, behavioural traditions and cultural evolution
456 in wild bonnet macaques. *J. Biosci.* **30**, 51–64 (2005).
- 457 82. Brent, L. J. N. *et al.* Genetic origins of social networks in rhesus macaques. *Sci. Rep.* **3**, (2013).
- 458 83. Laland, K. N. & Hoppitt, W. Do animals have culture? *Evol. Anthropol. Issues News Rev.* **12**, 150–
459 159 (2003).
- 460 84. King, A. J. & Sueur, C. Where Next? Group Coordination and Collective Decision Making by
461 Primates. *Int. J. Primatol.* **32**, 1245–1267 (2011).
- 462 85. Pennisi, A. & Giallongo, L. Animal Biopolitics: How Animals Vote. *Int. J. Semiot. Law-Rev. Int.*
463 *Sémiot. Jurid.* **31**, 491–499 (2018).
- 464 86. Carter, B. & Charles, N. Animals, agency and resistance. *J. Theory Soc. Behav.* **43**, 322–340
465 (2013).
- 466 87. Rader, K. *Making Mice: Standardizing Animals for American Biomedical Research, 1900-1955*.
467 (Princeton University Press, 2004).
- 468 88. Barbee, R. W. & Turner, P. V. Incorporating Laboratory Animal Science into Responsible
469 Biomedical Research. *ILAR J.* **60**, 9–16 (2019).
- 470 89. Voelkl, B. *et al.* Reproducibility of animal research in light of biological variation. *Nat. Rev.*
471 *Neurosci.* **21**, 384–393 (2020).
- 472 90. Savage-Rumbaugh, E. S., Rumbaugh, D. M. & Fields, W. M. Language as a window on rationality.
473 (2006).
- 474 91. Kaneko, T. & Tomonaga, M. The perception of self-agency in chimpanzees (Pan troglodytes).
475 *Proc. R. Soc. B Biol. Sci.* **278**, 3694–3702 (2011).

- 476 92. Zeagler, C., Gilliland, S., Freil, L., Starner, T. & Jackson, M. Going to the dogs: towards an
477 interactive touchscreen interface for working dogs. in 497–507 (2014).
- 478 93. Tomonaga, M. *et al.* A horse's eye view: size and shape discrimination compared with other
479 mammals. *Biol. Lett.* **11**, 20150701 (2015).
- 480 94. Jacobson, S. L., Kwiatt, A. C., Ross, S. R. & Cronin, K. A. The effects of cognitive testing on the
481 welfare of zoo-housed Japanese macaques (*Macaca fuscata*). *Appl. Anim. Behav. Sci.* **212**, 90–
482 97 (2019).
- 483 95. Croney, C. C. & Boysen, S. T. Acquisition of a Joystick-Operated Video Task by Pigs (*Sus scrofa*).
484 *Front. Psychol.* **12**, (2021).
- 485 96. Belsey, P. P., Nicholas, M. A. & Yttri, E. A. Open-Source Joystick Manipulandum for Decision-
486 Making, Reaching, and Motor Control Studies in Mice. *eNeuro* **7**, ENEURO.0523-19.2020 (2020).
- 487 97. Washburn, D. A., Rulon, M. J. & Gullledge, J. P. A new breed of computer users: Rats control a
488 cursor via joystick manipulation. *Behav. Res. Methods Instrum. Comput.* **36**, 173–179 (2004).
- 489 98. Bussey, T. J. *et al.* The touchscreen cognitive testing method for rodents: How to get the best
490 out of your rat. *Learn. Mem.* **15**, 516–523 (2008).
- 491 99. Bussey, T. J., Muir, J. L., Everitt, B. J. & Robbins, T. W. Triple dissociation of anterior cingulate,
492 posterior cingulate, and medial frontal cortices on visual discrimination tasks using a
493 touchscreen testing procedure for the rat. *Behav. Neurosci.* **111**, 920–936 (1997).
- 494 100. Delotterie, D. F. *et al.* Touchscreen tasks in mice to demonstrate differences between
495 hippocampal and striatal functions. *Neurobiol. Learn. Mem.* **120**, 16–27 (2015).
- 496 101. Slutzky, M. W., Jordan, L. R., Bauman, M. J. & Miller, L. E. A new rodent behavioral paradigm for
497 studying forelimb movement. *J. Neurosci. Methods* **192**, 228–232 (2010).
- 498 102. Nielsen, B. *Asking Animals: An Introduction to Animal Behaviour Testing*. (CABI, 2020).
- 499 103. Nielsen, B. L. Making sense of it all: The importance of taking into account the sensory abilities
500 of animals in their housing and management. *Appl. Anim. Behav. Sci.* **205**, 175–180 (2018).

