

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

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Abstract: This naturalistic note presents a series of observation of interspecies sexual behaviour involving Japanese macaques (*Macaca fuscata yakui*) and Sika deer (*Cervus Nippon yakushimae*) on Yakushima Island, Japan. The initial observation in 2015 revealed a male macaque's attempt to engage in sexual activity with female deer, displaying mate-guarding behaviour. Subsequent observations in 2020, 2021 and 2023 showed the continuation of this behaviour and potentially the propagation to other macaques. We categorised this rare behaviour as a case of reproductive interference and explored hypotheses regarding its functionality. While some suggest nutritional benefits for the deer, others propose learning, incomplete species recognition, or mate deprivation hypotheses. This behaviour may also be selectively neutral, offering no direct fitness benefits, but rather represents a behavioural by-product of other interactions between these two species, which may themselves be adaptive. Furthermore, we hypothesise that the observed propagation may underlie social transmission and highlight the potential cognitive capacities of Japanese macaques involving social learning mechanisms and the willingness to adopt non-instinctual behaviours.



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Introduction

Animal culture refers to behaviours, practices, and traditions that are learned socially within a species and passed down through generations. These behaviours, which are not inherited genetically but through social learning, challenge the belief that culture is unique to humans and offers insights into animal behaviour, evolution, and conservation (Whiten 2000; Laland and Janik 2006; Whiten and Schaik 2007; Duboscq et al. 2016). Animals, like humans, develop and transmit cultural traits, with different populations exhibiting distinct behaviours. For example, some chimpanzees use sticks to fish for termites, while others use stones to crack nuts, illustrating the variation in cultural behaviours between populations (Whiten et al. 1999, 2005, 2007; Biro et al. 2006; Matsuzawa 2017). The concept of animal culture originated in primatology, particularly through Kinji Imanishi's study of Japanese macaques in the mid-20th century. Imanishi's team observed the spread of potato-washing behaviour among macaques, providing the first documented example of cultural transmission in animals (Kawai 1965; Matsuzawa 2015). Jane Goodall's work with chimpanzees (*Pan troglodytes*) in the 1960s further solidified the idea of animal culture, particularly through her discovery of tool use, which was learned and transmitted socially within groups (Goodall 1986; Whiten et al. 1999). Since then, animal culture has been observed across various species. Humpback whales (*Megaptera novaeangliae*), for instance, exhibit cultural transmission through their songs (Garland et al. 2011), while New Caledonian crows (*Corvus moneduloides*) demonstrate cultural tool use (Rutz et al. 2018). Even species like fruit flies (*Drosophila sp.*) display cultural traditions in mate choice (Battesti et al. 2015). These findings highlight the importance of cultural diversity in animal conservation, emphasising that preserving cultural knowledge is as vital as protecting genetic diversity (Carvalho et al. 2022; Sueur 2022).

JAPANESE MACAQUES AND SIKA DEER CULTURES

Direct interactions between Japanese macaques and Sika deer provide a compelling example of the evolution of interspecies relationships. Initially, these species coexisted closely in terms of spatial proximity, with both benefiting from this arrangement. For instance, macaques, while feeding in trees, often drop food, which becomes an additional energy source for the deer, enhancing their foraging efficiency through gleaning (Tsuji et al. 2007). This interaction fosters a strong cohabitation dynamic between the two species. A particularly unusual aspect of this relationship is the deer's coprophagia, where deer consume the feces of macaques, especially around the latter's sleeping sites (Nishikawa and Mochida 2010). As their relationship change, some macaques have been observed grooming deer, a behaviour that suggests a deepening bond between the species. On Yakushima Island, this interaction has advanced into a co-culture (Co-culture is the mutual evolution of shared behaviours between different species that influence each other through direct or indirect interactions in a shared environment) (Sueur and Huffman 2024), with macaques even riding on the backs of Sika deer (Pelé et al. 2017). Similar behaviours have been observed between rhesus macaques (*Macaca mulatta*) and sambar deer (*Rusa unicolor*), suggesting that such complex interspecies interactions may arise in other environments and among different species (Prasad et al. 2013). Interestingly, these interactions have even led to interspecies sexual behaviours, as observed in both Yakushima and the Minoh Prefecture in Japan. Male macaques have been documented engaging in sexual activity with female Sika deer, and conversely, female macaques with male deer (Gunst et al. 2018). These instances illustrate the capacity for highly complex and unexpected behaviours to emerge between species living in close proximity. The evolution of their interactions –

