Nonhuman Mammalian Cultural Behaviors and the Animal Cultures Debate

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In fulfillment of the requirements for the degree of Master of Arts

Spring 2017

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Abstract

Although humans are a uniquely cultural species, many animal species have the ability to learn socially as individuals. Of these, a few have exhibited social learning that cascades through a population in a way that could be considered cultural. Chimpanzees, orangutans, humpback whales, and dolphins display clear socially learned behaviors that are practiced on a large scale, with geographical variation, and with no apparent genetic or environmental explanation for these differences. These behaviors have been described as cultural behaviors, despite the lack of a universally accepted definition of culture. An understanding of nonhuman mammalian cultural behaviors and their evolution may guide future research on the varieties and extent of mammalian culture.

Introduction

Currently there is no clear consensus on culture in nonhuman animals. The question of nonhuman animal culture is not a new one, and the debate has changed in several ways since its inception. Arguments against nonhuman culture were initially based upon a lack of evidence for socially learned behavior, and differences between human and animal cognitive processing. Modern arguments are characterized by disagreements over the definition of culture, mechanisms of transmission, and the question of whether human and other animal cultures are homologous or analogous. In this review, I discuss the currently contentious topics in the animal cultures debate, and describe the best documented examples of cultural behaviors of nonhuman mammal species that have assisted in the recent shift towards acceptance of socially learned and maintained behavioral transmission in nonhuman mammals.

Disagreements between definitions of culture often neglect behavioral science and rely more on semantic arguments and distinctions. Less scientific textbooks, for instance, state that culture is "what makes us human" or "is to humans like water to a fish" (reviewed in Laland and Galef, 2009). Some proposed definitions exclude nonhuman animals by attributing features to culture that the authors believe to be exclusive to humans, such as teaching with intent to pass on information (reviewed in Laland and Galef, 2009). The majority of these definitions that aim at specifically disallowing mammalian "culture" instead use the word "tradition", which could be considered evading the issue. A recent psychology article stated that there is no single definition of the evolutionary culture concept, and that instead the term "culture" is applied to multiple related phenomena (Driscoll, 2017). While this is true, of "culture" as of many other terms, the goal of behavioral science should be to mitigate the

disagreements and construct a definition that is as universal and generally applicable as possible. Some biological definitions of culture include all social learning without regards to spread through a population (de Waal, 2001), tie culture only to information without regard to behavior (Richerson and Boyd 2005), or consider culture as a system of behavior, without regard to information (Jablonka and Lamb 2005). The definition of culture to be used in this review will be "information transmitted between individuals or groups, where this information flows through and brings about the reproduction of, and a lasting change in, a behavioral trait" (Ramsey, 2013). This definition addresses social learning and group adoption of behavior. However, this definition does not address the relationship between such behaviors and the genes or environment, a matter which will be discussed later. Driscoll (2017) takes aim at this definition's lack of an explicit focus on the social group level and the breadth of the definition as weaknesses. However, the definition of culture should not be confused with the criteria for nonhuman culture. While group-level social transmitted behavior is not explicit in the Ramsey (2013) definition, it is not excluded. A broader or more open definition helps to facilitate further conversation about behaviors and evolution of behavior while avoiding semantic or tangential arguments.

Comparisons between human and nonhuman culture are another area of contention. Such comparisons are as old as nonhuman culture studies themselves. Determining the extent to which aspects of the evolution of human and nonhuman cultural traits are homologous versus analogous would be a milestone for cultural evolution research. Arriving on a universal definition of culture would allow or disallow the assignment of culture specifically to nonhuman species, however does nothing to address the assertion that humans are animals and that the study of human behavior is uniquely independent from Biology (Pagnotta, 2014). The key to such an understanding would be a detailed analysis of the ways in which the evolution of behaviors is shared across species. For instance, Guinea baboon (*Papio papio)* exhibit three features that are also characteristic of human cultural evolution: ratcheting, structural changes, and lineage specificity (Claidiere et al., 2014). Hamadryas baboons (*Papio*

hamadryas) demonstrate a variety social behaviors comparable to those characteristic of *Homo erectus,* the evolution of which may have occurred similarly due to environmental patchiness. (Swedell and Plummer, 2013). Moreover, models of the maintenance of cultural variation and the transmission of complex traits seem to apply equally well to humans and nonhuman species (Kempe et al., 2014). Archaeological discoveries indicate that the origins of human culture are more ancient than traditionally thought, which also suggests greater scope for continuity between human and nonhuman culture. There is evidence of differences between human and nonhuman culture, but features that are believed to be human-specific appear to have arisen later in human evolution (Whiten et al., 2011). Differences in proportion of tool development are higher in ancient human Acheulean (manufacturing of stone tools) behaviors than chimpanzees (*Pan troglodytes)* (Gowlett, 2015). Nonhuman apes also have very high levels of conservativism in cultural behaviors, however intraspecific variability is also higher within social groups (Gruber, 2016), which may lead to slower cultural evolution in nonhuman apes. This may be due to technological and social characteristics evolved much more recently in humans, rather than a human exclusive trait (Whiten, 2016). Whiten (2016) also cites geographical patterning of traditions, cultural behavior, and the social learning processes that handle cultural transmission, as factors for the similarity of behavioral maintenance in human and nonhuman species, all of which would be species dependent and therefore differ between humans and chimpanzees. Similarities between *Pan* and *Homo* indicate that several features of human and chimp culture might be homologous, although chimps are less socially and technologically advanced than humans.

