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ARTICLE

Cultural change in animals: a flexible behavioural adaptation to human disturbance

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ABSTRACT   In recent decades, researchers have increasingly documented the impact of anthropogenic activities on wild animals, particularly in relation to changes in behaviour. However, whether human-induced behavioural changes in wildlife may be considered evidence of cultural evolution remains an open question. We explored whether behavioural responses to different types of human activities in species already known to display behaviour transmitted through social learning, particularly non-human primates (NHPs), are suggestive of cultural evolution in the wild. Results indicate that human influence on NHP cultural repertoires includes the modification and disappearance of existing cultural traits, as well as the invention of novel traditions with the potential to become cultural. These examples are found mostly in the domain of food acquisition, where animals modify their diet to include new resources, and adopt novel foraging strategies to avoid humans. In summary, this paper suggests that human activities can act as a catalyst for cultural change in animals, both in terms of threatening existing traditions and fostering new ones. The current situation may echo environmental changes thought to have triggered major behavioural adaptations in our own evolutionary history and thus be useful for research on human cultural evolution. As wildlife is increasingly exposed to humans and their activities, understanding how animal behaviour patterns and cultures are impacted and change in response to anthropogenic factors is of growing conservation importance.

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Introduction

There has been a recent surge of interest in studying the impact of human activities on wild animal populations. Many species and/or populations cannot avoid humans and must therefore display behavioural strategies to cope with the ever-growing human disturbance in their environment (Candolin and Wong, 2012, McLennan et al., 2017, Barrett et al. 2019). This paper investigates animal, in particular non-human primate (NHP), potentially cultural responses to human activities (e.g., agriculture, hunting, road development). When these behavioural changes are deemed cultural (innovation is made by one or a limited number of individuals and is subsequently learned by others through social means (Fragaszy and Perry, 2003)), it suggests that humans can drive cultural change or cultural evolution (used synonymously; see below and Lamon et al., 2018; Mesoudi and Thornton, 2018) in other species. Our aim here is to collect behavioural adaptations to human disturbance that have possibly, or have the potential to, spread culturally in a given animal population.

Although numerous species exhibit behavioural variations in response to humans and their activities (see review in Barrett et al., 2019), our focus is on NHPs because of our joint expertise, but also because NHPs fulfil an unusual conglomerate of factors relevant to this question: (1) many NHP species are large-bodied and slow reproducing, long-lived species (Charnov and Berrigan, 1993, van Schaik et al., 2006) for which behavioural flexibility is the main (if not the only) way to respond quickly to environmental changes; (2) there is an extensive literature on NHP social learning and culture in both captive and wild settings, with some records spanning over 50 years on the same populations (Whiten et al., 1999, Kawai, 1965, Hirata et al., 2001), and with growing evidence that wild NHPs need to learn their skills during development through socially aided learning (Schuppli et al., 2016, Lamon et al., 2017); (3) NHPs provide the opportunity to discuss possible drivers of human cultural evolution through homology (Whiten et al., 2010). Nevertheless, there are also many examples of non-primate cultures that are impacted by humans and are possibly subject to cultural evolution (Brakes et al., 2019). Rather than an exhaustive catalogue of possible animal cultural behaviours that might be impacted by humans, this piece provides a theoretical framework for understanding how humans may impact non-human cultures, and calls for conservation strategies to take account of behavioural diversity to ensure that 'cultural units' (i.e., identifiable patterns of behaviour that have a socially learnt origin) are preserved (Whitehead, 2010, Greggor et al., 2014).

Evidence for flexible behavioural adaptation to human disturbance

Some species cope with human disturbance through genetic adaptation (e.g., Marnocha et al., 2011). However, for species with slow life histories genetic adaptation is difficult to achieve over short time periods. Another strategy in response to locally changing conditions (e.g., anthropogenic food sources, McLennan and Hockings, 2014) is proximately induced behavioural flexibility (Sih et al., 2011), that is "behavioural responses to changing local conditions, reflecting solutions to ecological or social problems" (p215, Hockings et al., 2015a). A prime example of behavioural flexibility in animals is the documented adaptation to ongoing human-provoked climate change (Beever et al., 2017). If such climate-change-led adaptations fit the cultural criteria, this will constitute strong evidence that humans alter animal cultures indirectly. However, because there is currently limited evidence of the connection between climate change and animal cultures (but see Wild et al. (2019) who report that culture may alleviate the effects of climate variation in bottlenose dolphins (*Tursiops*