ranging from shared foraging and grooming to more intricate behaviours like riding and interspecies sexual activities – demonstrates significant social and behavioural adaptation between these two distinct species. These behaviours are categorised as ‘highly complex’ due to the active feedback loops between the species, which foster reciprocal adaptations, and the layered nature of their interactions – from foraging and grooming to intricate behaviours like riding and interspecies sexual activities – indicating cognitive processes, social transmission, and behavioural innovation that evolve through mutual influence. They appear to learn from one another and have developed co-cultural behaviours (Sueur and Huffman 2024).

BEHAVIOURAL ANALYSIS

Original study

During his presence on Yakushima Island, Japan, from October 10 to November 6, 2015, the photographer Alexandre Bonnefoy observed for the first time the intriguing behaviour of an adult male Japanese macaque (figure 1a, Video 1). A timeline and a map are present in figure 2. This male, seemingly a peripheral member or part of a group of peripheral males (Sprague 1991), exhibited a case of heterospecific sexual behaviour, characterised by the mounter performing pelvic thrusting (i.e. rhythmic movements of the mounter’s pelvic girdle toward the mountee’s back or hindquarter). While this behaviour was documented for the first time in our study (Pelé et al. 2017), it does not mean that it did not exist before our observation. Nonetheless, our colleagues on the site had never reported witnessing this sexual behaviour until we shared our video findings with them. The male lived among other males and did not appear to be part of a multi-male, multi-female group. On November 6, the macaque male engaged in sexual activity with at least two female Sika deer. Notably, the macaque did not display aggression toward the deer but actively chased away other peripheral macaque males that approached the ‘guarded’ deer. Its initial interaction with one female deer involved mounting and displaying sexual behaviours with pelvic thrusting, although penetration did not occur. These behaviours occurred at consistent intervals between the same macaque male and the same deer female, with about ten mounts taking place approximately every 4–5 minutes over the course of an hour of observation before the animals disappeared into the forest. The male subsequently attempted to mount another female deer, which rejected the sexual advances. She tried to evade the macaque through movements, accelerating her pace, turning around, and exhibiting threatening gestures. Interestingly, shortly after, a 2018 study revealed that five female macaques exhibited similar mounting behaviour toward male deer in the Meiji Memorial Forest of Minoh Quasi-National Park, Minoh Prefecture, near Osaka, Japan – over 600 kilometres away from Yakushima (Gunst et al. 2018).

In October 2017, we (Marie Pelé and Cédric Sueur) came back for a week to Yakushima to assess whether the male macaque continued to display this behaviour and whether social transmission was observed, but we only saw the male macaque close to a deer without sexual behaviour. During this week we observed from 9 a.m. to 5 p.m. macaques *ad libitum*, going from group to group on the side of the unique road along the national park, identifying from three to nine groups per day. We cannot provide detailed descriptions of each group since we were unable to identify them specifically. Out of the numerous groups in Yakushima, only three are closely monitored. Our knowledge is limited to certain individual identification and insights into the home range and group size of macaques, with observations of up to nine groups per day. The density of macaques in Yakushima is exceptionally high. Within the lowland coastal zone, ranging from 0 to 300 metres above sea level, it is estimated that there were about 4.8 troops and between 62.4 to 99.8 monkeys per square kilometre. To

enhance the reliability of our observations based on video evidence provided by local inhabitants and researchers, we have corroborated these recordings with extensive local knowledge of the area's wildlife and the consistent behaviour patterns of the subjects over time. This approach has allowed us to mitigate some of the limitations associated with the opportunistic nature of data collection.

