

## Comments

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Social customs are ubiquitous across human cultures. But, the habits we learn from others (de Waal 2001) or “the way we do things” (McGrew 2004) can be so engrained in our everyday behavior that we are sometimes unaware of their significance until we encounter people for whom customs differ from our own. These cultural differences, whether subtle or extreme, have been documented by cultural anthropologists through detailed ethnographies (e.g., Mead 1928), and used to explain psychological processes from cognition to child development (e.g., Heine 2011).

Although the ethnographic method is not without flaws (Aunger 1995), objective observation and detailed description provide the necessary foundation for understanding the behavior of individuals and groups. But, whether it is a valid tool for studying social customs and other cultural behaviors in nonhuman primates has been debated. Ingold (2001), for example, argued that the ethnographic method cannot be applied to the study of nonhuman primates because it “fails to achieve an understanding that is sensitive to the intentions and purposes of the people themselves, to their values and orientations, to their ways of perceiving, remembering, and organizing their experience, and to the contexts in which they act” (337). More recently, Laland and Janik (2006) have argued that the ethnographic method is weak for both conceptual and interpretive reasons. In particular, Laland and Janik criticize the method of exclusion, through which genetic and ecological explanations for patterns of behavior must be ruled out, yet has been the primary method of recognizing cultural behaviors in nonhuman primates for at least the last 15 years. In recent years, enhanced phylogenetic analysis (e.g., Lycett, Collard, and McGrew 2007, 2009), improvements in detailed genetic analyses of primate groups (e.g., Langergraber et al. 2011) and focused ecological studies specific to purported cultural behaviors (e.g., Gruber et al. 2012; Koops, McGrew, and Matsuzawa 2013) have contributed to the debate.

Yet, as Nakagawa et al. point out, the majority of studies reporting on, or examining the innovation and transmission (via social learning) of, cultural behaviors in primates have focused on food-related (Watson and Caldwell 2009) and technological/subsistence behaviors for which the method of exclusion may be a more relevant tool. Thus, I agree with Nakagawa et al. that “social behaviors are less susceptible to the criticism that they were simply an adaptation to local environmental conditions due to their seemingly arbitrary nature.” Moreover, as with the customs that are definitive of human cultures, social customs often go unnoticed to ob-

servers familiar to the group (Nakamura and Nishida 2006), but are not any less important to our understanding of the evolution of culture.

Nakagawa and colleagues provide a welcomed report on social customs among nonhuman primates. Importantly, this research adds breadth to a literature that is mostly dominated by reports of social customs in one species—chimpanzees (for exceptions, see works cited in target article). Together with the recent paper by van Leeuwen et al. (2014) describing the “grass in ear” behavior of chimpanzees, the study by Nakagawa et al. should serve as reminder that to fully understand cultural behavior patterns we must not forget the root of cultural primatology and to look for the often subtle ways in which group-living individuals do things, even if the exact purpose cannot be determined.

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## Arbitrary Cultural Behavior Patterns Are Not Unique to Humans

While there is increasing evidence for cultural variation in a wide range of animal taxa, some behavioral domains are far more represented than others in the literature. On the one hand, there are numerous examples of animal material culture, including food preferences, food processing techniques, tool use, and medicinal plant use. On the other hand, reports on animal social culture, such as communicative rituals, courtship displays, allogrooming patterns, social play behaviors, and interspecific interactions, are relatively rare (reviewed in Fragaszy and Perry 2003; Laland and Galef 2009). By providing additional data to the latter, the study by Nakagawa and his colleagues is a timely and important contribution to the field of cultural primatology. Their findings have the potential to fuel the debate between evolutionary biologists who claim that culture is present in thousands of species (Lumsden and Wilson 1981) and sociocultural anthropologists who argue that “animal behavioral traditions” and “human culture” should be considered analogous rather than homologous because the content of what is transmitted is radically different (i.e., simple food-related utilitarian behavioral patterns versus elaborate social norms/conventions and ceremonial/symbolic customs based on complex beliefs; Hill 2009).

In nonhuman animals, material and social cultures differ in several ways. The former involves physical objects (e.g., food items, plant materials, and tools) that are used in subsistence-related contexts (e.g., feeding, self-medication) via the expression of adaptive behaviors that are reinforced by direct benefits to the performers and become the primary targets of natural selection. Thus, the form and sequence of

the motor patterns found in animal material culture are generally nonarbitrary. For example, efficient nut-cracking behavior requires the combination of specific objects with precisely coordinated and hierarchically organized behavioral patterns (Inoue-Nakamura and Matsuzawa 1997; but see Leca et al. 2011 for a notable example of arbitrary material culture in nonhuman animals).