Mechanisms of social transmission are currently an area of interest for those interested in animal culture. Imitation is a driving force of culture in both human and nonhuman culture. Initial arguments against imitation as a force in cultural evolution claimed that teaching was a requirement for culture (Kruger and Tomasello 1996). More recently, cumulative cultural evolution, which some believe to be exclusive to humans, has been argued to be necessary for culture (Tomasello, 2016). Humans are unique

and remarkable in cumulative cultural evolution (Whiten, 2017). Evidence of nonhuman cumulative culture is weak, which may be due to lack of verbal instruction and a lower level of prosocial tendencies (Dean, 2013), although chimpanzees have shown capacity for cumulative cultural evolution (Pescini and Whiten, 2007). The intent involved in teaching is not required for imitation and innovation to occur. Since imitation together with the ability to modify learned behaviors can facilitate cumulative cultural evolution, teaching should not be viewed as necessary for culture. Despite behavioral conservatism, chimpanzee groups have been shown to modify behaviors and even combine several learned behaviors (Davis et al., 2016). Chimpanzees in Yerkes National Research Center, for example, have been observed in what appears to be maintaining behavioral differences between groups (Grant, 2007). Cultural activities must originate in existing social groups, and must remain somewhat conserved across generations in the process of propagation. Imitation is a mechanism of social transmission that fulfills both requirements (Claidiere and Sperber, 2010). Environments with high cultural variety are more likely to contain individuals that commit errors in imitation (Castro and Toro, 2014), which may account for variability or innovations in larger populations with more complex behaviors. Observations of animals show evidence of both public information, and information gathered from a tutor while decision making. Animals have even used acquired information to make incorrect decisions in food gathering studies (Rieucau, and Giraldeau, 2011). Such observations show that conformity through imitation can in some cases be crucial for an individual, and may be adhered to, even detrimentally. Conformity has been shown to stabilize between-group differences and increase in-group homogeneity (Claidiere and Whiten, 2012). When individual trial-and-error learning is costly and an individual can learn valuable information by observing others, this socially learned information can be advantageous. Such socially learned information can transfer between populations as well. A cost of abandoning a traditional behavior will tend to maintain a behavior as cultural (Thornton and Clutton-Brock, 2011). Imitation

appears to be a more common and less costly way of transmitting social behaviors than teaching, and does not necessarily sacrifice individualism and variation caused by mistakes and innovation.

The most concrete evidence of culture in nonhuman animals can be found in birds. Roughly half of bird species are songbirds, whose songs are socially learned. Many songbird songs are shown to change over time due to mate preferences and inconsistent imitation (Beecher and Brenowitz 2005). Changes in bird song over time have clear implications for nonhuman animal culture. However, this review focuses on the evidence of culture in mammals. Evidence of culture has been observed in primates and cetaceans, with a few examples in other mammals. Since primates, specifically chimpanzees, are the closest human relatives, they are the species most appropriate for the question as to what features of culture are homologous or analogous between humans and other animals. Cultural evolution interacts with both environmentally-induced (noncultural) changes and genetic evolution of behaviors. Cultural behaviors can substantially alter local ecology, and further reinforce cultural behaviors or affect the rate and direction of cultural evolution (Marlor, 2016). Cultural evolution can also lead to rapid genetic change (Foote et al., 2016). Thus, a variety of mechanisms can be responsible for changes in behavior even if they are considered culturally evolving; hence some of the examples provided here of cultural evolution might involve other mechanisms as well. Below are well-documented behaviors in nonhuman mammals that either exhibit the capacity to be cultural, or have provided direct evidence of cultural evolution.

Nonhuman Primates

Primates are a high-interest target of nonhuman culture studies due their social complexity, high intelligence, and close relatedness to humans. Nonhuman apes such as chimpanzees exhibit cultural behaviors regarding food acquisition, mate selection, and possible predator avoidance. Since higher ranking males are imitated more, chimpanzees are likely to adopt and transmit specific behaviors depending on which member of a population is displaying the behavior (Poirier and Fitton, 2001). This

may result in innovations by juveniles not becoming widespread in populations, leading to higher levels of conservatism. This also accounts for high variability of behaviors between social groups of a species, due to immigrating individuals usually being low ranking (Kendal et al., 2015). This might be the underlying mechanism of all primate culture.