Cues indicating a propagation

In 2020 and 2021, new videos were recorded by an inhabitant of Yakushima (Cameron Riki Joyce) documenting interspecies sexual behaviour. No information had been disclosed about his daily visits to the park, including key details such as the location and duration of the observations. On August 23, 2020, a male macaque looking like the one previously observed in 2015 and 2017 was seen riding a female deer and engaging in sexual behaviour for nine seconds (figure 1b, Video 2). This male was identified by his distinct almond-shaped eyes, though we cannot be certain, with 100% accuracy, that he was the same individual. However, this does not affect the overall aim and conclusions of this note. In the video, the male was not seen with any other macaques. However, on March 12, 2021, the male was observed surrounded by other macaques, including one male, at least six females and three juveniles (Video 3). On the same day, a young female climbed onto a male deer, quickly groomed it, and then engaged in two sequences of sexual behaviours (with pelvic thrusting as behavioural units lasting five and seven seconds, respectively), followed by an extended period of grooming the deer (figure 1c, video 3). We defined a sequence of sexual behaviour as at least three consecutive pelvic thrusting behaviour. Later, another female, older than the first one described (differentiated through the body size and corpulence), also briefly engaged in a sequence of sexual behaviour with a male deer before being ejected by the deer (figure 1d, video 4). On November 29, 2023, a female exhibited mounting behaviour with pelvic thrusting on a male deer. Video 5, provided by A. Otsuyuki Ohshima, showcases activities within the national park during the week of November 27, capturing moments from dawn until dusk. Observations were made *ad libitum*, moving between groups along the roadside.

The sexual behaviour displayed by female macaques toward male deer differs from the typical mating behaviours observed with male macaques, as the pelvic movements are slower, less rhythmic, and lack the thrusting intensity usually seen in heterosexual interactions. Instead, these movements resemble the slower pelvic motions often observed in female-female homosexual interactions among macaques. These observations indicate two significant findings: firstly, if it indeed is the original male observed in 2015, the macaque exhibited a continuation of the original behaviour, and secondly, these observations suggest possible propagation (Duboscq et al. 2016) of this behaviour to other group members though further data and evidence are needed to confirm this transmission. Notably, this propagation occurred between macaques of different sexes, from one male to, at least, two females.

The appearance of rare and unique behaviours, such as the interspecies interactions documented here, highlights the value of non-standard methods like citizen science. As we see in this study, videos captured by photographers and tour guides provide invaluable insights, serving as powerful complements to rigorous scientific methods and expanding the scope of discovery beyond standard observational approaches alone (Silvertown 2009; Nelson and Fijn 2013; Sueur et al. 2020; Fraisl et al. 2022).

