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The Influence of Ecology on Chimpanzee (*Pan troglodytes*) Cultural Behavior: A Case Study of Five Ugandan Chimpanzee Communities

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The influence of ecology on the development of behavioral traditions in animals is controversial, particularly for chimpanzees (*Pan troglodytes*), for which it is difficult to rule out environmental influences as a cause of widely observed community-specific behavioral differences. Here, we investigated 3 potential scenarios that could explain the natural variation in a key extractive tool behavior, “fluid-dip,” among several communities of chimpanzees of the *Pan troglodytes schweinfurthii* subspecies in Uganda. We compared data from previous behavioral ecological studies, field experiments, and long-term records of chimpanzee tool-using behavior. We focused on the quality of the available food, dietary preferences, and tool sets of 5 different communities, and carried out a standardized field experiment to test systematically for the presence of fluid-dip in 4 of these communities. Our results revealed major differences in habitat, available diet, and tool use behavior between geographically close communities. However, these differences in ecology and feeding behavior failed to explain the differences in tool use across communities. We conclude that ecological variables may lead both to innovation and loss of behavioral traditions, while contributing little to their transmission within the community. Instead, as soon as a behavioral tradition is established, sociocognitive factors likely play a key maintenance role as long as the ecological conditions do not change sufficiently for the tradition to be abandoned.

Keywords: ecology, tool use, *Pan troglodytes schweinfurthii*, culture

Chimpanzees are some of the most accomplished tool users in the animal kingdom, a finding that has considerable implications for understanding the evolutionary origins of human cognition and capacity for culture. However, it is also well established that wild chimpanzee communities vary in their use of tools and, notably, that some communities hardly show any tool use (McGrew, 1992, 2010; Whiten et al., 1999). An ongoing source of contention concerns the nature of the mechanisms that have led to the ob-

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served behavioral diversity and whether such behavioral differences qualify as culture (Galef, 2009; Tomasello, 2009). Here, we define *culture* as a community-specific set of behaviors that an individual is exposed to and can socially learn from others (Gruber, Muller, Strimling, Wrangham, & Zuberbühler, 2009). A common line of reasoning is that if the ecological and genetic differences between the different communities are minimal, then, by default, any observed behavioral difference must be "cultural" (de Waal, 1999). However, other authorities in the field have argued that the habitats of wild chimpanzees are too complex to rule out ecological explanations a priori or without specific empirical data (Galef, 1992; Tomasello, 1999). An intermediate position is that group-specific behavioral differences will always be a product of interactions among ecological, genetic, and social factors (Krützen, van Schaik, & Whiten, 2007; Laland & Janik, 2006, 2007), a stance also adopted by recent field studies (Möbius, Boesch, Koops, Matsuzawa, & Humle, 2008; Schöning, Humle, Möbius, & McGrew, 2008).

Previously, we have experimentally shown that one widespread chimpanzee tool behavior, fluid-dip, is absent in the Sonso community of Budongo Forest, whereas it is present in the geographically close Kanyawara community of Kibale National Park, less than 200 km away (Gruber, Muller, Reynolds, Wrangham, & Zuberbühler, 2011; Gruber et al., 2009). Our studies have suggested that this difference should be interpreted in cultural terms, notably because the observed behavioral differences appear to have a cognitive underpinning. In particular, our suggestion was that the Sonso chimpanzees had never learned to consider sticks as relevant to manufacture a tool to extract food (Gruber et al., 2011). However, this interpretation has remained tentative because it has not been possible to rule out that subtle ecological differences between the two communities are responsible for the observed variation. Here, we aim to address the origin of the observed variation in tool use by comparing ecological, experimental, and observational data available for different chimpanzee communities in Uganda.

At least three hypotheses have been proposed to explain group-specific variation in animal behavior: local adaptation, ontogenetic flexibility, and cultural difference (van Schaik, et al., 2009). Under the first scenario, the local adaptation hypothesis, the presence or absence of fluid-dip is due to genetic differences between groups. In our case, this scenario is very unlikely, given the small distance between Budongo and Kibale forests. Moreover, the subspecies *P. t. schweinfurthii* has very low genetic diversity (Goldberg, 1996; Goldberg & Ruvolo, 1997b), suggesting that genetic differences are unlikely to explain the observed behavioral differences. Finally, the Kanyawara and Ngogo communities of Kibale Forest show different patterns of tool use despite being genetically indistinguishable (Langergraber et al., 2011). For these reasons, we conclude that it is simply unreasonable to propose that genetic factors alone could explain the observed behavioral differences in stick use across the Ugandan communities.

According to the second scenario, the ontogenetic flexibility hypothesis, ecological differences are the main cause for behavioral differences, which develop in response to local ecological conditions. The prediction here is that individuals affected by the same local ecology will develop group-specific behavior (Tennie, Call, & Tomasello, 2009). Thus, tool use differences in feeding-related behaviors are interpreted as responses to variation in food availability. The prediction is that communities with similar diets should also be similar in tool use. Communities that differ in fluid-dip, in other words, should differ more strongly in their diet than communities that are the same. To test this hypothesis, we compared the ecology of three Ugandan communities, that is, at Sonso, Kanyawara, and Ngogo, using published data collected with comparable methods (Sonso: Fawcett, 2000; Newton-Fisher, 1999; Tweheyo, Lye, & Weladji, 2004; Kanyawara: Wrangham, Chapman, Clark, & Isabirye-Basuta, 1996; Wrangham, Conklin, Chapman, & Hunt, 1991; Wrangham et al., 1993; Ngogo: Potts, Watts, & Wrangham, 2011). We complemented these data with preliminary results from two other communities within Budongo Forest, the Kaniyo Pabidi and Busingiro communities.

