

1 Propagation of interspecies sexual behaviour between Japanese macaques and Sika deer: First evidence

2
3 Cédric Sueur^{1,2,3}, Atsuyuki Ohshima⁴, Marie Pélé²

4 ¹IPHC UMR7178, CNRS, Université de Strasbourg, Strasbourg, France

5 ²ANTHROPO-LAB, ETHICS EA 7446, Université Catholique de Lille, Lille, France

6 ³Institut Universitaire de France, Paris, France

7 ⁴Atsuyuki Ohshima photography, Kyoto

8 9 **ABSTRACT**

10 This study presents a series of observation of interspecies sexual behaviour involving Japanese
11 macaques (*Macaca fuscata yakui*) and Sika deer (*Cervus Nippon yakushimae*) on Yakushima Island,
12 Japan. The initial observation in 2015 revealed a male macaque's attempt to engage in sexual activity
13 with female deer, displaying mate-guarding behaviour. Subsequent observations in 2020, 2021 and
14 2023 showed the continuation of this behaviour and propagation to other macaques. We categorised
15 this rare behaviour as a case of reproductive interference and explored hypotheses regarding its
16 functionality. While some suggest nutritional benefits for the deer, others propose learning, incomplete
17 species recognition, or mate deprivation hypotheses. Furthermore, we hypothesise that the observed
18 propagation may underlie social transmission and highlight the potential cognitive capacities of
19 Japanese macaques involving social learning mechanisms and the willingness to adopt non-instinctual
20 behaviours.

21 **Keywords:** tradition, culture, reproductive interference, primate, cervid, behaviour

22 23 24 **INTRODUCTION**

25 Animal culture refers to behaviours, practices, and traditions that are learned socially within a species
26 and passed down through generations. These behaviours, which are not inherited genetically but
27 through social learning, challenge the belief that culture is unique to humans and offers insights into
28 animal behaviour, evolution, and conservation (Whiten 2000; Laland and Janik 2006; Whiten and
29 Schaik 2007; Duboscq et al. 2016). Animals, like humans, develop and transmit cultural traits, with
30 different populations exhibiting distinct behaviours. For example, some chimpanzees use sticks to fish
31 for termites, while others use stones to crack nuts, illustrating the variation in culturally transmitted
32 behaviours between populations (Whiten et al. 1999, 2005, 2007; Biro et al. 2006; Matsuzawa 2017).
33 The concept of animal culture originated in primatology, particularly through Kinji Imanishi's study of
34 Japanese macaques in the mid-20th century. Imanishi's team observed the spread of potato-washing
35 behaviour among macaques, providing the first documented example of cultural transmission in
36 animals (Kawai 1965; Matsuzawa 2015). Jane Goodall's work with chimpanzees in the 1960s further
37 solidified the idea of animal culture, particularly through her discovery of tool use, which was learned
38 and transmitted socially within groups (Goodall 1986; Whiten et al. 1999). Since then, animal culture
39 has been observed across various species. Humpback whales, for instance, exhibit cultural
40 transmission through their songs, while New Caledonian crows demonstrate cultural tool use (Garland

41 et al. 2011). Even species with simpler cognitive abilities, like fruit flies, display cultural traditions in
42 mate choice (Battesti et al. 2015). These findings highlight the importance of cultural diversity in
43 animal conservation, emphasising that preserving cultural knowledge is as vital as protecting genetic
44 diversity (Carvalho et al. 2022; Sueur 2022).