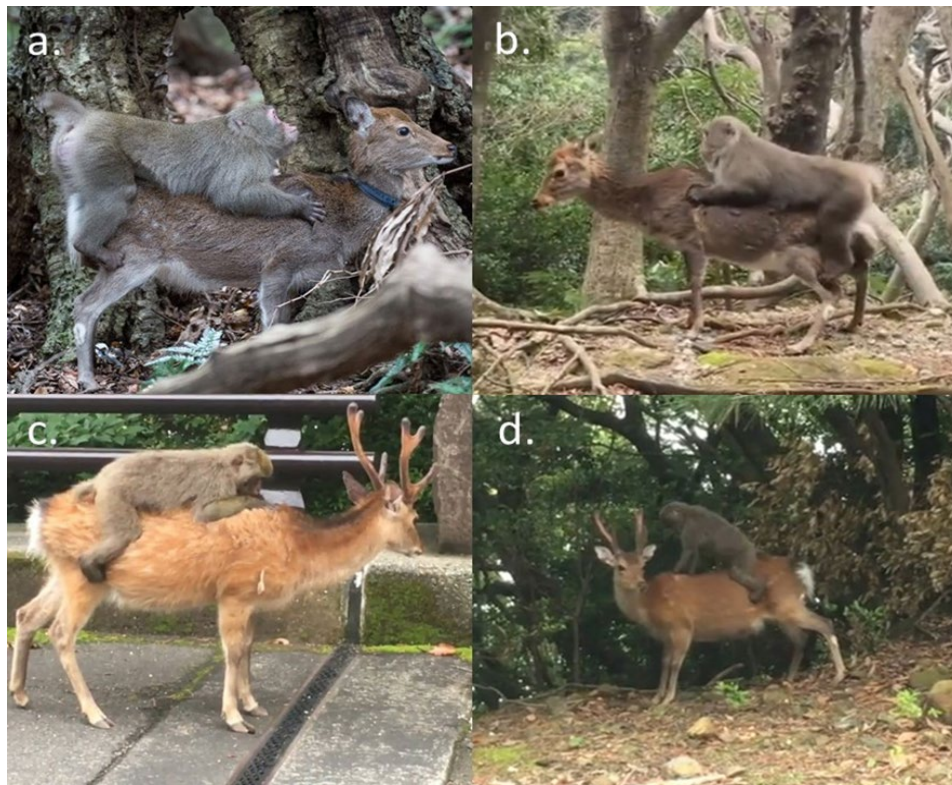


Figure 1. Cases of heterospecific sexual behaviour between Japanese macaques and Sika deer. a. First observation made in 2015, a male macaque on a female deer. b. Second observation of probably the same male macaque on a female deer made in 2020. c. and d. Observation of female macaques on male deer indicating a social transmission.

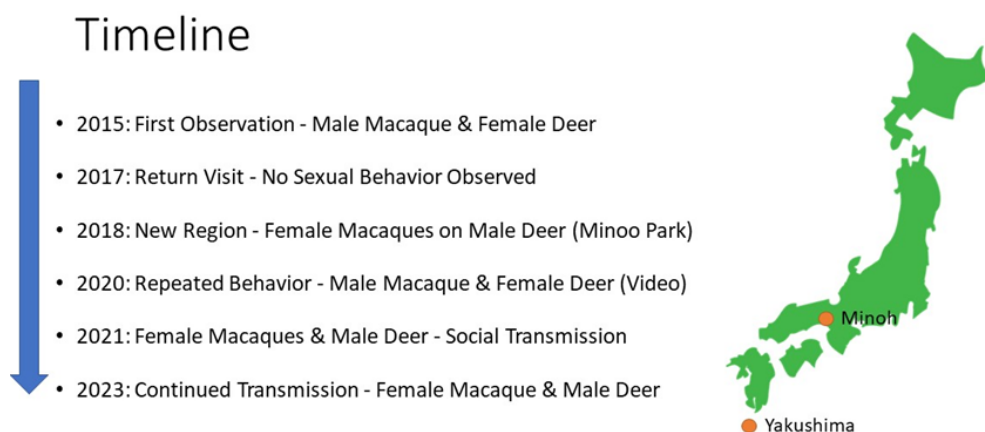


Figure 2: timeline and maps of events. 2015: The first observation of interspecies sexual behaviour between a male Japanese macaque and a female Sika deer on Yakushima Island was documented. The male macaque displayed mating behaviours toward the deer without aggression, guarding the deer against other male macaques. 2017: Cédric Sueur and Marie Pelé returned to Yakushima for a week to assess whether the male macaque continued this behaviour and to observe potential social transmission. However, no further sexual behaviour was observed during this visit. 2018: Observations in the Meiji Memorial Forest of Minoh Quasi-National Park near Osaka (over 600 km from Yakushima) documented five female Japanese macaques displaying similar mounting behaviour toward male deer, indicating a spread of this behaviour to other regions and individuals. 2020: A video recorded by a Yakushima resident (Cameron Riki Joyce) captured a male macaque engaging in sexual behaviour with a female deer for nine seconds. The male macaque was identified by unique physical features but could