The third scenario, the cultural diversity hypothesis, requires evidence that social learning has been responsible for the observed differences in tool behavior. In our previous experiments at Sonso and Kanyawara, we found complete segregation in how the two communities solved an identical experimental task (Gruber et al., 2009, 2011). Although this supports the cultural diversity hypothesis, a strong test would require evidence of novel, ideally experimentally seeded, tool use behavior to spread throughout the community via social learning, which we have not been able to address in this study. Instead, our strategy was to (a) empirically test the main alternative, the ontogenetic flexibility hypothesis, and (b) assess the plausibility of the cultural diversity hypothesis indirectly in light of what is known about the evolutionary history of the East African forests.

Method

Study Sites and Subjects

Kibale and Budongo forests are home to the largest populations of chimpanzees (*Pan troglodytes*) in Uganda. Budongo Forest consists of three main blocks, separated by two roads and surrounded by several disconnected satellite forests and forest fragments (Plumptre, 1996; Reynolds, 2005). The entire forest contains approximately 640 chimpanzees, about eight to 10 communities overall, with a density of 1.36 individual/km^2 (Plumptre, Cox, & Mugume, 2003). Other additional communities live in the satellite forests surrounding the main forest block (McLennan, 2011a). Three communities living in the main forest block have been habituated to human observers, at Busingiro, Sonso, and Kaniyo Pabidi (see Figure 1). The Sonso community has been habituated most extensively for research and consists of approximately 70 individuals. The Kaniyo Pabidi community has been partly habituated for ecotourism but its exact group size is still unknown. At Busingiro, chimpanzees were tolerant of human presence in the 1960s (Sugiyama, 1968), but this was no longer the case during our study and group size was also unknown.

Kibale Forest contains about 1,400 chimpanzees, or 2.32 individuals/km^2, possibly the highest density of chimpanzees in Africa (Plumptre et al., 2003). Local densities at Kanyawara and Ngogo are 1.4 and 5.1 individuals/km^2, respectively. Most recently, the Kanyawara community counted 51 members, and the Ngogo community consisted of more than 150 individuals (Potts et al., 2011). These two communities, separated by 12 km, are about 180 km from Sonso (Budongo Forest; see Figure 2).

