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## **Co-Cultures: Exploring Interspecies Culture Among Humans and Other Animals**

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### **Abstract**

The concept of 'co-culture' is introduced as a novel framework for understanding the mutual cultural evolution between animal species, including, but not only, humans. It explores the dynamics of interspecies interactions, particularly in how different species influence each other's behavioural and cognitive adaptations. Various instances of interspecies cultural exchange are highlighted such as the acquisition of medicinal plants from animals resulting in a shared medicinal culture, adaptive behaviours of urban wildlife, and cooperative behaviours between animal species. Co-culture challenges the notion of species-specific culture, underscoring the complexity and interconnectedness of human and animal societies, and between animal societies. Further research into co-culture is advocating and emphasising its implications for conservation, urban planning, and a deeper understanding of animal cognition and behaviour.

**Keywords:** learning, niche construction, cultural evolution, cultural coadaptation

## Learning in animal cultures

Responses to new situations across different environments in the animal kingdom have increasingly been the focus of study, underscoring the extensive and intricate nature of interspecies interactions. Interspecific **learning** (see **Glossary and Box 1**), where animals can acquire and adopt novel behaviours from other species [1,2], demonstrates the fluidity and adaptability of animal behaviour in the face of interactions with different species. For instance, studies have shown that wild songbirds utilise networks of interaction between species to spread information, influencing their survival tactics and behaviours [3]. However, much of the existing research has focused predominantly on one species adapting and modifying its behaviour in response to another, while the process might be more accurately described as bidirectional. In this context, we introduce the concept of '**co-culture**' or interspecies culture.

## Defining the concept of co-culture

In their pioneering work, Marzluff and Angell [8] introduced the concept of cultural **coevolution**. Despite its significance, research on 'co-culture' in human and animal evolution remains limited. This coevolution involves humans and other culturally developing species with a cultural process on both sides. Interactions between humans and these species can accelerate cultural evolution for both. Additionally, this process, although not well documented, can occur between non-human species as well. The concept suggests concurrent and reciprocal behavioural development between different species, visible in some populations, leading to joint cultural evolution over time (figure 1) [4]. For co-culture to manifest, it is essential for the populations of both species involved to occupy the same geographical space and to participate in either direct or indirect interactions.

The co-culture concept not only implies that two cultures are co-evolving in two populations sharing spaces and interacting, meaning a cultural drive on both sides, but that the two populations are sharing a common culture, or that their cultures are strongly influenced by the other's due to the synchrony of activities. Co-culture implies a deeper level of interaction where behaviours and knowledge are not only observed and assimilated but where the behaviours of one species actively shape the cultural evolution of another, and vice versa. Both species truly interact and may change and adapt their behaviours actively. This framework aligns with and extends the concepts of co-creation and coevolution [5] in understanding how linked processes lead to the formation of new cultural and genetic coevolution. It also considers how these processes are intertwined with cultural and ecosystem changes over time. This reflects a dynamic and mostly symbiotic evolution of interspecies relationships, underlining the interactive and interdependent nature of these associations. Furthermore, due to their adaptable nature, cultures are prone to rapid transformations in response to the changing dynamics of ecological or social environments. This fluidity propels a cycle of dynamic interactions and fine-tuning to the local environment, highlighting the malleable and responsive character of these interspecies relationships [4]. Co-culture can be seen as a specific form of **niche construction**, where the focus is on cultural modifications of the niche (figure 1) [6].

The concept of co-culture, while resonating with aspects of Cultural Niche Construction, extends beyond it by highlighting the reciprocal and evolving behaviors among non-human animals. Unlike Cultural Niche Construction, co-culture explicitly emphasizes the parallel cultural adaptation between populations, showcasing the dynamic interplay and mutual cultural processes across species boundaries [7]. While Cultural Niche Construction encompasses various elements present in co-culture, it does not explicitly underscore the intricate and synchronous cultural adaptation observed between populations, a distinctive feature accentuated by the concept of co-culture.

### **Drivers of co-cultures**

Interspecies learning (Box 1) is a driver of co-culture but this learning may be favoured and developed into stronger and more complex interactions between species in some conditions:

- **Mixed groups and interspecies proximity**

Mixed species groups of bats roosting in Costa Rica's rainforests reveal that bats' roosting choices are influenced by the presence of other bat species (twelve in total), suggesting benefits like thermoregulation and interspecific information transfer [8]. Mixed-species associations [9] (Box 2 for an example) formed by groups of two or more species that coordinate their activities for the benefit of feeding and predator defence in a shared habitat [10] demonstrate a wide range of interspecies interactions, from similar species gaining group-size-related benefits to different species providing complementary advantages. Due to the lack of historical studies, we cannot definitively label these instances as co-culture; however, they do showcase some form of interaction and learning between species.