not be definitively confirmed as the same individual observed in 2015 and 2017. 2021: Another video captured a young female macaque climbing onto a male deer, engaging in grooming and short sequences of mating-like behaviours, followed by grooming. Later, an older female macaque also briefly displayed similar behaviour with a male deer, suggesting possible social transmission. 2023: On November 29, a female macaque was observed displaying mounting behaviour with pelvic thrusting on a male deer. This observation further supported the possibility of social transmission, as behaviours now involved both male and female macaques.

FUNCTIONAL ANALYSIS AND HYPOTHESES

This rare instance of heterospecific sexual interaction attempt is categorised as one of the seven cases of reproductive interference as defined by Gröning and Hochkirch (2008). They define reproductive interference as any interspecific interaction occurring during mate acquisition that detrimentally impacts the fitness of at least one species involved, resulting from incomplete species recognition. They categorise reproductive interference into seven distinct types: signal jamming, heterospecific rivalry, misdirected courtship, heterospecific mating attempts, erroneous female choice, heterospecific mating, and hybridisation. However, the likelihood that Japanese macaques misrecognise sika deer as conspecific is minimal. This improbability is underscored by the long-term coexistence and frequent interactions these two species share on Yakushima Island. Instead, the observed interspecies interactions, including sexual behaviours, likely emerge from the close proximity and the complex, reciprocal interspecies dynamics that have developed, rather than from errors in species recognition.

The first observation and second observations involve sexual interaction between a male Japanese macaque and a female Sika deer, although there was no penetration. In the other observations, it involves female macaques and male deer. Unlike some cases of interspecific interactions that involve sexual harassment or coercion (Clutton-Brock and Parker 1995), these behaviours appeared different; the deer are always in the vicinity of macaques looking for food left by the macaques or eating the feces of the monkeys (Tsuji et al. 2007; Nishikawa and Mochida 2010; Pelé et al. 2017). The female deer's behaviour, specifically licking the macaque's seminal fluid, suggests that it might see this behaviour as a source of nutrition. However, this hypothesis cannot explain why the male deer let females climb on them. We first suggested that the hormonal surge during the macaque breeding season, coupled with their kind-of cooperative interactions as grooming exchange and play with Sika deer, may have contributed to this heterospecific sexual behaviour. In our 2017 paper (Pelé et al. 2017), we proposed alternative explanations for this behaviour. One theory suggested it might serve as a learning mechanism for copulation. Another considered the possibility of incomplete species recognition which is quite improbable. Additionally, we introduced the 'mate deprivation hypothesis', which posits that males with limited access to females might be more inclined to engage in such behaviour. This hypothesis is particularly relevant in species facing intense sexual competition. Similar patterns have been observed in other sexual behaviours among Japanese macaques, such as masturbation (Thomsen and Soltis 2004) and homosexual behaviour (Leca et al. 2015).

However, these new observations do not confirm these hypotheses. The male continued displaying interspecies sexual behaviour despite appearing to be dominant within his group, as shown in the video where he is seen chasing and threatening other group members. This behaviour may also be selectively neutral, offering no direct fitness benefits, but rather represents a behavioural by-product of other interactions between these two species, which may themselves be adaptive.