Evidence of culture in Chimpanzees

Of the nonhuman apes, chimpanzees display the most elaborate cultural profile (Whiten, 2007). Human and chimpanzee culture share several characteristics, such as conformity and imitation, and with each characteristic human culture appears to have unique or more advanced aspects. These characteristics were most likely present in our most recent common ancestor (Whiten, 2011). Studies of nestedness (number of members of a species spread across the number of sites) for example, reveal non-random cultural variability, implicating cultural relatedness between chimps and humans that was absent in orangutans (*Pongo spp)* (Kamilar, and Atkinson, 2014). Chimpanzee populations build their nests at varying heights in trees, likely in an effort to avoid predation (Stewart and Pruetz, 2013), though evidence of nest building being socially learned is lacking. Social groups of chimpanzees are highly uniform in behavior, and conservative despite immigration. Incoming immigrants often take on the cultural behavior of the group (Luncz, and Boesch, 2014). Observations of wild chimpanzee moss-sponging and leaf-sponge re-use reveals that moss-sponging is significantly socially learned. 85% of observations were linked to social learning, with a fifteen-fold increase in transmission potential when learned by a juvenile (Hobaiter et al., 2014). Imitation also tends to occur if a behavior can be easily identified as more successful. For example, Vale et al. (2014) report on chimpanzees watching video screen demonstrations of extraction of resource-rich and resource-poor food options. Subjects picked the nutrient-rich food options more than chance would predict.

While chimpanzee culture is seen as the most advanced example of culture outside of humans, there are distinct differences between the two. Nonhuman apes, including chimpanzees, express culture without knowledge or understanding of culture, which may be a key difference between current human and nonhuman culture (Gruber et al., 2015). Human children use social information more than chimpanzees in food retrieval studies (van Leeuwen, 2014). Chimpanzees are also more conservative with cultural behaviors than human children in food acquisition studies (Haun et al., 2014), though food studies may not be an accurate measure of cultural behaviors that are not food acquisition related (Watson and Caldwell, 2009). Contradicting chimpanzee conservatism, however, chimpanzees that observed immigrant individuals with knowledge of how to consume the food previously unpalatable learned to eat the food themselves (Vale et al., 2017).

Detailed analyses have been performed on several cultural behaviors in chimpanzees, such as termite and ant fishing, with a focus on geographic variation and change over time. Fishing, first observed by Goodall in the 1960's (Lonsdorf, 2017), is present in several chimpanzee populations, with differences in frequency, and is absent in many populations. Chimps use the midrib of a leaf that they usually alter and shape by removing the outer leaf, to probe the inside of a termite or ant mound, and remove insects for consumption. Populations that fish for termites vary in the tools and processes they use (Sanz et al., 2004). Brush-tipped fishing probes are created in Congo basin populations as a deliberate design feature, but are absent in other East African chimpanzee populations (Sanz, 2009). The length of the probe of chimpanzees fishing for ants is dependent on the species of ant, with black ants typically requiring shorter probes and hand-feeding, and red ants requiring long probes and feeding directly to the mouth (Humle and Matsuzawa, 2002). Claims that these differences were caused by environmental differences prompted a study of how chimpanzees find and create probing tools. There were notable differences in the expression of functional tool use between immature and mature individuals within populations in The Goualougo Triangle, leading to a largely homogeneous outcome, but varying in

elements of process (Sanz, 2009). Ecological differences often provide opportunities to innovate and maintain variation in cultural behavior. For example, chimpanzees in Seringbara do not fish for termites, but only for ants (Koops et al., 2014). This effect has been seen in other ant-fishing populations as well, even in places where termites are abundant (Luncz and Boesch, 2015). Ecology, social dynamics, and both social and individual learning affect rates of tool use acquisition and right hand favorability in chimpanzees (Humle, 2016). Ecological studies on habitat, available diet, and tool use found high variability in behavior between geographically close communities, but a relationship between tool use and environment was not observed (Gruber et al., 2012). Fishing in Gombe differs from other populations in the predominant raw material used, and suggests that termite-fishing technology might vary with geographic distance and population connectivity. Even neighboring communities of chimpanzees differ in their fishing techniques (Sanz et al., 2004). Termite-fishing tools are similar in size and material in the long-studied communities of chimpanzees in western Tanzania and in West Africa, but tools are not similar in central African populations even though the same materials are present (Stewart et al., 2013). Neighboring populations of chimpanzees with variable tool length had no ecological differences (Koops et al.,2015). Evidence that termite fishing behavior was socially learned, specifically with the assistance of mother-offspring interaction, was observed when time spent with mother chimpanzees showed a positive correlation with the offspring's acquisition of critical elements of the skill (Lonsdorf, 2005). In the absence of evidence of genetic or environmental contributions to the behavioral variation, we can assume that the difference in behavior is due to socially learned behavior.

Hand clasp grooming (HCG) is another behavior used to study culture in chimpanzees, due to its high visibility, long duration, and high frequency in populations that practice it. First observed by McGrew in 1978, chimpanzees will find a grooming partner and raise one hand in the air and interlock hands, while grooming each other with the other hand. This is believed to be a means of communication that increases trust while grooming a partner (McGrew and Tutin, 1978). Grooming pairs typically share a