- **Urban environments**

The novel behaviours of animals in urban environments are a specific case of interspecies learning between animals and humans. Japanese macaques' behaviours, influenced by human interactions, exemplify co-culture. In designated monkey parks, feeding by keepers fosters peaceful coexistence [11]. Conversely, in areas where macaques are seen as pests, aggressive human actions provoke fear or hostility. These cases showcase diverse co-cultural dynamics between humans and macaques [12]. This phenomenon of co-culture, reflecting varying degrees of pacifism or aggression, is not limited to Japanese macaques but is also evident in interactions between humans and other primate species, such as rhesus macaques (*Macaca mulatta*) and gray langurs (*Semnopithecus entellus*) in India [13], toque macaques (*Macaca sinica*) and purple-faced langurs (*Semnopithecus vetulus*) in Sri Lanka [14], and chacma baboons (*Papio ursinus*) in South Africa [15]. These examples underscore the broader concept of human-wildlife coexistence in urban and anthropogenic environments, where shared behaviours and adaptations emerge from the ongoing interaction between species. These co-cultures are majority symbiotic coadaptations in our mind but can also be not symbiotic but negative as farmers and maize-stealing crows, tourists, and bears or corvids [16]. It is essential to recognise that for a cultural process to be considered co-culture, there must be a mutual adaptation from both involved parties. Simply put, if humans alter their architectural styles and birds adjust by nesting in new locations

representative of nesting environments similar to what they used previously, this represents a unidirectional change, not fitting the criteria of co-culture. True co-culture occurs when both species modify their behaviours or practices in response to one another - for example, humans changing architectural designs and birds adapting their nesting habits in tandem.

### **Co-culture cases**

#### **- Finding resources**

The concept of co-culture in interspecies interactions is exemplified in several remarkable examples that underscore its importance. A notable instance is the mutualism between humans and the greater honeyguide (*Indicator indicator*) in Tanzania and Mozambique [17]. In this unique interaction, honeyguides lead humans to honeybee (*Apis mellifera*) nests, with humans harvesting honey and bee larvae while the birds feed on beeswax. This relationship is facilitated by specialised communication sounds, with recent studies showing honeyguides responding preferentially to local signals, suggesting cultural coevolution with cultural process on both sides [18]. Another example is the common raven (*Corvus corax*) strategic association with grey wolves (*Canis lupus*), particularly in winter [19]. Ravens may signal wolves to the location of carcasses, benefiting from their ability to tear the flesh apart. This behaviour showcases a sophisticated level of interspecies interaction and adaptation. In the high alpine oak forests of the western Himalayas, Himalayan black bears (*Ursus thibetanus*) with young cubs will follow below on the ground picking up the highly nutritious acorns dropped to the ground by central Himalayan langur (*Semnopithecus schistaceus*) groups foraging in the trees; avoiding the risk of infanticide by not leaving their cubs unprotected on the ground [20].

#### **- Cooperative hunting**

Cooperative hunting among different species illuminates the concept of 'co-culture', where distinct animal groups adapt behaviours for mutual benefit. A classic example is the collaboration between humans and bottlenose dolphins (*Tursiops aduncus*) in fishing, where dolphins herd fish towards the shore, signalling fishermen to cast their nets, enhancing foraging success for both [21,22]. This cooperation fosters socio-economic and cultural ties but faces challenges from environmental changes and tourism, underscoring the delicate nature of these interspecies relationships. Adding to this, the Erabu sea krait (*Laticauda semifaciata*) demonstrates another facet of cooperative hunting [23]. These sea snakes engage in communal hunting with both conspecifics and other predatory fish in the complex reef habitats of Southern Lombok, Indonesia. This strategy, observed in 52 instances, suggests a higher cognitive capacity in sea kraits to coordinate activities during these communal events, enhancing their ability to locate and capture elusive prey. Furthermore, the joint hunting efforts of false killer whales (*Pseudorca crassidens*) and bottlenose dolphins (*Tursiops truncatus*) off New Zealand's coast represent another intriguing example [24]. Here, over 300 individuals from both species employ a 'carouselling' technique to herd fish into dense clusters, demonstrating a shared hunting culture.