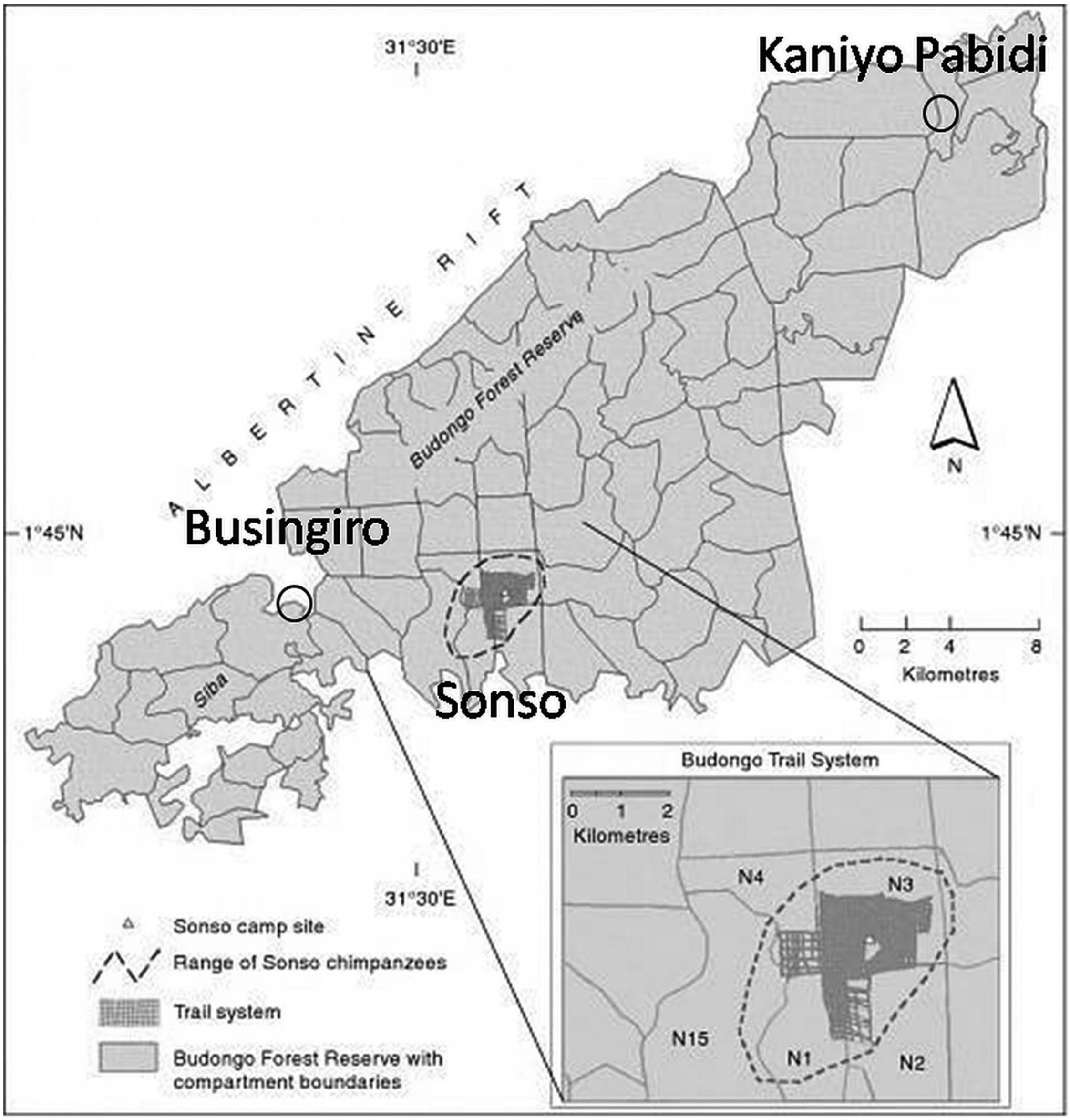


Figure 1. Map of the Budongo forest showing the location of Busingiro, Sonso, and Kaniyo Pabidi. From *The Chimpanzees of the Budongo forest: Ecology, behaviour and conservation*, by L. Hazzah and M. Reuling, 2005. Oxford, United Kingdom: Oxford University Press. 2005 by Oxford University Press. doi:10.1093/acprof:oso/9780198515463.001.0001. Reprinted with permission.

Tool use is surprisingly rare at Sonso, with only one of 11 (9.1%; Whiten et al., 1999) tool behaviors used for extractive purposes. At Kanyawara, the rate is two of 11 (18.2%; Whiten et al., 1999), and at Ngogo, four of 11 (36.4%; Watts, 2008). Although the three communities use leaves to manufacture sponges to extract water from cavities, only the Kanyawara and Ngogo chimpanzees use sticks to extract honey from beehives. In addition, Ngogo individuals also use sticks to enlarge existing holes, and some individuals have been observed to use twigs to fish for insects. Overall, the Sonso and Kanyawara communities have the lowest extractive tool-using diversity of all Eastern communities described so far (McGrew, 2010), and the Ngogo community only makes irregular use of tools (Watts, 2008).

Experimental Tool Tests

In the following, we briefly describe the experimental protocol followed at Kanyawara (Kibale Forest) and Sonso (Budongo Forest). For a more extensive description, see Gruber et al. (2009, 2011). The basic idea was for chimpanzees to encounter a log with a cavity that contained a desirable but not directly accessible food. Our apparatus thus consisted of a 25-cm wide log of a standardized length of 50 cm with an artificial hole with a 5 × 4 cm opening and 16 cm depth. We prepared several such logs, which we then positioned at places the chimpanzees were likely to visit. The hole was filled with honey to 10 cm below the surface every morning before the chimpanzees arrived. Honeycombs were used to cover