45

46 **JAPANESE MACAQUES AND SIKA DEER CULTURES**

47 Direct interactions between Japanese macaques and Sika deer provide a compelling example of the
48 evolution of interspecies relationships. Initially, these species coexisted closely in terms of spatial
49 proximity, with both benefiting from this arrangement. For instance, macaques, while feeding in trees,
50 often drop food, which becomes an additional energy source for the deer, enhancing their foraging
51 efficiency through gleaning, as noted by (Tsuji et al. 2007). This interaction fosters a strong
52 cohabitation dynamic between the two species. A particularly unusual aspect of this relationship is the
53 deer's coprophagia, where deer consume the faeces of macaques, especially around the latter's
54 sleeping sites (Nishikawa and Mochida 2010). As their relationship evolved, some macaques have
55 been observed grooming deer, a behaviour that suggests a deepening bond between the species. On
56 Yakushima Island, this interaction has advanced into a unique co-culture, with macaques even riding
57 on the backs of Sika deer (Pelé et al. 2017). Similar behaviours have been observed between rhesus
58 macaques (*Macaca mulatta*) and sambar deer (*Rusa unicolor*), suggesting that such complex
59 interspecies interactions may arise in other environments and among different species (Prasad et al.
60 2013). Interestingly, these interactions have even led to interspecies sexual behaviours, as observed
61 in both Yakushima and the Minoo prefecture in Japan. Male macaques have been documented
62 engaging in sexual activity with female Sika deer, and conversely, female macaques with male deer.
63 These instances illustrate the capacity for highly complex and unexpected behaviours to emerge
64 between species living in close proximity. The evolution of their interactions – ranging from shared
65 foraging and grooming to more intricate behaviours like riding and interspecies sexual activities –
66 demonstrates significant social and behavioural adaptation between these two distinct species. They
67 appear to learn from one another and have developed co-cultural behaviours (Sueur and Huffman
68 2024).

69

70 **BEHAVIOURAL ANALYSIS**

71 **Original study**

72 During his presence on Yakushima Island, Japan, from October 10 to November 6, 2015 (Pelé et al.
73 2017), the photographer Alexandre Bonnefoy observed for the first time the intriguing behaviour of an
74 adult male Japanese macaque (figure 1a, Video 1). This male, seemingly a peripheral member or part
75 of a group of peripheral males (Sprague 1991), exhibited a unique case of heterospecific sexual
76 behaviour, characterised by the mounter performing pelvic thrusting (i.e. rhythmic movements of the
77 mounter's pelvic girdle toward the mountee's back or hindquarter). While this behaviour was
78 documented for the first time in our study, it does not mean that it did not exist before our observation.
79 Nonetheless, our colleagues on the site had never reported witnessing this sexual behaviour until we
80 shared our video findings with them. The male lived among other males and did not appear to be part