COGNITIVE ANALYSIS AND HYPOTHESES

Regarding the interspecies sexual behaviour

Sexual behaviours observed among species can be attributed to their close proximity and frequent interactions. Indeed, complex interspecific interactions have been observed in various species, ranging from mixed-species groups to mutual exchanges of services between different species. These interactions have been documented in different contexts and can have various benefits (Axelrod and Hamilton 1981). For example, mixed-species groups can benefit from proximity to members of other species, leading to indirect advantages such as increased vigilance against predators or access to dropped fruits from trees (Tsuji et al. 2007; Nishikawa and Mochida 2010). In the case of Japanese macaques and Sika deer on Yakushima Island, direct interactions occur and may have conducted to these remarkable sexual behaviours between the two species. Indeed, the macaques drop food from trees, which serves as an energy source for the deer, enhancing their foraging efficiency. This results in a close cohabitation between the two species. Additionally, the deer engage in coprophagia by consuming the feces of Japanese macaques, particularly around macaque sleeping sites. Some macaques have even been observed grooming the deer and attempting to ride them without sexual behaviour involved. Similar interactions have been reported between rhesus macaques and sambar deer in India (Prasad et al. 2013). The sexual behaviour may have emerged from the close proximity and existing rodeo-like behaviours at a particular moment.

Regarding the potential social transmission

The observation of interspecies sexual behaviour between Japanese macaques and Sika deer has revealed complex interactions that point to both cognitive capabilities and the potential for social transmission of behaviours. The objective here is to clarify the differences between the cognitive processes implied by these behaviours and the hypothesis regarding social transmission (Whiten 2000; Hoppitt and Laland 2013; Duboscq et al. 2016). Regarding cognitive capacities and behavioural innovation, the initial sightings in 2015 suggested a novel aspect of macaque behaviour, although it is unlikely to be the first occurrence of this innovation given the absence of systematic, long-term data collection and similar behaviours observed in other populations. However, this was the first documented instance, as other colleagues regularly present in the field had never previously observed it. These innovations illustrate the macaques' ability to adapt and innovate by exploring mating opportunities outside their species, an indicator of behavioural flexibility and curiosity (Vancatova 2008; Aplin et al. 2015). Additionally, the guarding behaviour observed may reflect a level of understanding in managing competition for mates. This guarding may serve not only as a reproductive strategy but also as a way to protect the deer as a social or play-related resource rather than as a direct mating partner (Vasey 2004; Gunst et al. 2018). The different responses observed in female macaques engaging in reproductive interference with male deer also raise intriguing questions about their ability to discern between potential mating partners. This behaviour implies that some level of cognitive processing may be influencing their decision-making processes in these interactions (De Petrillo and Rosati 2021).

The social transmission hypothesis is supported by observations from 2020 to 2023, during which macaques of both sexes exhibited similar interspecies interactions. These findings may align with the hypothesis that social learning and transmission are at play, as the spread of this behaviour across different individuals, potentially from males to females, suggests an advanced form of social learning.

This behaviour indicates that macaques may be open to adopting behaviours culturally transmitted in this species (Zhang and Watanabe 2007, Zhang et al. 2007, Huffman et al. 2010).

We recognise the limitations posed by the opportunistic nature of our observations, including the potential for previous unrecorded instances of this behaviour among females before 2015. The absence of long-term, continuous observation precludes definitive conclusions about the origins and spread of this behaviour among macaques. Despite these limitations, our interpretation of the data is suggestive evidence of behaviour in multiple individuals within the same social group, a pattern that aligns with documented instances of social learning in non-human primates. While we cannot definitively rule out individual learning or independent innovation as explanations for the observed behaviour, the simultaneous occurrence in closely associated individuals suggests a social component to the behaviour's acquisition. Our suggestion of social transmission is also informed by comparative analysis with documented cases of social learning in primates, where behaviours spread through observation and imitation within social groups. We also acknowledge the possibility of alternative explanations for the observed behaviour, including individual learning or a shared environmental influence as some studies have not found any evidence of observational learning or imitation in primates (Nagell et al. 1993, Tomasello and Call 1994, Call et al 2005, Tennie et al 2006, Clay and Tennie 2018, Neadle et al. 2021).