close relationship such as kinship, and those in closer relationships will groom more frequently, with most mating pairs grooming about every 2.4 hours (de Waal, 2006). Observations of HCG have shown an increase in frequency over multiple observed sites across Africa, showing increases of over 500% between 1992 and 2006 (de Waal, 2006). The number of HCG partners per individual increases from mothers, to other females, and then to males. Palm to palm clasping is a variety of HCG in which both chimpanzees lay their palms over one another. Palm to palm clasping is highly consistent in matrilines, which implies conservation of matriarchal grooming techniques (Wrangham et al., 2016). The number of HCG partners also increases with age (Nakamura and Nishida, 2013). Young males have also been observed performing HCG with larger numbers of partners than young females do. This is most likely due to mating-related social structures in chimpanzees (Nakamura Nishida, 2013). However, very few populations participate in HCG, and several nearby populations that do practice it differ in their methods. Van Leeywen et al. (2012) studied variation in HCG method and the distance between individuals participating in HCG behavior in four neighboring chimpanzee populations. They found that HCG style, in terms of whether hands, palms, or wrists were linked and the amount of elevation, could be systematically linked to the chimpanzee's group membership (Van Leeuwen et al., 2012). These behaviors showed spatial consistency both within and between groups, and the arm-length differential between partners could not account for distance (Van Leeuwen et al., 2012). Strange variants of HCG have been observed such as the "social-scratch", and the " leaf-clip". The social-scratch is when, after finishing HCG, the grooming chimpanzee rakes the hand up and down the partners back. The social-scratch has been observed in Mahale Mountains National Park, but has not been observed in the nearby Gombe, nor has it been observed at any other site (Nakamura et al., 2000). Leaf-clipping chimpanzees take a break from grooming their partners to bite a nearby leaf instead, and then return to grooming their partner. This activity has also been seen outside the context of HCG (Nishida, 1980). These differences in observed hand clasp grooming techniques are difficult to account for by genetic and

environmental differences due to their high variability; therefore, it is likely to have been socially transmitted.

Nutcracking is also a behavior in chimpanzees that has been adopted by several chimpanzee populations, while neighboring populations do not practice the behavior. First published in 1982, nutcracking behavior was originally thought to be widespread across Africa (Boesch and Boesch, 1982). Later, however, nutcracking was found to be limited to a very small area in Tai National Park within the evergreen forest perimeter, amid several surrounding populations that do not nutcrack. In Côte d'Ivoire, the N'Zo-Sassandra river is the dividing line between populations of nutcracking and non-nutcracking chimpanzees. Chimpanzee population density, the density of nut-producing trees, the availability of anvil and hammer-like tools, genetic diversity, and the type of forest, all differed between populations on the west and east sides of the river (Boesch and Boesch, 1994). Individuals consider four factors when choosing a tool. They preferred stones over wooden clubs, and hard woods over soft woods. Heavy stones were also selected, and showed a distance decay effect, meaning that the weight decreased as the stone was located farther from the anvil. Very light hammers were selected when nuts were being cracked directly on the tree (Sirianni et al, 2015). The material and size of the hammers used differed not only with the hardness of the nuts, but also between neighboring chimpanzee groups (Sirianni et al., 2015; Luncz et al., 2012). The tool selection process provides insight into possible traditions because the tools vary by location and population, but not according to environmental factors.

One site, "Panda 100”, contained more than 40 kilograms of casings from crushed opened nut shells. The tools discovered were deemed to be approximately 4300 years old (Mercader et al., 2007), and even the type of nuts opened was determined by analysis of starches on the shell casings (Mercader et al., 2007). The findings provide evidence that chimpanzees have likely been cracking nuts with stone

tools for thousands of years. The stone tools found at this site also exhibited a distance-decay effect (Luncz et al., 2016).

Young chimpanzees learn the skillful handling of the nutcracking tool by watching, and attempting to use the hammer of the mother. The mother not only shares nuts with her children for years, but also seems to demonstrate her methodology (Boesch 1991). Perhaps the strongest evidence of culture in nutcracking behavior comes from a recent study illustrating that immigrant females will change tool type when nutcracking to match the population they are immigrating into (Luncz et al., 2015). All signs point to nutcracking being transmitted socially, and having differences in methodology that cannot be explained by genetic or environmental factors. It is one of the clearest examples of culture in chimpanzees. Other behaviors that show evidence of being cultural in chimpanzees are pestle pounding (Yamakoshi and Sugiyama, 1995), tooth clacking (Marshall et al., 1999), and biting twigs into a pillow (Laland and Galef, 2009). One chimpanzee has even been observed wearing a blade of grass sticking out of her ear for no functional reason, and having several flattering copycats (van Leeuwen, 2014). This activity may be extremely informative due to it not having any function, but only fashion.

All claims of chimpanzee culture are contingent upon whether chimpanzees can learn from their peers. Transmission of habits through social learning in chimpanzees has been well demonstrated experimentally. In a study on social transmission, chimpanzees were given straws to use as tools for the acquisition of fruit juice, and were separated by the method they employed to use the straw to drink. Of the nine chimpanzees tested, four used the straw to suck the juice out, and five used a much less effective method of dipping the straw into the juice and scooping out the juice. When paired together, four of the five chimpanzees that used the scooping method switched to using the straws to suck the juice rapidly, and the fifth learned after being placed in a chamber with a plastic window neighboring a conspecific using the straw-sucking method. All chimpanzees that changed their methodology appeared