aduncus)) and specifically NHP cultures, our focus will be on behavioural adaptations in response to direct encounters with humans or human activities. Habitat loss and fragmentation have been shown to reduce movements in numerous mammal species worldwide (Tucker et al., 2018), with many mammals (e.g., elephants, (*Loxodonta africana*, Bates et al., 2007)) or chimpanzees (*Pan troglodytes*, Hicks et al., 2013)) modifying their behaviour to avoid contact with humans. However, avoidance behaviour can be the result of a variety of processes (e.g., predator or threat avoidance, neophobia), which are not specifically connected to human activity or necessarily learned. An example of direct avoidance of humans is the development of nocturnal crop-foraging behaviour in one community of chimpanzees at Sebitoli in Uganda (Krief et al., 2014). Such behavioural responses, far from being isolated (see review in McLennan et al., 2017 and Table 1), suggest that novel behaviours in wild NHPs and other species may enter their behavioural repertoire as a result of human activities. However, it is important to determine whether these behavioural modifications are cultural.

Culture and cultural change

The analysis of culture as a biological and evolutionary phenomenon (Boyd and Richerson, 1985), and the existence of socially transmitted behavioural variation between groups or subgroups of the same species in non-humans, reminiscent of human culture (Laland and Galef, 2009), is now well accepted. Reports of cultural transmission in non-humans, including in Japanese macaques (*Macaca fuscata*, Imanishi, 1952), great tits (*Parus major*, Fisher and Hinde, 1949) and chimpanzees (Goodall, 1973), have launched a strong debate on the nature of culture in animals and how it compares to humans (Tomasello 1990, Galef, 1992, Laland and Galef, 2009). A cultural species displays patterns of behaviour (or 'traditions') acquired in part through socially aided learning processes (Fragaszy and Perry, 2003). Classically, if controversially (Laland et al., 2009), variation in behaviour between groups of the same species is used to detect such social learning by excluding genetic or ecological factors as underlying sources of the variation (the exclusion method: Whiten et al. 1999). A major concern is that the exclusion method can generate false positives or negatives in part because of our inability to isolate all relevant ecological factors that come into play in the appearance of a behaviour (Laland and Janik, 2006); in addition, the method does not provide direct evidence for social learning itself (Kendal et al., 2010b). Such criticism has in turn led to a wealth of studies aiming to further investigate ecological drivers of NHP behaviour (Möbius et al., 2008, Gruber et al., 2012, Spagnoletti et al., 2012, Langergraber et al., 2010, Schöning et al., 2008, Krützen et al., 2007) and create diverse methods for identifying social learning in wild animals, particularly NHPs (Luncz and Boesch, 2014, Hobaiter et al., 2014, Aplin et al. 2015, Allen et al., 2013, Kendal et al., 2010a, Hoppitt and Laland, 2011). The resulting evidence has allowed the debate to shift from the existence of non-human cultures to the issue of whether non-humans possess cumulative cultures, that is, the process by which cultural groups progressively improve their behavioural traits through innovative modifications and social transmission over generations (Mesoudi and Thornton, 2018, Dean et al., 2014). While recent findings suggest that non-human animals are able to adopt increasingly efficient or complex techniques to meet their goals (Sanz et al., 2009, St Clair et al., 2018, Sasaki and Biro, 2017, Lamon et al., 2018), data on cumulative cultural evolution in wild animals remain controversial and lacking (Dean et al., 2014). Although not universally accepted (Mesoudi and Thornton, 2018), the ratcheting up of complexity or efficiency of a