To fully understand the learning mechanisms underlying this behaviour, additional data would be required on several fronts, as noted by reviewers. First, establishing the timing of behaviour innovation and duration within the group is critical; although we noted the first recorded occurrence in 2015, this likely does not reflect the initial appearance of deer mounting. Second, without continuous monitoring, it remains unclear if other individuals practised this behaviour prior to the second observation, when females were noted engaging in deer mounting. We, therefore, lack data on the original innovator of the behaviour and the potential pathways of social transmission within the group, if any. It is equally possible that all members began engaging in this behaviour independently, with no social learning involved. To rigorously assess the role of learning, controlled experimental data would be essential, ideally involving naïve individuals exposed to social stimuli in a controlled setting. These experiments would require testing individuals confirmed to be naïve to deer mounting and systematically introducing the behaviour to discern the mechanisms behind its emergence. Given that this behaviour has also been observed in a separate group of macaques (Gunst et al. 2018), a simpler assumption may be that complex social learning mechanisms are not required for this behaviour to manifest; rather, exposure to the stimulus – in this case, the deer – may be sufficient for its appearance.

EVOLUTIONARY CONSIDERATIONS

Interspecific interactions in animals can have both negative and positive outcomes. Negative interactions are exemplified by prey-predator relationships (Freedman and Waltman 1984), where one species benefits at the expense of the other. Positive interactions are seen in mutualism (Axelrod and Hamilton 1981), where both species benefit. Heterospecific sexual behaviour, which involves sexual interactions between individuals of different species, has been mainly described in closely related species and has been studied in terms of its effects on fitness, hybridisation, and species survival (Burdfield-Steel 2012; Kyogoku 2015; Shuker et al. 2015). There have been few documented cases of heterospecific mating between individuals of distantly related species, and these instances have primarily occurred in captive or human-animal interaction settings (Beetz 2004; Gröning and Hochkirch 2008; Beirne 2009). One study reports sexual harassment of king penguins by Antarctic

fur seals, where some penguins were killed and eaten at the end of their mating behaviour (de Bruyn et al. 2008; Haddad et al. 2015). This note underscores the relative scarcity of research on interspecies sexual behaviour, particularly among distant species in natural settings. It also highlights the potential consequences and complexities associated with such interactions, which can range from fitness implications to survival challenges, depending on the circumstances and species involved (Sueur and Huffman 2024). The rarity of heterospecific sexual interactions between distant species makes our observations significant, providing insights into the evolution of interspecific mating behaviour in the animal kingdom and its potential relevance to understand zoophilia in humans (Beetz 2004; Beirne 2009).

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

CONCLUSION

In conclusion, this note on interspecies interactions between Japanese macaques and Sika deer on Yakushima Island reveals a complex dynamic that extends beyond mere coexistence. The documented instances of macaques engaging in heterospecific behaviours with deer, including grooming, riding, and sexual behaviours, suggest significant cognitive and social dimensions. These interactions highlight the adaptability and behavioural innovation within macaque populations, which may stem from close proximity and regular interspecies encounters. The possibility of social transmission of these behaviours among macaques implies that such interactions could become culturally embedded within specific groups, similar to previously documented cultural behaviours. While heterospecific sexual behaviour is rare and has largely been observed in closely related species, its occurrence here offers insights into the cognitive and social flexibility of macaques. However, these findings remain preliminary due to the opportunistic nature of observations. Further research is needed to determine the mechanisms underlying these behaviours, their evolutionary implications, and the potential for social learning among individuals. This note adds a unique dimension to our understanding of animal culture and cross-species interactions, urging a deeper exploration of how such behaviours evolve and persist in animal societies.

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Availability of material:

Video 1: [https://youtu.be/l8HFDnM7Sdw?si=qdaFyeCqfRTRh9pP](https://youtu.be/l8HFDnM7Sdw?si=qdaFyeCqfRTRh9pP;);

Video 2: <https://youtube.com/shorts/wfDaskQICb0?si=85BG8v5F7PxxvMbmK> ;

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

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

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

Authors' contributions: Data curation: AO, CS & MP. Visualisation: CS & MP. Original draft: CS. Writing, review and editing: AO, CS & MP.

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