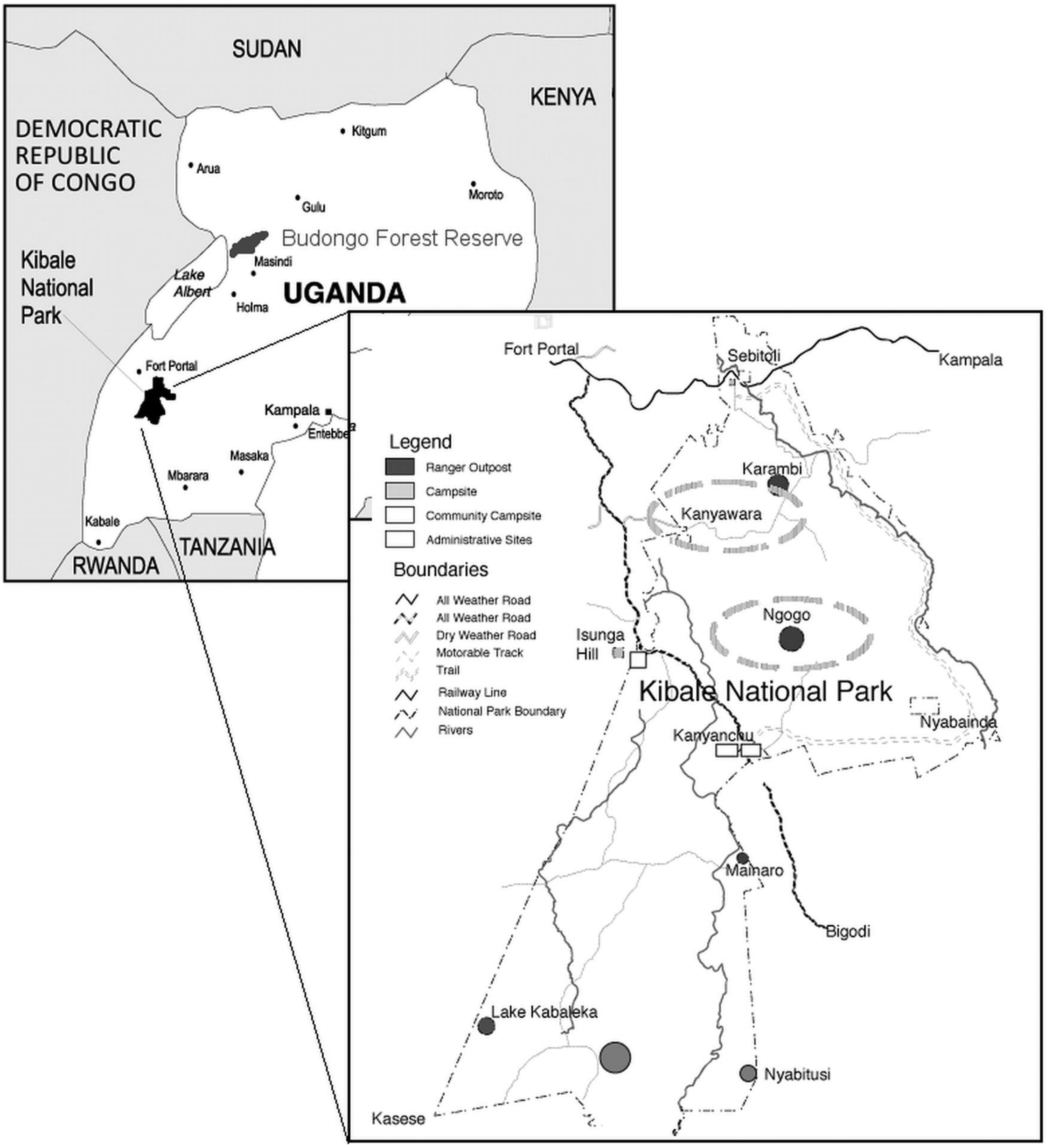


Figure 2. Map of Uganda with location of Kibale National Park and Budongo Forest Reserve with zoom on Kibale National Park showing the locations of Kanyawara and Ngogo.

the hole to protect it from insect invasion and to provide a visual cue.

At all sites, data were acquired with a motion-sensitive video camera (DVREye, PixController, Export, PA), which was positioned to survey the apparatus and a surrounding area of about 20 m^2. Complementary recordings were made by the observers with Canon Legria FS100 camcorders. As a tool, we provided a 40-cm long branch of an *Alstonia sp.* stripped of all leaves over half of its length, the “leafy stick.” In previous experiments at Sonso, we have shown that no individual discovered the functional tool properties of the leafy stick, that is, its usefulness as a “stick” or a “brush” (Gruber et al., 2011). In these experiments, we exposed individuals to the following conditions: (a) no tool, (b) tool next to the hole, and (c) tool inside the hole.

Habitat Ecology

To describe the different habitats, we used data published by Chapman, Wrangham, Chapman, Kennard, and Zanne (1999) for the Kanyawara and Ngogo study areas. For Budongo, a major ecological survey was conducted in 1992, which resulted in a series of publications, notably Plumptre and Reynolds (1994) and Plumptre, Reynolds, and Bakuneeta (1997), both of which were used in these analyses. Both the Kibale and Budongo studies used comparable methods to describe the composition of the forests. Specifically, the authors documented all trees with a diameter at breast height > 10 cm following the trails cut throughout the core area of the three chimpanzee communities, therefore encompassing both the areas where they spent most of their time (Chapman & Wrangham, 1993; Newton-Fisher, 2000) and the diversity of their habitats. The Kibale Forest is a moist evergreen forest transitional between lowland and mountain rain forest (Chapman et al., 1999). The Kanyawara site is composed of mature forest, swamp, grassland, plantation, and secondary forest (Emery Thompson & Wrangham, 2006; Struhsaker, 1997). The Ngogo site is characterized as closest to a lowland forest (Potts, Chapman, & Lwanga, 2009). Budongo Forest is a lowland moist evergreen forest, composed of four main types: a mature *Cynometra*-dominant forest, a mixed secondary forest, a colonizing forest, and a swamp forest, all present in the Sonso study area (Plumptre & Reynolds, 1994). The purpose of the surveys was to produce an accurate estimate of the tree diversity in the study areas. The three sampled areas were comparable in size (Sonso: 3.3 ha; Kanyawara: 2.4 ha; Ngogo: 4.8 ha). These data allowed us to generate a database of tree densities at each site and to compare the three sites in terms of their tree composition (Supplemental Material S1). Data by Plumptre et al. (1997) served to estimate the overall tree composition of Budongo Forest. We used Pearson chi-square tests to compare the proportion of edible and nonedible trees in the home range of the three study groups (Sonso, Ngogo, and Kanyawara).

Comparison of Dietary Preferences

To compare dietary diversity between Ngogo, Kanyawara, and Sonso, we calculated their Shannon–Wiener indices ($H' = -\Sigma [Pi.\ln Pi]$, where Pi is the proportion of the species i in the overall diet). Diversity is calculated by relating each consumed food type to its frequency over a given time period. Larger H' values indicate greater diversity. A related measure is the standardized Shannon–Wiener diversity index (J'), or Hill's equality index (Hill, 1973), which is defined as $J' = H'/\ln(x)$, with x being the total number of food types included in the diet during the sampling period. J' therefore is a score between 0 and 1, with 1 indicating maximum equitability of feeding time among all food types.