to do so by attempting to imitate more successful individuals (Yamamoto et al., 2013). Similarly, in a lab experiment, two chimpanzees were trained to manipulate a box containing food to receive a reward. Upon successful retrieval of the food, the trained chimpanzee was relocated and was used to demonstrate the task to another chimpanzee. Two separate means of obtaining the food reward were taught to the initial chimpanzees, "lifting" and "sliding", and the individuals that were trained were placed in separate groups. Chimpanzees in the group with the lifting expert did not adopt the sliding method, nor did sliding chimpanzees adopt the lifting. Members of a control group of chimpanzees were unable to obtain any food reward (Horner, 2006). These types of social learning results are much harder to achieve in wild chimpanzees; however, some experiments have revealed similar results. Two types of nuts, coula, and panda, were introduced into a new nut-cracking Bossou community, whose members had previously cracked and eaten only oil palm nuts. These nuts were collected from nearby sites, as they were unavailable in the region, and left in small piles in a clearing where nut cracking typically took place. Only one individual initially attempted to crack the coula nuts; an adult female immediately cracked and ate them. This caused juvenile chimpanzees to show interest, with several juveniles attempting to crack the new nuts, despite their initial lack of interest. Over a series of four coula nut presentations between 1993 and 2002, the number of adults who successfully cracked coula nuts rose by 67% (Matsuzawa and Humle, 2001).

Chimpanzees are a prime example of a nonhuman species that exhibits culture. No other species outside of humans is as well documented culturally, and many characteristics of chimpanzee culture are shared in human culture. While there are differences in behavior maintenance, information processing, and communication, there are multiple similarities in nearly all aspects except for cumulative culture. Chimpanzee show little signs of cumulative culture, but many signs of capacity for culture, and several behaviors that are culturally maintained. Future chimpanzee research attempting to demonstrate

culture should attempt to provide evidence of teaching to appease those that see it as a requirement for culture, or to demonstrate tool ratcheting in wild chimpanzee populations.

Evidence of culture in Orangutans (*Pongo pygmaeus*)

While chimpanzees have been the most valuable primate when it comes to understanding primate culture, research on orangutans has added a great deal of information due to their geographic isolation and their similarity to humans in some respects. Following Whiten's geographic chimpanzee study, van Schaik in 2003 documented differences in orangutan behavior based on geography. These differences included forms of tool use such as using leafy branches to swat insects, gathering water leaves to use as napkins, and poking sticks into tree holes to obtain insects and seeds. He even observed play behaviors such as "snag-riding" (surfing towards the ground on a falling tree), and emitting sounds such as "raspberries" and "kiss-squeaks". Several orangutans used plant products to amplify their sounds, or built cover during rainy and hot sunny days (van Schaik, 2003). Some orangutans were observed making what appeared to be dolls out of leaves, and sleeping with them (van Schaik, 2003). Van Schaik's observations are good examples of complex intelligence in orangutans, but the differences in behavior also provide evidence of culture. Several behaviors commonly observed in certain populations of orangutans were absent in nearby populations. For instance, orangutans on one side of a barrier river used tools to extract seeds from fruit with large barbs, while those on the other side did not (Van Shaik, 2001). Highlighting these differences does little to illustrate culture, however, unless genetic and environmental factors can be eliminated as sources of the differences. A genetic and environmental analysis of Van Shaik's (2003) data calculated differences in mtDNA and environmental variability. Genetic differences among orangutan populations explained very little of the geographic variation in

behavior, but environmental differences explained much more, indicating the importance of plasticity. There was, however, no correlation between plasticity and cultural behaviors (Krutzen et al., 2011).

Evidence of social transmission is also required to demonstrate culture in nonhuman animals. Multiple studies on orangutans illustrate transferring of behavior socially. An experiment nearly identical to the chimpanzee modeling behavior study (Whitten, 1999) was done in orangutans (Dindo et al., 2011). Orangutans were taught to either lift or slide a section blocking them from receiving a food reward. Two orangutans were initially taught by modeling, and then those orangutans each taught one new orangutan, which was used as the start of the transmission chain. The results were conclusive, and identical to the chimpanzee study (Whiten, 1999): socially learned behaviors were maintained, and the technique was transmitted along both experimental chains, with significant preferences for the modeled method. There was no control group in this experiment; however, individuals taught by video showed no interest in the video screen (Dindo et al., 2011). There is also evidence that orangutan diet is culturally transmitted, by juveniles watching what their mothers eat. Mothers have highly variable diet between individuals. Bornean orangutans copied their mothers' dietary choices, with an individual's diet being over 80% identical to that of its own mother (Jaeggi et al., 2010). Dietary choices were copied even if they were seen as poor choices by humans, such as eating cardboard (Jaeggi et al., 2010). Orangutans intently observe conspecifics, primarily while foraging and nest-building; orangutans seen "peering" at mothers often mimicked their food preferences. Periods of orangutan development with the highest levels of peering often coincided with nest-building practice. Also, as age increased, orangutans peered more at conspecifics other than their mother at higher levels (Schuppli et al., 2016). These results suggest vertical social transmission of diet, and imply that offspring that are with their mothers often, and offspring of mothers with more complex diets, would learn more through social learning.