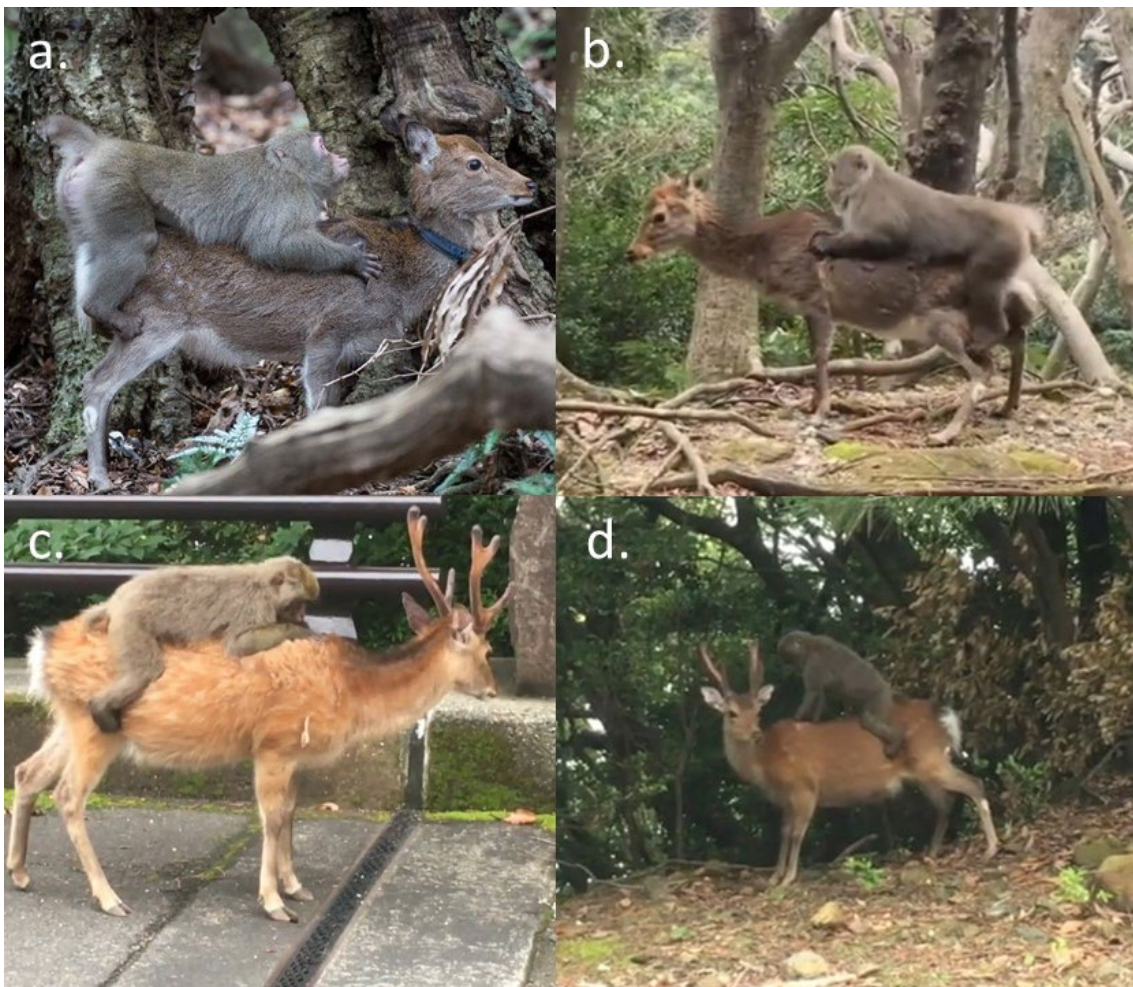
81 of a multi-male, multi-female group [2]. On November 6, the macaque male engaged in sexual activity
82 with at least two female Sika deer [2]. Notably, the macaque did not display aggression toward the deer
83 but actively chased away other peripheral macaque males that approached the 'guarded' deer. Its initial
84 interaction with one female deer involved mounting and displaying sexual behaviours with pelvic
85 thrusting, although penetration did not occur. However, when the male approached a second female
86 deer, her response was markedly different, as she resisted vehemently, attempting to evade him through
87 movement, increased speed, turning around, and displaying defensive behaviours. These behaviours
88 occurred at consistent intervals between the same macaque male and the same deer female, with a ten
89 mounts taking place approximately every 4–5 minutes over the course of an hour of observation before
90 the animals disappeared into the forest. The male subsequently attempted to mount another female
91 deer, which rejected the sexual advances. She tried to evade the macaque through movements,
92 accelerating her pace, turning around, and exhibiting threatening gestures. Interestingly, shortly after, a
93 2018 study revealed that five female macaques exhibited similar mounting behaviour toward male deer
94 in the Meiji Memorial Forest of Minoo Quasi-National Park, Minoo Prefecture, near Osaka, Japan – over
95 600 kilometres away from Yakushima. (Gunst et al. 2018). In October 2017, we (Marie Pelé and Cédric
96 Sueur) came back a week to Yakushima to assess whether the male macaque continued to display this
97 behaviour and whether a social transmission was observed but we only saw the male macaque closed
98 to a deer without sexual behaviour. During this week we observed from 9 a.m. to 5 p.m. macaques *ad*
99 *libitum*, going from group to group on the side of the unique road along the national park, identifying
100 from three to nine groups per day. We cannot provide detailed descriptions of each group since we were
101 unable to identify them specifically. Out of the numerous groups in Yakushima, only three are closely
102 monitored. Our knowledge is limited to certain individual identification and insights into the home range
103 and group size of macaques, with observations of up to nine groups per day. The density of macaques
104 in Yakushima is exceptionally high. Within the lowland coastal zone, ranging from 0 to 300 metres above
105 sea level, it is estimated that there were about 4.8 troops and between 62.4 to 99.8 monkeys per square
106 kilometre. To enhance the reliability of our observations based on video evidence provided by local
107 inhabitants and researchers, we have corroborated these recordings with extensive local knowledge of
108 the area's wildlife and the consistent behaviour patterns of the subjects over time. This approach has
109 allowed us to mitigate some of the limitations associated with the opportunistic nature of data collection.