We calculated the average monthly standardized Shannon–Wiener diversity indices for all three groups using diet data published by Potts et al. (2011) and Newton-Fisher (1999) and compared them using independent *t* tests. Although the years when the studies were conducted differed, we controlled for seasonality by comparing overlapping months (e.g., January–June or June–December periods at both sites) assuming that seasonal patterns had remained largely similar over time (National Water Development Report, 2005, pp. 38–39), although we acknowledge that this analysis may have lowered the similarity estimates for nonannual tree species that did not fruit during the years of the studies. We used Pearson chi-square tests to compare the different diet components (e.g., ripe fruits, flowers) of the three communities.

Quantitative comparisons of extractive tool use behaviors were not possible because of low variability (Sonso, Kanyawara, Ngogo: $n = 1, 2, 4$, respectively). Instead, we focused on the presence or absence of fluid-dip, a tool behavior that is present throughout wild chimpanzee communities, but curiously absent in the Sonso community.

Results

Field Experiments

We carried out the honey-trap experiment with the Kaniyo Pabidi and Busingiro communities to assess the presence of fluid-dip in Budongo Forest. Chimpanzees were exposed to the test apparatus with or without a multifunctional tool, the leafy stick. At Kaniyo Pabidi, five individuals were tested on nine occasions on seven different days in both the "no tool" and "tool inside the hole" conditions. Subjects engaged with the hole for a total of 18 min 9 s. Responses were similar to those of the Sonso chimpanzees, with no instance of using the leafy stick as a stick or brush. In contrast to Sonso, however, no individual was seen manufacturing a leaf sponge, using the tool or other material. Instead, all individuals used their hands to try to access honey (see video 1 of the online supplemental materials). At Busingiro, at least 10 individuals were tested over 7 days. Individuals engaged with the hole for a total of 30 min 22 s. Reliable identification of individuals was not possible, as the community was not habituated at the time of the study. No individual used the provided tool or any other tool to try to retrieve honey (see video 2 of the online supplemental materials).

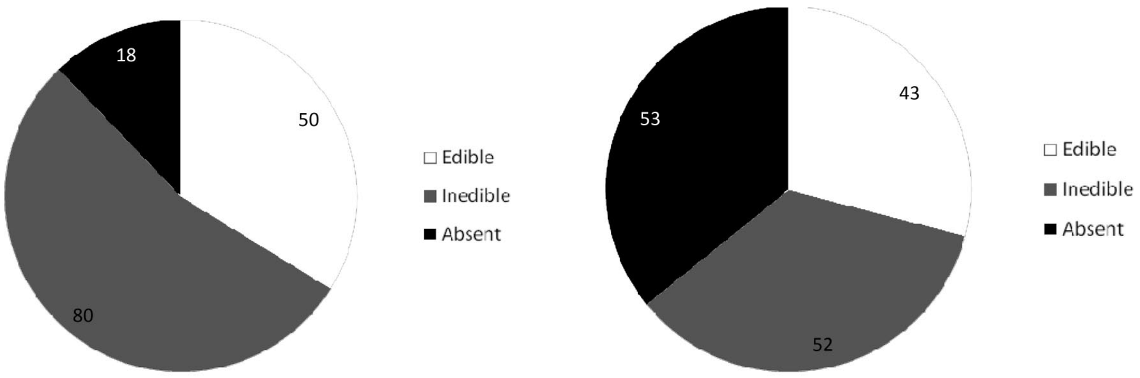
Comparative Ecology of Budongo and Kibale Forests

Using published records, we identified 148 tree species throughout the home range of the three main study groups at Sonso, Kanyawara, and Ngogo (Chapman et al., 1999; Plumptre et al., 1997). At Sonso, 95 tree species were identified, 45.2% of which were eaten by chimpanzees. At Kanyawara and Ngogo, 61 and 59 species were identified, respectively, 26.2% and 25.9% of which were eaten (see Figure 3 and Supplemental Material S1). In pairwise comparisons, we found that 44 of 148 (29.7%) trees differed between Kanyawara and Ngogo, with 10 of 44 being edible. The difference in the ratio of edible to nonedible trees between Sonso and Kanyawara was 41 of 108 (38.0%), similar to that between Sonso and Ngogo, 39 of 106 (36.8%, $\chi^2 = 0.031$, $p = .86$).