Table 1 Possible non-human primate cultural variants impacted by human influence

Human influence	Species	Specific disturbance	Response	Reference	Evidence for cultural behaviour
Human presence in the environment	Chimpanzee (*Pan troglodytes*)	Increased hunting pressure	Decrease in ground nesting (D)[a]	Tagg et al. (2013)	Matsuzawa, and Yamakoshi (1996)
			Deactivation of snares (I)	Ohashi and Matsuzawa (2010)	Ohashi and Matsuzawa (2010)
	Long-tailed macaques (*Macaca fascicularis*)	Presence of local farm dogs at foraging sites at the shore	Decrease of stone tool use (D)	Gumert et al. (2013)	Tan (2017)
Introduced and novel food items	Orang-Utans (*Pongo pygmaeus*)	Oil palm mono cultures	Dispersal into mature plantations, use oil palm trees for nesting, and feeding on mature fruits (M)	Ancrenaz et al. (2014)	van Schaik et al. (2003)
	Chimpanzee (*Pan troglodytes*)	Newly human-introduced trees or crops for animals living in the vicinity of human settlements	Crop-feeding (I)	McLennan and Hockings (2014)	Whiten et al. (1999)
			Emergence of leaf tools used for the consumption of Raphia palm wine (M)	Krief et al. (2014).	Hockings et al. (2015a, 2015b).
			Crop-feeding during the night (M)		
	Chimpanzee (*Pan troglodytes*)	Proliferation of natural fig species due to controlled forest poisoning and introduction of non-native species in the core area	Loss of stick tool use (D)[a]	Gruber (2013)	Gruber et al. (2009)
	Chimpanzee (*Pan troglodytes*)	Newly human-introduced plant species	Nest manufacture (M)	McCarthy et al. (2017)	Matsuzawa, Yamakoshi (1996)
	Japanese macaques (*Macaca fuscata*)	Introduction of potatoes and corn (though direct provisioning)	Food washing (I)	Kawai (1965)	Schofield et al. (2018)
	Japanese macaques (*Macaca fuscata*)	Visitor (e.g., fishermen) leaving raw fish to dry or providing on Koshima island	Consumption of raw fish (I)	Watanabe (1989)	Watanabe (1989)
	Japanese macaques (*Macaca fuscata*)	The influence of the occurrence and frequency of food provisioning on object-directed play behaviour in Japanese macaques	Stone handling (M)	Leca et al. (2008)	Leca et al. (2008)
	Long-tailed macaques (*Macaca fascicularis*)	Co-occurrence of provisioning and co-habitation with humans at a temple	Innovation and diffusion of token-mediated exchange between humans and long-tailed macaques (I)	Brotcorne et al. (2017)	Brotcorne et al. (2017)
	Long-tailed macaques (*Macaca fascicularis*)	Introduction of oil palm trees	Development of oil palm nut-cracking (I)	Luncz et al. (2017)	Tan (2017)
Habitat alterations and/or decrease in natural foods	Chimpanzee (*Pan troglodytes*)	Disappearance of naturally occurring decaying Raphia that provided specific nutrients	Emergence of moss sponging (M)	Reynolds et al. (2015)	Hobaiter et al. (2014)
	Gibbons	Forest fire smoke	Decrease in song and call pattern (D)[a]	Cheyne (2010)	Koda et al. (2013)

Note: Invention is defined as novel behaviour resulting from independent asocial learning, i.e., there is no immediate prior information (that may be socially learned) from which the impetus for the innovation directly emerges, while Modification is defined as a novel behaviour resulting from asocial modification of an existing behaviour or evaluation of prior information (that may have been gleaned socially). See Carr et al. (2016) for additional definitions. Further we posit that incorporation of a new plant part (e.g., tuber) or food type (e.g., fish) previously not eaten would be invention, but that consumption of a new fruit species by a species that already eats fruit is modification
D Decrease of a behaviour pattern, I invention innovation, M modification innovation
[a]denotes cases that are more speculative in our current list

behavioural trait (Tennie et al. 2009) remains a major criterion when attributing cumulative cultural evolution to a given species. Key in identifying cumulative cultural evolution is consideration that innovation has two forms: innovation by modification and innovation by invention (Reader and Laland, 2003). Innovation by (beneficial) modification of an existing trait (or 'ratcheting') is crucial for cumulative culture (Carr et al., 2016), while innovation by invention increases the repertoire of cultural traits (Dean et al., 2014) resulting in cultural evolution (or change) but not cumulative cultural evolution. Here, we will refer to cultural evolution if there is evidence for social learning in the spread of a new behavioural trait in a substantial portion of a group/population (Lamon et al., 2018, Mesoudi and Thornton, 2018).