### - **Medicinal cultures**

Throughout human history, the acquisition of some medicines has been attributed to the observation of wild animals' use of many different plants to treat perceived illness or otherwise alter their physiological or psychological state for positive benefits [25,26]. Recently this practice became a science in itself, proposed as a means of acquiring new medicinal plants for human use in the face of antibiotic resistance [27]. The study of animal self-medication has revealed many examples of shared pharmacopeia by humans and animal species sharing the same habitats [28–30]. Not only do humans acquire animal medicines, but wild animals whose habitats are encroached upon by expanding human-dominated landscapes also acquire new plants of medicinal value [31,32]. This exchange highlights the dynamic relationship between human-animal or animal-animal knowledge systems.

### — **Signal convergence**

Interspecies signal convergence, as described in the context of bird species [4] using similar acoustic signals in proximity, aligns closely with the concept of co-culture. In co-culture, different species develop concurrent and interrelated behaviours through direct or indirect interactions. The phenomenon of signal convergence among bird species represents a form of co-culture where interspecies communication networks extend beyond individual species boundaries, leading to clustered and synchronised signals. This may also occur in other species as tamarins [33]. This convergence indicates a deeper level of social communication that transcends species-specific boundaries, highlighting a form of co-cultural evolution. Not only do similar ecological niches play a role, but crucially, it is the interactions between species that drive this convergence. This suggests that rather than signals diverging to minimise interference, they have evolved to become more alike, effectively enhancing interspecies communication. However, this phenomenon must extend beyond merely sharing similar environmental conditions; there must be an element of learning occurring between the species. This pattern contradicts the traditional view of signal divergence to avoid misidentification and represents a novel form of interspecies interaction and adaptation, a core aspect of co-culture.

## **Future research perspectives**

### - **Interspecies social networks**

The study of **interspecies social networks** aligns with the concept of co-culture by examining how different species interact, learn and adapt their behaviours within shared environments [34]. These interactions form complex social networks where each species influences and learns from the other, leading to shared patterns of behaviour, risk taking, and resource utilisation [35]. This mutual adaptation and learning exemplify co-culture, where species co-evolve and co-create shared sociological spaces and networks [36]. These studies demonstrate that through social networks, interspecies relationships are not just incidental but are integral to the behavioural and ecological strategies fostering a dynamic, bidirectional exchange.

## - **Wild animals in urban environments**

Studying **urban animal cognition** [37] in relation to co-culture reveals how animals adapt their cognitive abilities to urban environments, distinct from their natural habitats. This adaptation involves mutual influence between wild animal and human behaviours and environments. Urban animals modify their behaviours, learning, and problem-solving skills to cope with urban challenges, reflecting a dynamic response to urban landscapes. Similarly, humans alter their urban spaces, influencing wildlife behaviour and evolution. This reciprocal adaptation between humans and wildlife is fundamental to understanding co-culture [38]. Do animals in urban environments engage culturally with human societies as Japanese macaques can do, or do they merely adapt – both ontogenetically and potentially culturally – to an environment predominantly moulded by human activities? It is crucial to study the cognitive mechanisms behind this urban cultural adaptation.

## - **Cultural and genetic coevolution**

The concept of co-culture, where both species involved evolve and change, offers a nuanced understanding of **cultural and genetic coevolution** (figure 1) [39–42]. In co-culture, both species mutually influence and adapt to each other's presence, leading to joint evolutionary changes. This process reflects a bidirectional interaction, where the cultural behaviours and potentially over generations genetic traits of one species shape and are shaped by those of the other with feedback between both species. Cultural selection and genetic selection may not always occur simultaneously; their concurrence depends on several factors. For instance, the extent to which a cultural behaviour is intertwined with the fitness of a population in a specific environment can influence this relationship. Cultural behaviours that enhance survival or reproductive success in a particular setting can lead to changes in population habits that, over time, could drive genetic selection. This implies that cultural adaptations, by altering behaviour or environmental interactions, can pave the way for genetic changes if those cultural traits significantly affect reproductive success and survival. Thus, the interplay between cultural and genetic selection is complex and context-dependent, highlighting the nuanced ways in which culture and genetics can co-evolve, shaping the trajectory of population evolution (Figure 1). Such interactions between genes and cultures result in shared adaptations that are beneficial for both species, underscoring a symbiotic relationship rather than one dominated by control. These species proximity and interactions may accelerate evolution as suggested in the evolution of spatial mosaic hypothesis of Thompson and collaborators [43]. Domesticated animals are an example where mutual cultural evolution has led to genetic change as with wolf-human tolerance and learning leading to dogs [44]. This perspective emphasises the collaborative aspect of domestication, viewing it as a co-evolutionary process rooted in mutualism, with both species playing active roles in shaping this dynamic evolutionary pathway. Co-culture extends and enriches Henrich's ideas about the collective brain and cultural evolution [45] as well as evolution of networks [46]. Henrich's argument that our dominance as a species stems not from individual intelligence but from our ability to socially interconnect with individuals of our species and of other species, and learn across generations, illuminating the mechanisms

behind cultural behaviours impacting genetic selection. Further research is essential to explore this area in more depth, particularly on other animal species.