110

111 **Cues indicating a propagation**

112 In 2020 and 2021, new videos were recorded by an inhabitant of Yakushima (Cameron Riki Joyce)
113 documenting interspecies sexual behaviour. No information had been disclosed about his daily visits to
114 the park, including key details such as the location and duration of the observations. On August 23,
115 2020, a male macaque looking like the one previously observed in 2015 and 2017 was seen riding a
116 female deer and engaging in sexual behaviour for nine seconds (figure 1b, Video 2). This male was
117 identified by his distinct almond-shaped eyes, though we cannot be certain, with 100% accuracy, that
118 he was the same individual. However, this does not affect the overall aim and conclusions of the study.
119 In the video, the male was not seen with any other macaques. However, on March 12, 2021, the male
120 was observed surrounded by other macaques, including one male, at least six females and three

121 juveniles (Video 3). On the same day, a young female climbed onto a male deer, quickly groomed it,
122 and then engaged in two sequences of sexual behaviours (with pelvic thrusting as behavioural units
123 lasting five and seven seconds, respectively), followed by an extended period of grooming the deer
124 (figure 1c, video 3). We defined a sequence of sexual behaviour as at least three consecutive pelvic
125 thrusting behaviour. Later, another female, older than the first one described (differentiated through the
126 body size and corpulence), also briefly engaged in a sequence of sexual behaviour with a male deer
127 before being ejected by the deer (figure 1d, video 4). On November 29, 2023, a female showed
128 mounting behaviour with pelvic thrusting on a male deer (video 5 provided by A.O., showcases the
129 activities within the national park during the week of November 27th, capturing moments from dawn until
130 dusk, observations were made *ad libitum*, going from group to group on the side of the road). The sexual
131 behaviour of females is not looking like the ones displayed with males but the ones displayed during
132 homosexual behaviours. These observations indicate two significant findings: firstly, if it indeed is the
133 original male observed in 2015, the macaque exhibited a continuation of the original behaviour, and
134 secondly, there is likely evidence of propagation (Duboscq et al. 2016) of this behaviour to other group
135 members. Notably, this propagation occurred between macaques of different sexes, from one male to,
136 at least, two females.



137
138 **Figure 1.** Cases of heterospecific sexual behaviour between Japanese macaques and Sika deer. *a.* First
139 observation made in 2015, a male macaque on a female deer. *b.* Second observation of the same male

140 *macaque on a female deer made in 2020. c. and d. Observation of female macaques on male deer*
141 *indicating a social transmission.*

142

143 **FUNCTIONAL ANALYSIS AND HYPOTHESES**

144 This rare instance of heterospecific sexual interaction attempt is categorised as one of the seven cases
145 of reproductive interference as defined by Gröning and Hochkirch (Gröning and Hochkirch 2008). In the
146 first observation and second observation, it involves sexual interaction between a male Japanese
147 macaque and a female Sika deer, although there was no penetration. In the other observations, it
148 involves female macaques and male deer. Unlike some cases of interspecific interactions that involve
149 sexual harassment or coercion (Clutton-Brock and Parker 1995), these behaviours appeared different;
150 the deer are always in the vicinity of macaques looking for food let by the macaques or eating the feces
151 of the monkeys (Tsuji et al. 2007; Nishikawa and Mochida 2010; Pelé et al. 2017). The female deer's
152 behaviour, specifically licking the macaque's seminal fluid, suggests that it might see this behaviour as
153 a source of nutrition. However, this hypothesis cannot explain why the male deer let females climb on
154 them. Having food from the macaques may be a reason why the deer allow this behaviour. We first
155 suggested that the hormonal surge during the macaque breeding season, coupled with their kind-of
156 cooperative interactions as grooming exchange and play with Sika deer, may have contributed to this
157 heterospecific sexual behaviour. Similar proximity and cooperation have been reported in other species,
158 such as Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*)
159 (Herzing and Elliser 2013). In our 2016 paper [1], we proposed alternative explanations for this
160 behaviour. One theory suggested it might serve as a learning mechanism for copulation. Another
161 considered the possibility of incomplete species recognition. Additionally, we introduced the 'mate
162 deprivation hypothesis', which posits that males with limited access to females might be more inclined
163 to engage in such behaviour. This hypothesis is particularly relevant in species facing intense sexual
164 competition. Similar patterns have been observed in other sexual behaviours among Japanese
165 macaques, such as masturbation [10] and homosexual behaviour [11]. However, these new
166 observations do not confirm these hypotheses, as the male continued having this interspecies sexual
167 behaviour while it belongs to a group where it seems to be the dominant as we observed the male in
168 the video chasing and threatening other group members.