Drivers of cultural evolution in non-human cultures
Human landmark behavioural innovations have often correlated with significant ecological changes (e.g., Potts, 2013, Vrba, 1985, Potts, 1996, de Menocal, 2011, Trauth et al., 2005), suggesting that the latter may drive cultural evolution. Similarly, current day human-induced rapid environmental changes can, despite their usually devastating effects on wild animals (see above), also foster behavioural variation, and thus potentially also cultural change. To innovate is to potentially maximise exploitable resources to increase the efficacy of one's behaviour and circumvent novel challenges or threats (Reader and Laland, 2003). Thus innovations (and potential subsequent cultural change) can arise due to 'necessity' mediated by variation in environmental pressures,

leading to a reduction in resource availability and animals investigating alternative resources when necessary (Gruber et al. 2016, Lee and Moura, 2015, Grund et al., 2019). Likewise, innovations often arise due to 'opportunity': e.g., innovations may be fostered by frequent exposure to certain substrates and importantly, by exposure to novel stimuli (Luncz et al. 2017, Spagnoletti et al., 2012, Koops et al., 2014). Humans can play a key role for both 'opportunity' and 'necessity' in providing new opportunities or limiting them. Indeed, human impact often leads wild animals to be exposed to novel stimuli, which is a potent catalyst of innovations but a rare event under natural conditions (van Schaik et al., 2016). For example, the recent introduction of oil-palm (*Elaeis guineensis*) nuts provided the 'opportunity' for long-tailed macaques (*Macaca fascicularis*) to develop nut-cracking behaviour from habitual cracking of hard-shelled marine invertebrates within roughly a decade (Luncz et al., 2017). Elsewhere, in a comparison of crops consumed by chimpanzees at two sites with differing histories of exposure to agriculture (Bossou in Guinea, and Bulindi in Uganda), chimpanzees showed increased foraging adaptations to cultivated landscapes over time, with crop selection by chimpanzees gradually becoming less selective and including more non-fruits such as underground storage organs and pith (McLennan and Hockings, 2014). In addition, intrinsic factors such as personality (Brosnan and Hopper, 2014) or the ability to overcome neophobia (Forss et al., 2017) also interact with these ecological correlates, leading both extrinsic and intrinsic factors to influence the likelihood of innovation in some individuals, and the potential for cultural change if the new behavioural variant is

learned by the individual and subsequently copied by others (see Carr et al., 2016 for a review).

Human-induced changes in social behaviour in animals may also impact culture by influencing the grouping patterns, and general social behaviour of animals towards one another. For example, in West Africa, chimpanzee party sizes did not differ when foraging on wild resources and human crops. However, likely due to the need to survey potential threats from humans, party cohesiveness during crop foraging was greater than wild resource foraging (Hockings et al., 2012). This increased cohesiveness leads animals to spend more time in proximity to one another, which could foster the spread of novel behaviours and lead to new cultural traditions within a group. However, human pressure can also force individuals to migrate to survive, potentially leading to further conflicts with conspecifics, humans and other non-human species (e.g., Meric de Bellefon, 2017; Table 1). Forest fragmentation and human infrastructure can result in the fragmentation of animal groups and displacement of individuals which may reduce the transmission of cultural variants as they spread among close associates (Lamon et al., 2017). Likewise, birds and cetaceans often react to human-produced noise by reducing their singing patterns (Nowacek et al., 2007, Davidson et al., 2017), a particular threat to vocal cultures (Slater, 1986, Garland et al., 2017). Thus human activities can potentially disorganise the social complexity of animal societies leading to the loss of cultural behaviour (van Schaik, 2002). Nevertheless, immigrant individuals may also constitute 'cultural vectors', who introduce new innovations and diversify local cultures (Mörchen et al., 2017, Biro et al., 2003, O'Malley et al., 2012, Luncz and Boesch, 2014, Luncz et al., 2015), potentially buffering against human impacts.