### **Concluding Remarks**

The exploration of co-cultures, highlighting interspecies culture among humans and animals, and between non-human animal species, opens a transformative perspective on how different species co-evolve and mutually influence each other's behaviour and cognition. This concept challenges the traditional understanding of culture and learning as species-specific phenomena, emphasising the intricate dynamics of interspecies interactions in various contexts, notably in urban environments (see Outstanding Questions). This research underscores the significance of co-culture in understanding the dynamics of interspecies relationships, where behaviours evolve concurrently and mostly symbiotically, leading to novel cultural coevolution, and sometimes genetic coevolution. The study of co-cultures is a frontier in understanding the interconnectedness of life. It emphasises the need for further research in this field to unravel the complexities of these evolutionary processes and their implications for conservation, urban planning, and our broader understanding of animal cognition and behaviour (see Outstanding Questions).

#### **Box 1: Interspecies learning**

Mechanisms of **learning** transcending species boundaries are remarkably diverse, encompassing a spectrum from explicit imitation to more nuanced forms of influence such as **stimulus enhancement** or **social facilitation** [1]. This domain of animal cognition is particularly salient in the interactions between non-human animals and humans, especially pronounced in urban environments [37]. Such settings, with their unique blend of challenges and opportunities, become fertile grounds for novel forms of adaptation and interspecies interaction. A case in point is the observed behaviour of herring gulls (*Larus argentatus*), which have adapted to mimic human food preferences during foraging, demonstrating a form of interspecies stimulus enhancement [47] as tits (*Parus sp.*) with opening milk bottles [48]. In a similar vein, wild mockingbirds (*Mimus polyglottos*) and ravens (*Corvus corax*) living in urban areas have shown the capacity to differentiate between individual humans, suggesting a level of social cognition that equips these birds to adeptly navigate the complexities of human-dominated landscapes [49,50]. The process of learning is a crucial element in defining co-culture. For example, migratory flycatchers (*Ficedula sp.*) adopting habitat preferences through learning from resident great tits (*Parus major*) demonstrate increased interspecies habitat overlap [2]. Under human-created conditions, the possible transmission of a form of solitary object play, stone handling to a previously non-stone handling group of rhesus macaques from a stone handling group of Japanese macaques living adjacent to them has been reported [51]. Separated by a concrete wall with limited visual openings and climbing structures, two monkey groups could partially see and hear each other. Observations revealed that when the Japanese macaques engaged in stone handling, the rhesus macaques, seemingly influenced by the sounds, began similar activities. A comparison showed high similarity in their stone handling behaviours. Despite the lack of



direct contact, this artificial setup highlights the impact of visual and auditory stimuli in fostering shared cultural traditions between two species. Human-animal interactions, like human-dog (*Canis lupus familiaris*) play [52], pointing [53], learning detour tasks [54] or human-horse (*Equus caballus*) communication [55], reveal co-cognitive processes emerging from collective interactions. Farm animals [56] help to elucidate the underpinning concept of co-culture. Future research in interspecies learning [1,2] is crucial for a deeper comprehension of how species mutually shape each other's learning processes and behaviours within shared environments. These cross-species interactions result in behavioural adaptations and preferences that are not just incidental but represent a form of convergent evolution.