While orangutans as a species are less studied than chimpanzees, they might be as capable of social learning, both in lab studies and in the wild, as chimps are. Future research should attempt to document mechanisms of transmission, and ratcheting of any socially learned behavior. Cultural differences in orangutans may be lost due to illegal logging activity in Indonesia. It is important to attempt to conserve whatever orangutan culture differences exist. As with human cultures, if a cultural variant is lost, it cannot be recovered.

Evidence of culture in other primates

Evidence of culture has been reported in several other primate species. The first instances of reported nonhuman culture were documented in 1953, when a Japanese macaque (*Macaca fuscata*) named Imo was observed using fresh water to clean the dirt from sweet potatoes, the only individual in the population observed doing so (Kawamura, 1959). When surveyed again in 1958, 78.9% of macaques under the age of seven washed their sweet potatoes, and several had switched to washing in salt water (Matsuzawa and McGrew, 2015). Evidence of culture has since been reported in several other primate species. Western (*Gorilla gorilla)* and eastern gorillas (*Gorilla beringei)* exhibit a combined 23 behaviors that meet criteria for behaviors with cultural potential (Robbins et al., 2016). Roughly half of all variation in these traits are intraspecific, and the other half was differences between western and eastern gorillas (Robbins et al.,, 2016). Mountain gorillas have shown various methods of tool use to open fruits with strong conservation to techniques and social transmission (Byrne and Byrne, 1993). Bonobos (*Pan paniscus*) show similar geographic behavioral differences as chimpanzees (Hohmann et al., 2003), and savanna baboons (*Papio cynocephalus)* have populations that have shown lower levels of aggression than other populations due a tuberculosis epidemic affecting primarily the more aggressive males.(Sapolsky and Share, 2004). Monkeys such as the vervet monkey (*Chlorocebus pygerythrus)* (Hauser, 1988), rhesus monkey (*Macaca mulatta)* (de Waal and Johanowicz, 1993), and capuchin

monkey (*Cebus capucinus*), have all shown behaviors that appear to be socially learned and vary geographically. Juvenile vervet monkeys that were given sand-covered grapes imitated the washing techniques their mothers used, and mothers that displayed more than one technique had juveniles more likely to also explore other techniques (van de Waal, 2015). Vervet monkeys that witnessed a conspecific solve food acquisition task often mimicked the same technique (van de Wall, 2015). Of all monkeys, the capuchin has been studied the most regarding cultural behaviors. Wild capuchin monkeys play games such as hand sniffing, finger and toe sucking, and removing objects from each others' mouths. The games played, and the frequency of their play over time, vary among five sites in Costa Rica (Perry et al., 2003). Capuchins in Brazil have also been observed participating in culturally maintained nutcracking activity as well (Mendes et al., 2015). Capuchins also specialize in foods that use multi-step processing, and different techniques are used within the same groups with some amount of conservatism. Juvenile capuchins, especially females, tend to mimic the foraging techniques of their mothers (Perry 2011). The evidence for culture in these primates is not as strong as in chimpanzees or orangutans. Capuchins appear to have the highest capacity for culture of these primates, and more evidence must be collected to corroborate the claims that these species exhibit culture.

Evidence of culture in Cetaceans

A mélange of cetacean behaviors illustrates high intelligence, and evidence for a cultural basis for several behaviors has been documented in whales and dolphins. These behaviors are often harder to study in aquatic animals due to their large ranges, environmental variability, and the fact that the behaviors are drastically different than those seen in primates. For instance, tool use is less prevalent in aquatic creatures (Mann and Patterson, 2013) but other sorts of data such as audio recordings are more effective in demonstrating culture than in primates. Prior to Rendell and Whitehead (2001) cetaceans

were thought by some to have culture, but the article accumulated so much data and discussion that arguing against the presence of nonhuman animal culture became much more difficult. Rendell and Whitehead (2001) attempted to highlight all of the behaviors that might be considered cultural in multiple cetacean species, and facilitate discussion about why some still oppose it. While not all the cetacean species with possible cultural behaviors exhibit the same behaviors, many of the candidates are vocalizations and feeding techniques.

Humpback Whales

Humpback whales (*Megaptera novaeangliae)* exhibit differences in feeding practices such as lobtail feeding, and and also exhibit cultural evolution in song. Lobtail feeding is observed when a whale dives to blow bubbles under schools of fish, in order to raise them towards the surface. The whale slams its tail flukes onto the water prior to diving. The spread of this behavior is known in some detail, since it was recorded over a nine-year period in individuals known from photo-identification. These details provide clues to the transmission process (Weinrich et al., 1992). This behavior was observed first in 1981, and was practiced by nearly 50% of the population in 1989 (Weinrich et al., 1992). The observations might show some ratcheting effect, to improve the effectiveness of the technique. The behavior has also been shown to be adopted by younger humpback whales, which implies social learning (Rendell and Whitehead, 2001).