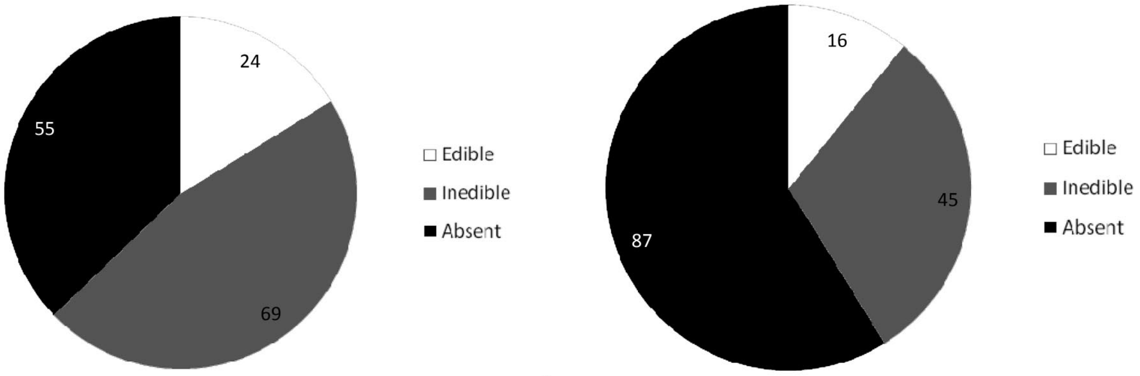
When a larger and more representative section of Budongo Forest consisting of six different sites (1992 census; Plumptre et al., 1997) was considered, we found that of all 148 species, only 18 were absent throughout Budongo Forest, two of 18 (11.1%) of which were eaten by chimpanzees. At Sonso, 53 of 148 species (35.8%) were absent, nine of which (17.0%) were eaten. In comparison, at Kanyawara, 87 of 148 (58.8%) were missing, 36 of which (41.4%) were eaten; and at Ngogo, 67 of 148 (45.3%) were missing, 30 of which (44.8%) were eaten. Thus, by all accounts, Budongo Forest represents an extremely diverse habitat for chimpanzees, with most edible and inedible trees of both forests represented, and Kibale Forest offers a more restricted range of tree species suitable as chimpanzee foods.

Core Diet

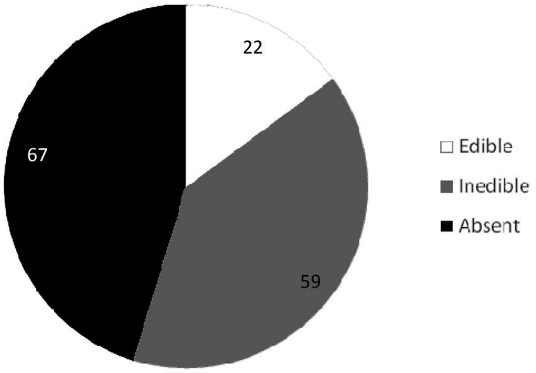
Differences in ecological composition do not automatically lead to differences in food availability. We therefore compared the chimpanzee diets recorded at the different study sites as follows. First, we compared the most commonly eaten foods at the three main sites following Newton-Fisher (1999) and Potts et al. (2011). At Kanyawara, the top-20 list consisted of 13 trees species and



a) Budongo c) Sonso



b) Kibale d) Kanyawara



e) Ngogo

Figure 3. Pie charts illustrating the proportion of species found in (a) Budongo and (b) Kibale forests relative to the combined pool of 148 species. Budongo is represented by a combination of six sites within the Budongo Forest (data extracted from Plumptre et al. 1997), including (c) Sonso. Kibale is represented as a combination of the (d) Kanyawara and (e) Ngogo sites.

seven species of terrestrial herbaceous vegetation (THV), each accounting at least for 0.95% of the total feeding time, or 89.5% total (range: 0.96–17.9). At Ngogo, the top-20 species consisted of trees only, each accounting at least for 0.7% of the total feeding time, or 91.5% total (range: 0.7–34.0). At Sonso, no top-20 list was available, but the top 17 tree species each accounted for more than 0.5% of chimpanzee feeding time. In addition, the chimpanzees fed on an unspecified number of THV and climber species, which accounted for 3.2% and 1.2% of feeding time, respectively. The 17 trees, climbers, and THV accounted for 97.7% total (range: 0.8–23.0; Newton-Fisher, 1999). In pairwise comparisons, eight species were shared between Kanyawara and Ngogo, five between Kanyawara and Sonso, and six between Sonso and Ngogo. Across the three communities, four species were common (see Table 1).

Comparing all foods, Sonso chimpanzees consumed more than 58 species (15-month study period; Newton-Fisher, 1999). Over a comparable period of time, the Kanyawara chimpanzees also consumed 58 species and the Ngogo chimpanzees consumed 53 spe-

Table 1
Favorite Plant Species Consumed at Kanyawara, Ngogo, and Sonso Sorted by Total Feeding Time and Item