169

170 **COGNITIVE ANALYSIS AND HYPOTHESES**

171 **Regarding the interspecies sexual behaviour**

172 Sexual behaviours observed among species can be attributed to their close proximity and frequent
173 interactions. Indeed, complex interspecific interactions have been observed in various species, ranging
174 from mixed-species groups to mutual exchanges of services between different species. These
175 interactions have been documented in different contexts and can have various benefits (Axelrod and
176 Hamilton 1981). For example, mixed-species groups can benefit from proximity to members of other
177 species, leading to indirect advantages such as increased vigilance against predators or access to
178 dropped fruits from trees (Tsuji et al. 2007; Nishikawa and Mochida 2010). In the case of Japanese
179 macaques and Sika deer on Yakushima Island, direct interactions occur and may have conducted to
180 these remarkable sexual behaviours between the two species. Indeed, the macaques drop food from

181 trees, which serves as an energy source for the deer, enhancing their foraging efficiency. This results
182 in a close cohabitation between the two species. Additionally, the deer engage in coprophagia by
183 consuming the feces of Japanese macaques, particularly around macaque sleeping sites. Some
184 macaques have even been observed grooming the deer and attempting to ride them without sexual
185 behaviour involved. Similar interactions have been reported between rhesus macaques and sambar
186 deer in India (PRASAD et al. 2013). The sexual behaviour may have emerged from the close proximity
187 and existing rodeo-like behaviours at a particular moment.

188

189 **Regarding the potential social transmission**

190 The observation of interspecies sexual behaviour between Japanese macaques and Sika deer has
191 unveiled complex interactions that suggest both cognitive capabilities and the potential for social
192 transmission of behaviours. Our analysis aims to clarify the distinction between the cognitive processes
193 inferred from these behaviours and our hypothesis on social transmission. (Whiten 2000; Hoppitt and
194 Laland 2013; Duboscq et al. 2016).

195 Cognitive Capacities and Behavioural Innovation: 1. Innovation in behaviour (Vancatova 2008; Aplin et
196 al. 2015): The initial sightings in 2015 suggested a novel aspect of macaque behaviour. Innovation
197 demonstrates macaque ability to innovate and adapt by seeking mating opportunities outside their
198 species. 2. Guarding behaviour (Vasey 2004; Gunst et al. 2018): The macaque's guarding behaviour
199 may indicate an understanding of competition for mates but also protect the deer as a non-reproductive
200 resource linked to social or play behaviour. 3. Differences in female responses (De Petrillo and Rosati
201 2021): The fact that female macaques have reproductive interference with male deer raise questions
202 about the ability of animals to discern between different mating partners. This implies some level of
203 cognitive processing in their decision-making.

204 Social Transmission Hypothesis (Hoppitt and Laland 2013; Duboscq et al. 2016): The behaviours
205 observed in 2020 and extending to 2023, where macaques of both sexes exhibited similar interspecies
206 interactions, may support the hypothesis of social learning and transmission. The spread of this
207 behaviour across different individuals, potentially from male to female, indicates a sophisticated level of
208 social learning, showing an openness to adopting non-instinctual behaviours.