### **Box 2: Japanese macaques and Sika deer interactions**

Direct interactions between Japanese macaques (*Macaca fuscata*) and Sika deer (*Cervus nippon*) exemplify the evolution of interspecies relationships (Figure I). Initially, these species developed close spatial proximity, benefiting mutually from their coexistence. Macaques, when feeding in trees, inadvertently drop food which becomes an energy source for deer, enhancing their foraging efficiency through gleaning, as noted by Tsuji et al. [57]. This interaction fosters a strong cohabitation dynamic between the deer and macaques. An unusual aspect of this relationship is the deer's **coprophagia**, particularly around macaque sleeping sites, where they consume the macaques' faeces [58]. As this relationship evolved, some macaques have been observed grooming deer, a behaviour suggesting a deepening of their interspecies bond. On Yakushima Island, this interaction has progressed into a unique co-culture, with macaques riding on Sika deer [59]. Interestingly, these interactions have led to interspecies sexual behaviours, as observed in Yakushima and Minoo, Japan. These instances involve male macaques engaging sexually with female Sika deer and, conversely, female macaques with male deer. These interactions are not passive, as evidenced by the behaviours and attitudes of macaques and deer, which signal their consent or dissent regarding the interaction. For example, certain deer may gaze at macaques and position themselves to show a readiness to interact or avoid each other. Consequently, various locations in Yakushima exhibit distinct forms of co-culture, reflecting the unique dynamics between local populations of deer and macaques. Such interactions highlight the capacity for highly complex and unusual behaviours to develop between different species living in close proximity. The evolution of their interactions – from shared foraging and grooming to more complex behaviours like riding and interspecies sexual activities – demonstrates a significant level of social and behavioural adaptation between two distinctly different species. They learned from each other and developed co-cultural behaviours.

### **Glossary:**

- **Co-culture:** Describes mutual cultural evolution and interaction between different species, like humans and animals, leading to collective cultural development through shared adaptations and behaviours resulting from direct or indirect interactions within the same environment.

- **Coevolution:** The reciprocal evolutionary influence between two or more species, where each exerts selective pressures on the others, leading to adaptations that can be beneficial, harmful, or neutral.
- **Coprophagia:** The act of consuming feces, which in interspecies interactions can be a nutritional strategy or a means of acquiring digestive enzymes, playing a role in co-culture between species.
- **Cultural and Genetic Coevolution:** Simultaneous evolution of cultural traits and genetic characteristics within and between species, reflecting the interplay between cultural behaviours and genetic adaptations, often leading to mutual benefits and enhanced survival strategies.
- **Interspecies Networks:** Complex systems of relationships and interactions between different animal species, including humans, encompassing various forms of cooperation, competition, and communication, influencing behaviours, survival strategies, and ecological roles.
- **Interspecies Learning:** The process where individuals from different species observe, learn, and imitate each other's behaviours, transcending species boundaries and including a range of behaviours from simple imitation to complex adaptations and problem-solving techniques.
- **Medicinal cultures:** Shared use and knowledge of medicinal plants and practices between humans and animals, involving the observation and adoption of healing behaviours and substances from one species to another, leading to a shared pharmacopoeia and medical practices.
- **Niche Construction:** The process by which organisms modify their own and each other's niches through their activities and choices, altering the physical environment, resources, and interactions within an ecosystem and affecting the evolutionary process.
- **Signal Convergence:** The development of similar communication signals by species through interaction and cohabitation, facilitating interspecies communication and cooperation, leading to effective coordination and mutual understanding.
- **Social Facilitation:** A phenomenon where the presence or actions of conspecifics or individuals from other species increase the likelihood of a behaviour being performed by an observer, leading to the spread of new behaviours within a group.
- **Stimulus Enhancement:** A form of learning where an individual's presence or behaviour draws attention to a particular object or environment, facilitating learning in others, occurring within or between species and influencing behavioural choices and preferences.
- **Urban Animal Cognition:** The study of how animals adapt their cognitive processes in urban environments, examining changes in animal behaviour, learning, memory, and

problem-solving abilities in response to challenges and opportunities presented by human-modified urban landscapes.