The humpback whale's song evolution is possibly the best example of a cultural phenomenon in cetaceans, and the most extensively documented whale behavior. Research has been conducted for decades on how these songs change over time, and how they are conserved. Songs vary in the number of repeats and phrases used. All males in a breeding population sing nearly the same song, but the song

evolves structurally over time, changing noticeably over a breeding season, and substantially over periods of a few years, but remains relatively unchanged over summer months (Payne & Payne 1985). Songs from Maui, Hawaii, and Islas Revillagigedo, Mexico (4,500 km apart) are similar at any time, but change in parallel over a two-year period (Payne & Guinee 1985). Cerchio and Darling (1993) suggested that evolving humpback song may form dialects, and that conformity to the current dialect may be socially significant in the same way that conformity to the local dialect can be in birds. This lead to several claims (Janik, 2001) that geographical clan data alone are not enough evidence to claim possible culture). This continuous evolution over such a large area in such a short period is difficult to explain. This became somewhat of an issue because it appeared to be travelling and evolving too fast to be matched by any cultural model (Kucaj, 2001). Humpback whale song transmission has been observed in the South Pacific to occur in cultural waves under high sexual selection pressure, and evolve at speeds that are "unparalleled" (Garland et al., 2011). Evidence also suggests that songs can transfer between populations when individuals transfer, and at feeding grounds (Garland et al., 2014). Centrally located social units in a vocal cluster have higher levels of song-sharing among populations than other clusters (Garland et al., 2015), indicating that levels of song evolution varied by region. Song structure within a humpback whale social group seems to be formed from a combination of innovation during song transmission and conservation (Cantor and Whitehead, 2013). Songs have also been shown to evolve during song revolutions by combining multiple complete phrases and themes from one of three song types, before transitioning through a hybrid phrase into the phrases and themes of another song type (Garland et al., 2016).

Lobtail feeding in humpback whales shows intelligence, coordination, and social transmission. Whale song transmission might be analogous and nearly identical to that of birdsong, which is considered one of the best examples of culture in animals. Future research on details of the mechanisms of song

evolution, speed of transmission, and selection behind song evolution would answer the majority of the current unanswered questions regarding humpback whale culture.

Sperm Whales

Sperm whales (*Physeter macrocephalus)* also have vocalizations that are indicative of culture, though this claim is much less well supported than in humpback whales. Sperm whale vocalizations are distinctive, stereotyped patterns of 3 to 12 clicks called codas, which are thought to function in communication (Watkins & Schevill 1977). Popular codas are conserved by imitation and transferred among conspecifics (Cantor et al., 2015). Smaller social units of whales gather periodically in larger clans exclusively with social units with similar codas (Whitehead et al., 2012). Clans contain thousands of females, but are sympatric and have distinctive vocalizations, and movement patterns (Whitehead et al., 2012). In the North Atlantic, social units rarely group with other social units, and there is no evidence for sympatric cultural clans. This difference is believed to be caused by an effort to prevent predation from killer whales (Whitehead et al., 2012.) Distinctive coda numbers and spacing are a feature of groups of about 20 female sperm whales, and have a matriarchal lineage (Weilgart & Whitehead 1997). Given female sperm whales' range of roughly 1,000km, (Dufault & Whitehead 1995) these dialects are effectively created in pockets of sympatric dialects of matriarchal clans, where social units sing with specific codas. mtDNA testing concluded that there was a correlation between mtDNA and coda type (Whitehead, 1998). Social units seem to form groups preferentially with other units within their clan. Sperm whales are then believed to be an example of sympatric culture on a global scale, in that songs are universal, though codas vary. Culture may therefore be an important determinant of sperm whale clans, even more so than genetics (Rendell and Whitehead 2003). In the Pacific Ocean, female sperm whales live in nearly permanent social units that typically contain about 11 females and immatures of multiple, unrelated matrilines (Rendell and Whitehead 2003).

Killer Whales

Orcas (*Orcinus orca)* have recently been receiving a lot of attention from scientists studying animal culture. A 2016 study reported evidence that, at some point close to 250,000 years ago, there was a drastic bottleneck in the orca population, and the remaining communities likely underwent ecological divergence and genetic drift, which resulted in a wide range of genetic differentiation between pairs of allopatric and sympatric communities. What then occurred is a rapid evolution of cultural behaviors and genetics (Foote et al., 2016). Orca calls have been compared to accents in human speech, in the way they are passed down from parent to offspring (Marino et al., 2007). Orcas form pods of closely related individuals, groups of pods gather together to form clans which use similar dialects. Despite innovation and mistakes in songs, conservation was observed within matriarchal lineages (Filatova and Miller 2015). Neither phylogeny of dialects nor similarity of syllables is correlated with associations between matrilineal units, although the number of syllables shows correlation (Filatova et al., 2017). Prior to this, killer whales were studied for several behaviors that varied geographically, such as grouping together and targeting prey as a hunting team to form a wave large enough to splash prey off a piece of ice (Rendell and Whitehead, 2001). The complex and stable vocal and behavioral cultures of sympatric groups of killer whales appear to have no parallel aside from humans, and represents an independent evolution of cultural faculties. Groups of killer whales will also greet each other using different motions and vocalizations (Rendell and Whitehead, 2001). These differences may be an example of culture, though such claims are not well supported. More information regarding transmission and maintenance is required.