Kanyawara		Ngogo		Sonso	
Plant species	Feeding time (%)	Plant species	Feeding time (%)	Plant species	Feeding time (%)
Ficus natalensis[a]	17.9	Ficus mucuso[a]	34.0	***Ficus capensis***[a]	23.0
Ficus sansibarica[a]	16.1	*Uvariopsis congensis*[a]	11.1	Broussonetia papyrifera[a]	22.7
Mimusops bagshawei[a]	8.3	Chrysophyllum albidum[a]	9.8	Ficus mucuso [a]	9.8
Ficus exasperata[a]	7.62	Pterygota mildbraedii	6.97	Maesopsis eminii	9.4
Celtis africana[a]	6.9	Teclea nobilis	5.5	Celtis durandii	8.4
unk THV[b]	5.4	*Mimusops bagshawei*	5.1	Celtis mildbraedii	4.6
Acanthus arborescens	5.3	*Ficus saussureana*	3.7	THV[b]	3.2
Ficus capensis	4.9	Morus mesozygia	2.6	Khaya anthotheca	2.9
Uvariopsis congensis	3.9	Pouteria altissima	2.2	Croton macrostachys	2.8
Aframomum spp.	2.9	***Ficus sansibarica***	1.7	***Ficus exasperata***	2.2
Lepistemon spp.	1.8	Treculia africana	1.24	Cordia millenii	1.7
Pennisetum purpureum	1.62	*Pseudospondias microcarpa*	1.15	Climbers	1.5
Ficus saussureana	1.4	Cassine buchananii	1.03	Desplatsia dewevrei	1.3
Ensete spp.	1.27	Cordia millenii	0.98	Cynometra alexandrii	0.9
Cordia abyssinica	1.17	***Ficus exasperata***	0.98	***Ficus sansibarica***	0.9
Pseudospondias microcarpa	1.14	***Ficus natalensis***	0.96	Raphia farinifera	0.6
Linociera johnsonii	1.05	Monodora myristica	0.95	***Ficus natalensis***	0.5
Cyperus papyrus	0.96	***Ficus capensis***	0.72	Ficus varifolia	0.5
		Cola gigantea	0.7	Cleistopholis patens	0.8
Total	89.5	Total	91.5	Total	97.7

Note. THV = terrestrial herbaceous vegetation; unk = unknown. Species appearing in the top foods of Kanyawara, Ngogo, and Sonso are shown in bold italic type. *S*pecies appearing in the top foods of Kanyawara and Ngogo are shown in italic type. Species appearing in the top foods of Sonso and Ngogo are underlined.
[a] Species accounting for more than 50% of total feeding time. [b] Common in the top foods of Sonso and Kanyawara, although the species are not mentioned.

cies (12-month study period; Potts et al., 2011). In terms of plant items (e.g., leaf, roots), the three communities fed on 118, 64, and 60 different items, respectively. At Sonso, fruits (64.5%), leaves (19.7%), and flowers (8.8%) accounted for most of the feeding time. At Kanyawara, fruits (66.5%), THV (17.4%), and leaves (10%) were most common; at Ngogo, fruits dominated the diet (92.2%). Overall, the diet composition of the three communities was significantly different ($\chi^2 = 50.88$, $p < .001$; see Table 2).

The average standardized Shannon–Wiener diversity index (J') was highest at Kanyawara ($J' = 0.70$; 12 months; Potts et al., 2011), followed by Sonso ($J' = 0.69$; 15 months; Newton-Fisher, 1999) and Ngogo ($J' = 0.58$; 12 months; Potts et al., 2011). Using H' data by Potts et al. (2011) and Newton-Fisher (1999) matched for calendar months to control for seasonal differences in rainfall, we found that dietary diversity was significantly different between Sonso and Ngogo but not between Sonso and Kanyawara: $N_{\text{Sonso}} = N_{\text{Ngogo}} = 7$, $t(1, 12) = 4.484$, $p < .001$; $N_{\text{Sonso}} = N_{\text{Kanyawara}} = 12$, $t(1, 12) = 0.385$, $p = .704$.

Table 2
Diet Composition at the Three Sites Displayed as Percentage of Feeding Time Over Comparable Periods (Sonso: 15 months; Newton-Fisher, 1999; Kanyawara and Ngogo: 12 months; Potts et al., 2011)

Type of food	Kanyawara	Ngogo	Sonso
Ripe fruits	64.6	80.5	54.6
Unripe fruits	2.0	11.0	9.9
Flowers	Included in Others	Included in Others	8.8
Leaves	11.4	3.5	19.7
THV	17.4	1.1	3.2
Others	4.6	3.9	3.8
Total	100	100	100

Note. THV = terrestrial herbaceous vegetation.

Key Food Species

At Sonso, four tree species (*Ficus sur*, *F. mucuso*, *Maesopsis eminii*, and *Celtis durandii*) accounted for more than 75% of the time spent eating fruits (equal to 49.4% of the total feeding time). Two more species, *Broussonetia papyrifera* and *Celtis mildbraedii*, also contributed considerably, albeit mostly with flowers. Adding a seventh species, *Khaya anthotheca*, accounted for more than 80% of total feeding time. The top three species, *F. sur*, *B. papyrifera*, and *F. mucuso*, accounted for more than 50% of feeding time. At Ngogo, the top three species, *F. mucuso*, *Uvariopsis congensis*, and *Chrysophyllum albidum*, also accounted for more than 50% of feeding time. At Kanyawara, the top four species, *F. natalensis*, *F. sansibarica*, *Mimusops bagshawei*, and *Celtis africana*, accounted for more than 50% of feeding time. Figs alone accounted for 45.5% of feeding time at Kanyawara, 37.5% at Ngogo, and 36.9% at Sonso (the measure in Kanyawara and Ngogo is based on 100% of the feeding time; the measure at Sonso is based on the time spent on all food species accounting for 0.5% or more of feeding time, which accounts for a total of 97.7% of feeding time; see Table 1).

Nonvegetarian Foods

All three communities hunt mammals, including other primates (Gilby, Emery Thompson, Ruane, & Wrangham, 2010; Mitani & Watts, 2001; Newton-Fisher, Notman, & Reynolds, 2002). Insects are also consumed and sometimes extracted with tools. In particular, a few Ngogo chimpanzees have been observed using twigs to feed on beetles, a behavior not seen at Kanyawara or Sonso (Sherrow, 2005). At Kanyawara and Ngogo, but not Sonso, chimpanzees use sticks to obtain honey from beehives (Gruber et al., 2009; Reynolds, 2005; Watts, 2008; Whiten et al., 1999).