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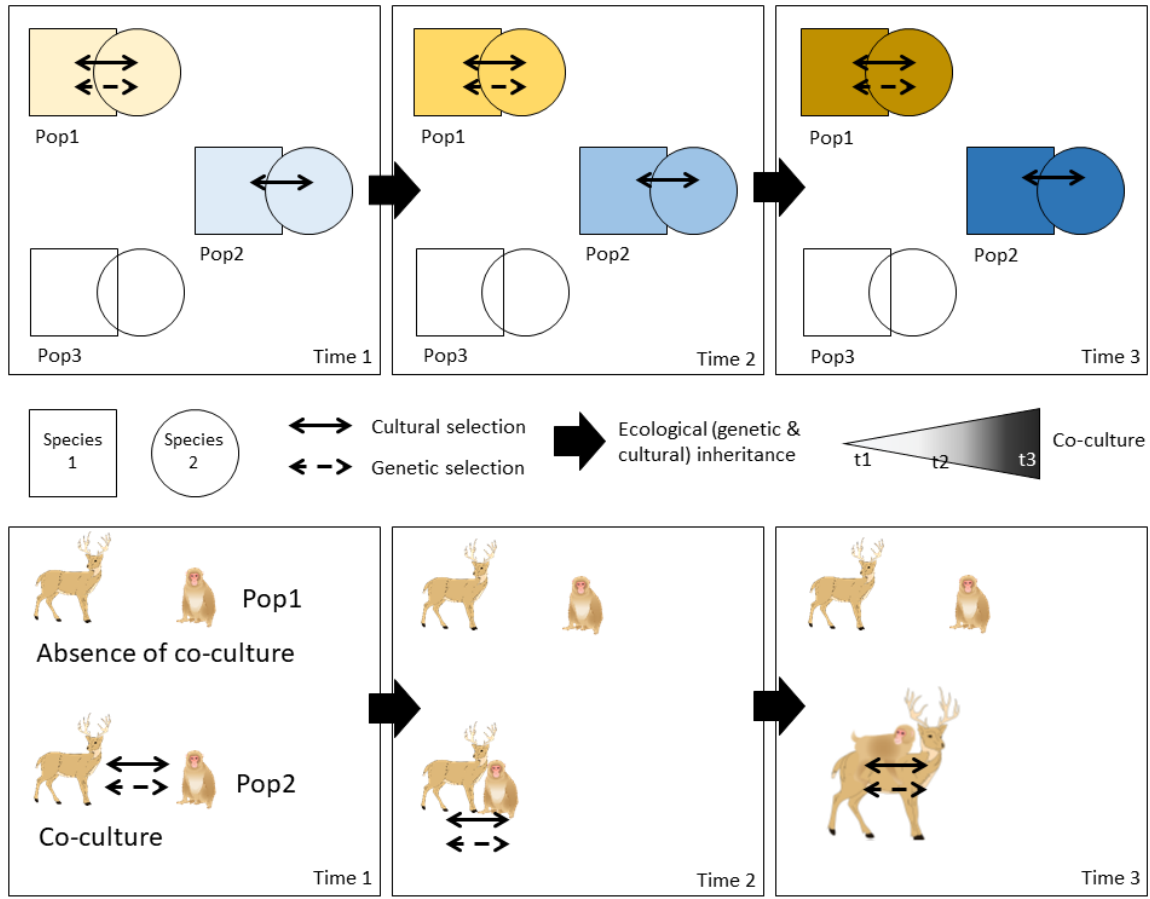


Figure 1: a model that melds the concepts of gene-culture coevolution with niche construction, illustrating the intertwined genetic and cultural evolution among several populations (Pop1, Pop2, Pop3, etc.) of two interacting species over various time points ( $t_1$ ,  $t_2$ , etc.). It highlights the diversity of phenotypes between populations as a result of the interplay between genetic factors, individual learning, and cultural transmission. The diagram traces the evolution of these populations through the inheritance of genetic and cultural traits over generations. Notably, Populations 3 of both Species 1 and Species 2 (blank) exhibit a lack of co-culture and so, of cultural and genetic coevolution over time, but populations 1 and 2 of both species are involved in co-culture. Yellow and Blue populations indicate the presence of co-culture. Colour changes indicate co-cultural variations. The interactions between Population 1 of Species 1 and Population 1 of Species 2 underline the dual influence on genetic selection, which affects inclusive fitness, and on cultural selection, which shapes the cultural viability of memes. This dual influence suggests that changes in genetic traits within these populations could potentially feed back to affect cultural evolution, leading to differences in evolutionary trajectories compared to populations where only cultural selection is at play. For example, the dietary customs of killer whales, *Orcinus orca*, have led to the development of population-specific genes that influence morphology and digestion[60], subsequently shaping their dietary preferences and learning patterns. However, only cultural selection acts on Populations 2 of Species 1 and Species 2. In these populations, the absence of genetic changes may limit the potential for feedback effects on

cultural evolution, resulting in evolutionary trajectories that are primarily driven by cultural factors. Such reciprocal dynamics between the populations of these species highlight the intricate relationship between genetic and cultural evolution, as depicted in the subsequent figure featuring Japanese macaques and Sika deer, demonstrating the complex mechanisms at play in evolutionary processes.



Figure I: Proximity between Japanese macaques and Sika deer (top left) leads to interactions such as grooming (top right), riding (bottom left) or play (bottom right). Credit: Alexandre Bonnefoy