- 501 104. Webb, C. E., Woodford, P. & Huchard, E. Animal ethics and behavioral science: An overdue
502 discussion. *BioScience* **69**, 778–788 (2019).
- 503 105. Laule, G. E., Bloomsmith, M. A. & Schapiro, S. J. The Use of Positive Reinforcement Training
504 Techniques to Enhance the Care, Management, and Welfare of Primates in the Laboratory. *J.*
505 *Appl. Anim. Welf. Sci.* **6**, 163 (2003).
- 506 106. Prescott, M. & Buchanan-Smith, H. Training laboratory-housed non-human primates, part I: a
507 UK survey. *Anim. Welf.-POTTERS BAR THEN WHEATHAMPSTEAD-* **16**, 21 (2007).
- 508 107. Schapiro, S. J., Bloomsmith, M. A. & Laule, G. E. Positive Reinforcement Training As a Technique
509 to Alter Nonhuman Primate Behavior: Quantitative Assessments of Effectiveness. *J. Appl. Anim.*
510 *Welf. Sci.* **6**, 175 (2003).
- 511 108. Prescott, M. J. *et al.* Refinement of the use of food and fluid control as motivational tools for
512 macaques used in behavioural neuroscience research: report of a Working Group of the NC3Rs.
513 *J. Neurosci. Methods* **193**, 167–188 (2010).
- 514 109. Matsuzawa, T. SAGA and GAIN for great apes. (2016).
- 515 110. Machado, C. J. & Nelson, E. E. Eye-tracking with nonhuman primates is now more accessible
516 than ever before. *Am. J. Primatol.* **73**, 562–569 (2011).
- 517 111. Ryan, A. M. *et al.* Non-invasive Eye Tracking Methods for New World and Old World Monkeys.
518 *Front. Behav. Neurosci.* **13**, (2019).
- 519 112. Basso, M. A. *et al.* Using non-invasive neuroimaging to enhance the care, well-being and
520 experimental outcomes of laboratory non-human primates (monkeys). *NeuroImage* **228**,
521 117667 (2021).
- 522 113. Costello, M. *et al.* Field work ethics in biological research. (2016).
- 523 114. Soulsbury, C. D. *et al.* The welfare and ethics of research involving wild animals: A primer.
524 *Methods Ecol. Evol.* **11**, 1164–1181 (2020).
- 525 115. MacKinnon, K. C. & Riley, E. P. Field primatology of today: current ethical issues. (2010).

- 526 116. Lopes, P. C. & König, B. Wild mice with different social network sizes vary in brain gene
527 expression. *BMC Genomics* **21**, 506 (2020).
- 528 117. Evans, J. C., Liechti, J. I., Boatman, B. & König, B. A natural catastrophic turnover event:
529 individual sociality matters despite community resilience in wild house mice. *Proc. R. Soc. B*
530 *Biol. Sci.* **287**, 20192880 (2020).
- 531 118. Raulo, A. *et al.* Social networks strongly predict the gut microbiota of wild mice. *ISME J.* **15**,
532 2601–2613 (2021).
- 533 119. Fehlmann, G. & King, A. J. Bio-logging. *Curr. Biol.* **26**, R830–R831 (2016).
- 534 120. Schofield, D. *et al.* Chimpanzee face recognition from videos in the wild using deep learning. *Sci.*
535 *Adv.* **5**, eaaw0736 (2019).
- 536 121. Ferreira, A. C. *et al.* Deep learning-based methods for individual recognition in small birds.
537 *Methods Ecol. Evol.* **11**, 1072–1085 (2020).
- 538 122. Poirotte, C. & Charpentier, M. J. E. Unconditional care from close maternal kin in the face of
539 parasites. *Biol. Lett.* **16**, 20190869 (2020).
- 540 123. Schaefer, A. T. & Claridge-Chang, A. The surveillance state of behavioral automation. *Curr. Opin.*
541 *Neurobiol.* **22**, 170–176 (2012).
- 542 124. Bout, H. J., van Vlissingen, J. M. F. & Karssing, E. D. Evaluating the ethical acceptability of animal
543 research. *Lab Anim.* **43**, 411–414 (2014).
- 544 125. Voelkl, B., Würbel, H., Krzywinski, M. & Altman, N. The standardization fallacy. *Nat. Methods*
545 **18**, 5–7 (2021).
- 546 126. Würbel, H. Behaviour and the standardization fallacy. *Nat. Genet.* **26**, 263–263 (2000).
- 547 127. Bierbach, D., Laskowski, K. L. & Wolf, M. Behavioural individuality in clonal fish arises despite
548 near-identical rearing conditions. *Nat. Commun.* **8**, 15361 (2017).
- 549 128. Bradford, M. A., Tordoff, G. M., Eggers, T., Jones, T. H. & Newington, J. E. Microbiota, fauna,
550 and mesh size interactions in litter decomposition. *Oikos* **99**, 317–323 (2002).