Cultural change in animals can be usefully viewed through the lens of niche construction (NC) whereby modifications to the environment where a species lives, as a result of their own or another species' activities, impact on the evolution of a species' behaviour or biology (Odling-Smee et al., 2003). Cultural niche construction (CNC) refers to significant feedback loops between innovations that become cultural and modifications of an organism's environment (Odling-Smee et al., 2003). Humans may

drive the evolution of animal cultures through two types of NC (Day et al., 2003). *Perturbational* NC refers to individuals actively changing the environment through their actions or responding to an environment altered by other species. Two textbook examples in the animal cultural literature, milk bottle opening in parids (Fisher and Hinde, 1949) and food washing in Japanese macaques (Kawai, 1965), describe cases of behavioural adaptations to novel food sources (a perturbation representing an innovation due to 'opportunity') provided by humans that subsequently spread through populations (but see Galef, 1992). *Relocatory* NC refers to cases where individuals actively move in space, exposing themselves to different environmental factors. A textbook example for *Relocatory* NC is that of black rats (*Rattus rattus*) that, due to human deforestation of oak forests in Israel in the early 20th century, were forced (innovation due to 'necessity') to relocate to relatively sterile pine forests where they thrived due to the new cultural trait of pine cone processing to extract and consume the seeds (Terkel, 1996).

Can flexible behavioural adaptations to human activity in non-humans be considered cultural?
It is essential to differentiate between adaptations that have the potential to be cultural from those that do not. First, it is important to stress that cultural change involves behavioural flexibility or phenotypic plasticity on the part of the individual innovator of the change (Reader and Laland, 2003), but also on the part of those who subsequently socially learn and adopt the new trait (see Harrison and Whiten, 2018 for a review). A change becomes cultural when it eventually spreads to the majority of a group, becoming part of their behavioural portfolio through a diversity of social processes (Whiten et al., 2009, Laland and Hoppitt, 2003, Hoppitt and Laland, 2008) and has longevity across generations (McGrew, 2004, Fragaszy and Perry, 2003). However, an obvious problem with the latter proposal is that human disturbance is often too recent compared with the lifespan of a species, for one to define many changes as fitting this criterion. Nevertheless, evidence of social transmission of a given behaviour between age classes (e.g., Fig. 1) is already a strong indicator of the potential for subsequent transmission and
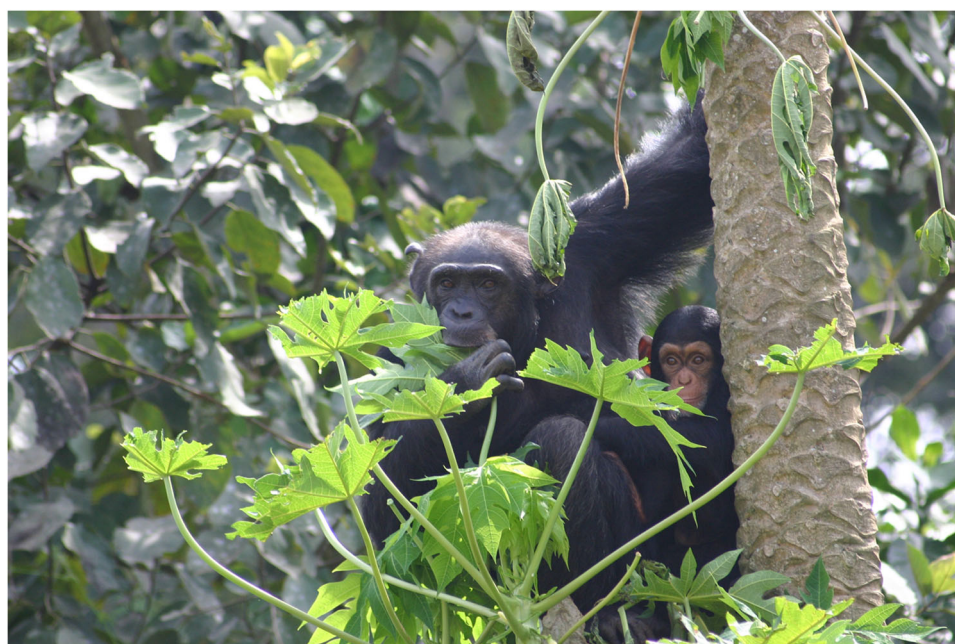