Dolphins

Bottlenose dolphins *(Tursiops truncatus)* are among the most intelligent mammals, and those in Shark Bay, Australia are said to have the most complex social relationships described so far in cetaceans, due

to fission-fusion grouping (social groups that change composition frequently) (Connor, 2007). These dolphins use the marine basket sponge (*Echinodictyum mesenterinum*) as a tool to protect their rostra during foraging (Smolker et al., 1997). Sponge foraging is primarily a female behavior, and appears to be learned via vertical social transmission (Mann et al., 2008). mtDNA analysis suggests dolphins that currently exhibit this behavior are very closely genetically related, almost exclusively descending from one matriarchal lineage. Of the calves observed foraging, 87% used a strategy identical to their mother (Mann et al., 2001). This points to the invention of using the sponge as a tool from a single "sponge Eve" (Krutzen et al., 2005). Fatty acid analysis of bottlenose dolphins reveals differences between populations of sponge users and non-sponge users (Krutzen, et al., 2014). It is also believed that not using echolocation, and instead digging with sponges, is beneficial for locating targets without swim bladders, for which echolocation is not as functional (Patterson & Mann, 2011). No other population of bottlenose dolphin on Earth has been observed using sponges as tools, and closely related individuals do not use the tool. It seems unlikely that the behavior is environmental or genetically rooted.

Dolphins exhibit other behaviors that are indicative of social transmission, such as characteristic vocalizations. These whistles are highly complex, and are generally conserved across a dolphin's lifetime. Male dolphins in alliances in Australia and Florida, have been observed modifying their original whistles in an effort to converge on a similar whistle type to that of their alliance partners (Smolker and Pepper, 1999). Whistle sharing may identify members of a group, separating them from others, an example of culture. High natural variation was observed in these calls, and usually are characteristic of a group. Humpback whales may have the most social vocalizations of the cetaceans, though much less is known regarding dolphin vocalization. Dolphin social vocalization may be even more complex, as demonstrated by their complex social transmission of whistles (Herman, 2001), and has even been seen to imitate the vocalizations of sea lions and turtles (Bauer & Harley, 2001).

Cetaceans are certainly difficult to study; however, observations show social transmission, evolution of vocalizations, tool use, and most other cultural observations witnessed in primates. The Whale and Dolphin Conservation Society compares cetaceans and primates, even calling cetaceans the "apes of the sea". It is difficult to say which group provides a better example of nonhuman animal culture because of the differences in the amount of research performed.

Evidence of Culture in other mammals

Few other mammals have behaviors that might be considered cultural. These mammals typically only demonstrate a single behavior that could be considered socially transmitted, and the evidence is generally incomplete. Black rats (*Rattus rattus)* have been shown to learn to strip open pine cones, and juveniles learn the technique from mothers that practice the technique. The technique acquired is a direct imitation of the mother (Terkel, 1996). Similarly, Norwegian rats *(Rattus norvegicus)* mimic food preference choices. Rats were trained by humans to choose a specific food source, and were imitated by those that were not trained (Galef, 1982). Spearnose bats *(Phyllostomus hastatus)* can discriminate among calls from different caves. This discrimination is believed to be based on whether calls are familiar or unfamiliar (Boughman and Wilkinson, 1998). Giant otter *(Phyllostomus hastatus)* vocalizations are categorically socially transmitted and show changes over time acquired by multiple groups (Leuchtenberger et al., 2014). African elephant *(Loxodonta africana*) fidelity to a site is a result of extended juvenile development and extensive ecological knowledge gained from observing conspecifics (Fishlock, 2016). Several other mammals can learn behaviors socially; however, those not mentioned may not be considered animal culture due to the lack of learning, or a genetic or environmental explanation for differences in behavior. Also, in most cases there is no documentation of a change in the behavior over time.

Conclusions

Humans have a history of self-aggrandizing, as exemplified by claims that culture is an exclusively human trait. Culture was attributed originally only to humans, and this bias likely led to the creation of definitions of culture that set human culture aside as unique. Studies then used these anthropocentric definitions of culture, to determine whether nonhuman species behaviors meet those definitions rather than universal criteria. Chimpanzees, orangutans, humpback whales, and dolphins display clear socially learned behaviors that are practiced on a large scale, with geographical variation, with no apparent genetic or environmental explanation for these differences. These behaviors meet the criteria set by previous definitions of culture, before teaching and cumulative culture were considered by some to be necessary. While these two specific features are characteristics of advanced human culture, they have not been clearly observed in nonhuman animals and might be distinctive features of human culture. Behaviors of other species have some but not all of the features listed above that are indicative of culture. Further research is needed to discern whether behaviors are subject to technological or communicative ratcheting, whether cumulative culture exists in any nonhuman species, and whether cultural features in humans are homologous with those in nonhumans. One promising experimental method would be the introduction of an individual with knowledge of a food acquisition technique to a wild population; researchers would then observe whether the population adopts the technique. A follow-up experiment demonstrating capacity for cumulative culture would involve introducing a further individual with a more efficient technique. If the improved technique is adopted, this would illustrate a two-step ratcheting of a socially learned behavior. While strong evidence of cumulative culture is currently unique to humans, all other aspects of culture have been observed in other animal species. Hopefully future research will lead to widespread adoption of universal definitions and criteria for culture, and ultimately identification of the ways in which human and nonhuman culture are homologous or analogous.

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