209 Study limitations: We recognise the limitations posed by the opportunistic nature of our observations,
210 including the potential for previous unrecorded instances of this behaviour among females before 2015.
211 The absence of long-term, continuous observation precludes definitive conclusions about the origins
212 and spread of this behaviour among individual macaques. Despite these limitations, our interpretation
213 of the data as suggestive evidence of social transmission is based on the observed emergence of
214 behaviour in multiple individuals within the same social group, a pattern that aligns with documented
215 instances of social learning in non-human primates. While we cannot definitively rule out individual
216 learning or independent innovation as explanations for the observed behaviour, the simultaneous
217 occurrence in closely associated individuals suggests a social component to the behaviour's acquisition.
218 Our suggestion of social transmission is also informed by comparative analysis with documented cases
219 of social learning in primates, where behaviours spread through observation and imitation within social

220 groups. We also acknowledge the possibility of alternative explanations for the observed behaviour,
221 including individual learning or a shared environmental influence.

222

223 **EVOLUTIONARY CONSIDERATIONS**

224 Interspecific interactions in animals can have both negative and positive outcomes. Negative
225 interactions are exemplified by prey-predator relationships (Freedman and Waltman 1984), where one
226 species benefits at the expense of the other. Positive interactions are seen in mutualism (Axelrod and
227 Hamilton 1981), where both species benefit. Heterospecific sexual behaviour, which involves sexual
228 interactions between individuals of different species, has been mainly described in closely related
229 species and has been studied in terms of its effects on fitness, hybridisation, and species survival
230 (Burdfield-Steel 2012; Kyogoku 2015; Shuker et al. 2015). There have been few documented cases of
231 heterospecific mating between individuals of distantly related species, and these instances have
232 primarily occurred in captive or human-animal interaction settings (Beetz 2004; Gröning and Hochkirch
233 2008; Beirne 2009). One study reports sexual harassment of king penguins by Antarctic fur seals, where
234 some penguins were killed and eaten at the end of the mating behaviour (de Bruyn et al. 2008; Haddad
235 et al. 2015). The study underscores the relative scarcity of research on interspecies sexual behaviour,
236 particularly among distant species in natural settings. It also highlights the potential consequences and
237 complexities associated with such interactions, which can range from fitness implications to survival
238 challenges, depending on the circumstances and species involved. The rarity of heterospecific sexual
239 interactions between distant species makes our observations significant, providing insights into the
240 evolution of interspecific mating behaviour in the animal kingdom and its potential relevance to
241 understand zoophilia in humans (Beetz 2004; Beirne 2009).

242 This interspecies sexual behaviour, if it is socially transmitted, which seem probable given past cultural
243 behaviours observed in macaques, may represent a form of cultural transmission among the macaques.
244 This cultural transmission can have profound implications for the evolutionary trajectory of a group (van
245 Schaik et al. 2012; Mattei 2014; Henrich 2017). It may allow for the spread of novel behaviours that
246 provide adaptive advantages. Cultural behaviours are well documented in Japanese macaques
247 (Bonney et al. 2016), with some serving practical functions, such as the use of hot springs for bathing
248 (Zhang et al. 2007), washing potatoes (Matsuzawa 2015), or forming strong aggregations known as
249 'saru-dango.' However, the functionality of certain other traditions, such as the stone-handling behaviour
250 (Leca et al. 2007; Huffman et al. 2010) or these heterospecific sexual interactions, remains a topic of
251 ongoing debate. These behaviours, nonetheless, illuminate the intricate social and cultural lives of
252 Japanese macaques. As researchers, it is imperative that we delve deeper into our observations and
253 analyses of these behaviours.

254

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263

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265 may have influenced the material presented in this article.

266

267 Availability of material:

268 Video 1: <https://youtu.be/l8HFDnM7Sdw?si=qdaFyeCqfRTRh9pP;>

269 Video 2: <https://youtube.com/shorts/wfDasKQICb0?si=85BG8v5F7PxxvMbmK> ;

270 Video 3: https://youtube.com/shorts/qK1SEW106D8?si=aNxzkhZ_uXldhBH ;

271 Video 4: https://youtu.be/peYCBla0fpk?si=L_5M_BoEzRTborHw ;

272 Video 5: https://youtu.be/Df0lw_tBRu8

273

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276

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