Fig. 1 Mother and infant chimpanzees, Jire and Joya, feeding on papaya (*Carica papaya*) leaf illustrating cross-generation crop-foraging in Bossou, Guinea (photo taken by K.Hockings)

fulfilment of stricter criteria for tradition formation. For example, while the Sebitoli chimpanzees' night crop-foraging is mostly led by adult males (Krief et al., 2014), younger individuals participate in this behaviour, making it likely that night time crop-foraging will be passed on to the next generation, even when the founder generation has disappeared. The same applies to other behaviours such as the ingestion of fermented raffia sap by chimpanzees at Bossou in Guinea whereby all age and sex classes use leaf tools, often co-feeding, to access this human resource (Hockings et al., 2015b). In contrast, a behavioural adaptation to human activities that is exhibited by some or most members of a given group may not automatically be associated with social learning because its distribution may represent independent discovery by each group member (Bandini and Tennie, 2017). For example, the concurrent availability of provisioned food and temple visitors (more specifically humans with long hair) appears to have led to the innovation of dental flossing in long-tailed macaques but, although it is a common behaviour in the group, there is no definitive evidence that the behaviour has spread socially (Watanabe et al., 2007, but see Masataka et al., 2009). Similarly, house or trash raiding observed in many species in close proximity to humans, such as chacma baboons (*Papio ursinus*) in South Africa (Fehlmann et al., 2017), appears unlikely to require social learning.

Table 1 provides examples of current behavioural changes in NHPs, which were induced by anthropogenic activities and likely to be cultural or to become cultural in the near future. To qualify for inclusion examples had to fulfil two criteria: there had to be evidence that (i) the trait belonged to the cultural repertoire of the species in the wild (i.e., being socially transmitted, ideally between age classes, or demonstrating longevity beyond the founder(s), although for some examples such requirement may not be fulfilled because of the recent appearance of the behaviour) and, (ii) that the observed change is attributable to human influence. For some of our examples (those denoted with an 'a' in Table 1), there is no direct connection between the evidence for social learning presented on the one hand, and the behavioural adaptation to human influence on the other, meaning these examples are relatively speculative. However, these examples were included in consideration of the fact that if no action is taken to study how animal cultures are influenced by human activities, populations exhibiting these potential cultural adaptations may well have disappeared by the time they are considered cultural (e.g., Sapolsky and Share, 2004). Indeed, clear unequivocal evidence that behavioural variants belong to the cultural repertoire of a species are notoriously difficult to obtain (Hobaiter et al., 2014, Allen et al., 2013, Hirata et al., 2001). The goal here is to identify behavioural adaptations that have the potential to be cultural responses to human activities and to spur further debate and research regarding the topic.

The examples in Table 1 can be linked to three major types of human influence, as they can be a reaction to: first, the mere presence of humans in the environment; second, the introduction of novel substrate by humans; and third, the human destruction of the environment (variously resulting in perturbational or relocationary NC due to opportunity or necessity). In agreement with previous analyses of innovation behaviour in NHPs (Reader and Laland, 2002), the majority (69%) of our recorded cases (9 of 13 cases) concern behavioural changes in the foraging domain. Of the 16 behavioural adaptations recorded within these 13 cases, 25.0% (4 of 16) represent a decrease or loss of behaviour (e.g., a decrease in stone tool use in long-tailed macaques, Gumert et al., 2013), 37.5% (6 of 16) represent a modification to an existing behaviour (e.g., chimpanzee nest manufacture using introduced plant species, McCarthy et al., 2017), and 37.5% (6 of 16) a novel

behaviour (e.g., development of fish eating in Japanese macaques, Watanabe, 1989).

The low number of cases so far may be due to the difficulty with which wild animal cultural traits are identified (Kendal et al., 2010b). The drawbacks of the exclusion method are known (Laland and Janik, 2006): it can be hard to gather data from enough groups to ascertain that a given variant is truly cultural; and social learning may be involved in the spread of a behaviour pattern even where its distribution is also influenced by ecology. A prime example of this type-II error is found in variations in diet, which may be both driven by ecology but also culture (Jaeggi et al., 2010). This is important as the inclusion of human-introduced trees or crops into the diet (McLennan and Hockings, 2014) are likely to constitute a major part of NHP behavioural responses to humans. Despite its known flaws, the exclusion method allows the identification of potential cultural traits by a simple and comparative ethological approach (Laland et al., 2009). In addition, alternative statistical methods that directly assess the presence of social learning in the transmission of a trait can be used when possible (Farine et al., 2015, Kendal et al., 2010b). Nevertheless, their application to non-intentional/non-experimental human-induced environmental change (e.g., Hobaiter et al., 2014) relies on serendipitously observing a population undergoing change. Here, paying closer attention to the responses of non-human animals to human induced change, especially those from long-term research sites, will provide the opportunity to gather the information necessary to infer evidence for cultural change (Box 1). Finally, correlational approaches that assess both the degree to which animal populations are exposed to human disturbance and the extent by which a possible cultural repertoire has varied over time will be instrumental to determine how the type and degree of human-provoked disturbance might modify species' cultural repertoires. Such approaches, however, necessitate knowledge of the extent of a given population's repertoire, which can often take several decades (Boesch and Boesch-Achermann, 2000). Therefore, this approach will be limited to the small (but growing) number of well-documented populations in NHPs and other species.