The latter involves social interactions whose usage is far less obvious, as they occur in the context of social conventions or playful activities (reviewed in Nakagawa et al.). Apparently, these interactions are not reinforced by direct benefits to the performers, and therefore, they may not be the primary targets of natural selection. As such, they can be categorized as non-adaptive cultural behaviors. Relaxed functional constraints on social culture generally result in flexible and arbitrary behavioral patterns. Indeed, contrary to stone tool use, there are no optimal hand-clasp grooming postures in chimpanzees (cf. McGrew et al. 2001) and no possible “mistake” in expressing social greetings through hand sniffing, eye poking, or any other social games observed in white-faced capuchins (cf. Perry et al. 2003). According to Stephenson (1973), behavioral arbitrariness is usually a function of individual experience, but can also be influenced culturally through social interactions with other group members. Despite Nakagawa et al.’s (undemonstrated) claim that embracing behavior in Japanese macaques may serve to reduce social stress, this social custom is not likely to affect survival or reproductive success. Arguably, the apparent lack of direct fitness consequences and the arbitrariness of embracing positions (i.e., ventro-ventral, ventro-lateral, and ventro-dorsal) and rhythmic movements (i.e., opening and closing palm and body rocking) make it easier to rule out obvious ecological factors and thereby examine cultural factors as potential causes of intergroup variation (cf. Leca et al. 2007).

Interestingly, a recent study found marked intergroup differences and covariation in the frequency and form of two types of nonconceptive sexual behaviors in female Japanese macaques (i.e., female-female mounts and female-male mounts; Leca et al. 2014). Whereas male mounting posture should be optimal (i.e., precisely coordinated and invariant) in order to achieve penile intromission during heterosexual copulation, female mounting is less functionally constrained, which allows for more flexible and arbitrary behavioral patterns. Leca et al. (2014) showed that the customary occurrence, high prevalence, and great diversity of female-female and female-male mounts at Arashiyama may be the result of combined favorable sociodemographic conditions, namely few resident males, most of them being old, sexually under-motivated, and less aggressive and controlling than the average male Japanese macaques living in the other study groups at Minoo and Jigokudani. They suggest that female-female and female-male mounts may be cultural sexual practices in the Arashiyama monkeys; in most other populations, all the aforementioned favorable sociodemographic conditions are not met, and although female mounting may occasionally be ex-

pressed by several group members, it does not reach the group-level cultural status. In line with Nakagawa et al.’s account for group-specific forms of embracing behavior, Leca et al. (2014) argued that although genetic explanations for such intraspecific variation cannot be ruled out, *arbitrary* behavioral patterns such as intergroup differences in female mounting postures in Japanese macaques could be purely cultural, as any alternative explanation is difficult to imagine. As group-level social tolerance is key to explain cultural variation (Bonnie and de Waal 2006), future research could explore whether embracing behavior is more common in groups with a “mellow” social style.

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Nakagawa et al. give us a valuable addition to the ethnography of nonmaterial culture in nonhuman primates, with their detailed description of stylized embracing in Japanese macaques. They rightfully point out that such social customs (i.e., those lacking any necessary contributions from external objects or the physical environment) have been reported far less often than the material cultural patterns of elementary technology and subsistence. Moreover, they offer a cross-populational comparison that reveals intergroup differences, suggesting that this behavioral constellation is flexible, perhaps as a result of social learning processes. The kneading versus rocking contrast is fascinating, as both involve kinesthetic cues. What follows here is a series of queries, posed in hopes that the authors will amplify or clarify some of the points that they have raised.

### Culture Defined

This has always been a thorny area, both conceptually and terminologically. For example, transgenerational, vertical cultural transmission may characterize traditions, but within-generational, horizontal cultural transmission may give rise to fads, or pop culture. Both are culture. Similarly, the differences between intra- versus inter- and population versus group comparisons need to be made clear.

### Material Culture

The authors’ distinction between social versus technological/subsistence seems to be confounded: 5 of their 11 examples (play nest, kiss squeak, stone bang, stone throw, branch shake) cited as social customs necessarily involve external objects. Perhaps a more clear-cut distinction might be material versus nonmaterial culture? (See McGrew 1992 and 2004 for fuller discussion.) A classic example of nonmaterial culture in Japanese monkeys is found in Green’s (1975a) wide-ranging