- 551 129. McCoy, K. D., Geuking, M. B. & Ronchi, F. Gut Microbiome Standardization in Control and
552 Experimental Mice. *Curr. Protoc. Immunol.* **117**, 23.1.1-23.1.13 (2017).
- 553 130. Xiang, Q. *et al.* Effects of diet on gut microbiota of soil collembolans. *Sci. Total Environ.* **676**,
554 197–205 (2019).
- 555 131. Montiel-Castro, A. J., González-Cervantes, R. M., Bravo-Ruiseco, G. & Pacheco-López, G. The
556 microbiota-gut-brain axis: neurobehavioral correlates, health and sociality. *Front. Integr.*
557 *Neurosci.* **7**, 70 (2013).
- 558 132. Boyer, F., Jaouen, F. & El Chérif Ibrahim, E. G. Deficits in social behavior precede cognitive
559 decline in middle-aged mice. *Front. Behav. Neurosci.* **13**, (2019).
- 560 133. Rosati, A. G. *et al.* Social selectivity in aging wild chimpanzees. *Science* **370**, 473–476 (2020).
- 561 134. Lacreuse, A., Raz, N., Schmidtke, D., Hopkins, W. D. & Herndon, J. G. Age-related decline in
562 executive function as a hallmark of cognitive ageing in primates: an overview of cognitive and
563 neurobiological studies. *Philos. Trans. R. Soc. B Biol. Sci.* **375**, 20190618 (2020).
- 564 135. Baker, N., Wolschin, F. & Amdam, G. V. Age-related learning deficits can be reversible in
565 honeybees *Apis mellifera*. *Exp. Gerontol.* **47**, 764–772 (2012).
- 566 136. Richardson, T. O. *et al.* Ant Behavioral Maturation Is Mediated by a Stochastic Transition
567 between Two Fundamental States. *Curr. Biol.* **30**, 1–8 (2020).
- 568 137. Wild, B. *et al.* Social networks predict the life and death of honey bees. *Nat. Commun.* **12**, 1110
569 (2021).
- 570 138. MacKay, J. R. D., Langford, F. & Waran, N. Massive Open Online Courses as a Tool for Global
571 Animal Welfare Education. *J. Vet. Med. Educ.* **43**, 287–301 (2016).
- 572 139. Watson, W. R., Kim, W. & Watson, S. L. Learning outcomes of a MOOC designed for attitudinal
573 change: A case study of an Animal Behavior and Welfare MOOC. *Comput. Educ.* **96**, 83–93
574 (2016).
- 575 140. Dawkins, M. S. *The Science of Animal Welfare: Understanding What Animals Want.* (Oxford
576 University Press, 2021).

- 577 141. Derrida, J. *The animal that therefore I am*. (Fordham Univ Press, 2008).
- 578 142. Savage-Rumbaugh, S., Wamba, K., Wamba, P. & Wamba, N. Welfare of Apes in Captive
579 Environments: Comments On, and By, a Specific Group of Apes. *J. Appl. Anim. Welf. Sci.* **10**, 7–
580 19 (2007).
- 581 143. Franks, B., Webb, C., Gagliano, M. & Smuts, B. Conventional science will not do justice to
582 nonhuman interests: A fresh approach is required. *Anim. Sentience* **4**, 17 (2020).
- 583 144. Pelé, M., Georges, J.-Y., Matsuzawa, T. & Sueur, C. Editorial: Perceptions of Human-Animal
584 Relationships and Their Impacts on Animal Ethics, Law and Research. *Front. Psychol.* **11**, (2021).
- 585 145. Donaldson, S. & Kymlicka, W. *Zoopolis: A political theory of animal rights*. (Oxford University
586 Press, 2011).
- 587
- 588