Humans as both threats to and catalysts of cultural change in animals

The working hypothesis of this paper has been that humans, both through their direct and indirect actions, must be considered a potential force for cultural evolution in wild animals. Table 1 presents tentative examples in NHPs, which may be good candidates for cultural behaviours whose appearance or modification is currently being influenced by human activities. In particular, human activities may lead to the reduction of displays of cultural traits (Kühl et al., 2019), but also to their modification or to the invention of novel behaviour that has the potential to become cultural. On the one hand, the examples we present in this study (although not exhaustive) suggest that the reduction of observed cultural behaviour is possibly linked to loss of opportunity, both in terms of the available ecological niche, but also of social opportunities for learning. On the other hand, new opportunities for social learning, particularly through the introduction of novel and edible foods in the environment can lead to the establishment of new potential traditions in animals. Our catalogue is by no means exhaustive and one reason for our limited sample size is that animals must exhibit behavioural flexibility and their capacity to learn from each other be documented in the first place to be considered capable of cultural change. For example, while many species exhibit 'automatic' (or genetically driven) tool use (Shumaker et al., 2011), only a limited number of species exhibit the flexibility that may allow them to adapt their tool use

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Box 1: Types of human disturbances and expected changes in animal cultural behaviour leading to cultural evolution

Type of disturbance	Expected changes in cultural behaviour
Human presence	Decrease in frequency of cultural behaviour display when humans/human activities are in the vicinity
	Innovation (and spread) of novel behaviour in response to human provided opportunities
Introduced food items	Introduction of a novel human-introduced food item in the diet
	Social adaptation to consumption of human-introduced food to avoid conflicts with humans
	Loss of natural cultural behaviour between generation as introduced easy-to-easy access resources become part of the diet vs. development of new cultural behaviour because of more time afforded by more relax feeding pressure
	Use of introduced plants for other purposes (e.g., nest-building)
	Raise of frequency of novel socially-transmitted behaviour at provisioning site
Habitat alteration	Direct impact on health that prevents animals from displaying their cultures
	Decrease in frequency of cultural behaviour because of the disappearance of the exploited resource
Methods to isolate whether change is cultural	
Evidence for social learning/against individual learning	1) No multiple individual innovation (e.g., Zone of Latent Solution)
	2) indirect evidence for social learning (e.g., Method of exclusion)
	3) Direct evidence for social learning (social networks and/or captive studies)
	4) Ontogenetic evidence for spread across age-classes
	5) Longitudinal evidence for longevity of trait beyond founders

See for references: (1) Bandini and Tennie, 2017, PeerJ. (2) Whiten et al., 1999, Nature. (3) Hoppitt and Laland, 2011, American Journal of Primatology. (4) Lamon et al., 2017, Science Advances. (5) Hirata et al., 2001 Primate origins of human cognition and behaviour.

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culturally to changes in their environment in the short term (Call, 2013, Jacobson and Hopper, 2019). In this respect it would be particularly interesting to study the types of behavioural adaptation shown by other famed flexible tool-users such as corvids (e.g. New Caledonian crows (*Corvus moneduloides*, Hunt and Gray, 2003, Rutz et al., 2010) or jackdaws (*Corvus monedula*, Greggor et al., 2016)). It is also important to stress that most of our examples are cases of adoption of new food sources (Reader and Laland, 2002), which may be less cognitively demanding than tool use, and thus require less social learning (Kendal et al., 2009). For these examples, as well as others found in the non-primate literature (e.g., Diaz Lopez, 2012), in order to show cultural evolution researchers will require evidence that an apparent behavioural tradition is socially transmitted (Jaeggi et al., 2010) rather than resulting from individual learning (Bandini and Tennie, 2017). Nevertheless, it is likely that more examples will be uncovered as more species are sampled, and more behavioural patterns receive scientific scrutiny. For example, the recent focus on the cultural dimension of travel routes in birds and ungulates (Sasaki and Biro, 2017, Jesmer et al., 2018) may provide additional examples of how animal knowledge—and culture—is being influenced or threatened by human activities. Finally, based on current information (Table 1) and attention to anthropogenic disturbance, it is appropriate to raise the question of human impact on animal cultures for the following reasons:

Humans are catalysers of cultural change. Humans are not the only driver of cultural change in animals. For example, a natural disaster may force animal populations to migrate to a novel environment, leading to the adoption of new behavioural traditions. However, this paper has argued that human activities, particularly in recent decades, have increased the likelihood of cultural changes, by directly tampering with the natural environment of animals. By physically modifying the environment where wild animals live, for instance by installing snares or encroaching on the forest, humans cause animals to develop behavioural counter strategies (e.g., snare deactivation techniques, Ohashi and Matsuzawa, 2010). Where these behaviours come to characterise certain groups compared with other less-impacted groups of the same species, and there is suggestive evidence that the distribution of the behaviour involves social learning, we may claim human induced changes to wild animal cultures. Indeed, most of our documented behavioural adaptations constitute novel behaviours, either through innovations by invention or by modification, that have the potential to be considered as new cultural variants. Such direct and indirect influence of humans therefore cannot be ignored when analysing culture in wildlife.

Human activities directly threaten animal cultural behaviour. The degree to which the behavioural flexibility of animals will enable them to survive in our rapidly changing world remains an open question. In a recent article, chimpanzee researchers found that human disturbance correlated with less observed behavioural diversity, suggesting that human presence directly threatens cultural diversity in chimpanzees (Kühl et al., 2019). The rapid pace of anthropogenic environmental change suggests that unless drastic measures are taken, all wild animal populations will be forced to respond to some form of human disturbance soon. The threat to animal cultures is therefore unquestionable and must be incorporated into conservation policy (Brakes et al., 2019).

Conclusions

The study of animal cultural evolution is still in its infancy yet we currently have a unique opportunity to study and understand its drivers. Some species display the behavioural flexibility to cope with or even take advantage of novel ecological opportunities, although this may only happen out of necessity due to increased cohabitation with humans. For various reasons, however, innovations may not always spread or be maintained in subsequent generations. We predict that the higher the impact of humans on a population's habitat, the more existing behavioural traditions may be lost because of human pressure; but, concurrently, the higher this impact, the more (potentially cultural) behavioural adaptations unique to that population should be observed as a direct result of exposure to novel anthropogenic stimuli. Nevertheless, there is also a clear risk of uniformization and loss of cultures as all populations are likely to face very similar threats from humans. Finally, another prediction is that behavioural adaptations will only spread, within and between populations, if social conditions are adequate, that is, if human disturbance does not fragment the population or lead to increased stress levels (Boogert et al., 2013) that might hinder social learning. To

operationalise these predictions, researchers will need evidence of human activities, as well as evidence of behavioural change in animals that may directly or indirectly result from these activities and to determine whether social learning is involved. As demonstrated in this paper, change in social structure resulting from human activities can directly influence the cohesiveness of animal groups, either increasing it and thus increasing opportunities for social learning, or not. Quantifying the instances (either ancient or new) for cultural behaviours that result directly from human activities will allow us to determine the impact of humans on animal cultural evolution.

As anthropogenic environmental change appears able to induce cultural change stemming from innovations by modification, one may also see an increase in the, hitherto sparse (Dean et al., 2014), evidence of cumulative cultural evolution in wild NHPs. This 'forced' modification of cultural traits differs from the spontaneous motivation to modify the complexity or efficiency of a trait associated with current human cumulative culture. However, it mirrors the beginnings of our own cumulative cultural abilities which were likely a product of altered selection pressures resulting from expansion into new environments (Stiner and Kuhn, 2006) and demographic changes (Derex and Boyd, 2016) during our evolutionary history. Studying human-induced animal cultural evolution, in an epoch some term the Anthropocene (Lewis and Maslin, 2015), may thus shed light on our own cultural evolution.

Data availability

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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Additional information

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