Discussion

Assessment of the Ontogenetic Flexibility Hypothesis: Comparisons of Habitat Quality and Extractive Tool Use Diversity

Our analyses have shown that, despite geographical proximity and similar histories, the three study sites are by no means identical in their ecology, no matter how similar they appear at first sight. Although all communities devote large amounts of time to feeding on ripe fruits, most extremely so at Ngogo, there are considerable differences in the availability of fruit trees, even within Kibale Forest. Ngogo has more fruit trees than Kanyawara (Chapman, Chapman, Wrangham, Isabirye-Basuta, & Ben-David, 1997), which may in part explain the unusually large group size of the Ngogo community (Hohmann et al., 2010; Mitani & Watts, 1999). However, diversity may also be a relevant factor (Felton, Felton, Lindenmayer, & Foley, 2009; Raubenheimer, Simpson, & Mayntz, 2009) if it buffers populations against periods of food scarcity. Our results show that the Sonso chimpanzees have the most diverse food availability, with no record of food scarcity during 15 years of observations (Newton-Fisher, 1999; Reynolds, 2005). Individuals devote only 54.5% to 70.0% of their feeding time to ripe fruits (Tweheyo et al., 2004), but they consume nearly twice as many items compared with the Kibale communities. The diet at Sonso also contains a high proportion of a nonnative species, *Broussonetia papyrifera*, from which all parts are being eaten, probably because they are free of tannins and thus offer readily digestible sugars (Reynolds, Plumptre, Greenham, & Harborne, 1998). Comparing Shannon–Wiener indices suggests that Kanyawara and Sonso chimpanzees have a similar dietary diversity, but our analysis shows that the two diets differ in quality. At Kanyawara, the diversity is largely due to THV, whereas at Sonso, it is due to leaves and flowers (Reynolds, 2005). Kanyawara chimpanzees thus appear to have the least favorable environment, which may require them to complement their diet with THV (Wrangham et al., 1996). In comparison, Ngogo chimpanzees have a richer habitat with a large number of fruit trees, which account for more than 80% of their feeding time. This fruit-rich diet, however, may create temporary food shortages if fruiting patterns are irregular between years. In this sense, the Sonso chimpanzees appear to have the least demanding habitat because individuals have access to a stable food supply that can be accessed without extractive tool-using techniques.

Can these ecological differences be related to observed differences in tool use? More specifically, do the relatively low food diversity at Ngogo and the relatively low food quality at Kanyawara promote extractive tool use? Our data suggest that the Kanyawara community has the least favorable environment of all three communities. The ontogenetic flexibility hypothesis thus predicts that Kanyawara individuals should develop the most extensive tool use catalogue. However, this is not the case because Ngogo individuals have more food-related tool-using behaviors, although their habitat offers the best food quality. Our data suggest that communities with high food diversity are less likely to develop extractive tool use compared with communities with low diversity, which are more likely to face periods of food shortage. These results are in line with other studies conducted with different chimpanzee subspecies or ape species. At Bossou, Guinea, it has been suggested that nut cracking was necessary for chimpanzees (*P. t. verus*) to cope with low food diversity and periods of food shortages (Yamakoshi, 1998, 2001). At Ketambe, Indonesia, Sumatran orangutans (*Pongo abelii*) consume strangler figs as part of their diet. Although these fruits are considered fallback food compared with other fruits, they are present throughout the year, assuring the Ketambe orangutans a constant supply (Morrogh-Bernard et al., 2009). Similar to the Sonso community, this community has been found to have a very small tool catalogue in comparison with other orangutan communities (van Schaik, 2009). It is interesting that this community is thought to live in a less favorable environment than the Suaq Balimbing community, which shows nonetheless a more developed extractive tool set (C. P. van Schaik, personal communication, 2011).

In summary, our study shows first that ecological conditions have to be analyzed at several levels when put in connection with tool use. Although a major factor is the number of trees with edible items in a given area, our data suggest that this variable is unrelated to the number of food-related tool behaviors in the communities we studied. However, food availability analyzed in terms of food diversity could play a role in the generation of such behaviors. High general reliance on fruits can make a community vulnerable to periods of food scarcity, which then requires individuals to search for food items that are concealed and hard to access. Variation in food availability over time thus may play an important role in the appearance and disappearance of food-related tool behaviors.

Second, our study shows that current ecological conditions are poor predictors of the extractive tool catalogue of the different chimpanzee communities, suggesting that they are unlikely to explain observed differences in extractive tool use behaviors from a developmental perspective. However, what cannot be ruled out is that past ecological conditions have been responsible for current patterns of tool use and other behavioral differences. In the following section, we review the evolutionary history of Ugandan forests in an attempt to explain the observed differences in tool use of the different resident chimpanzee communities.

Tool Use Presence in Relation to Ugandan Forests' Evolutionary History

During the Pleistocene, tropical forests in Africa experienced periods of expansion and contraction due to climatic changes (Kendall, 1969; Moeyersons & Roche, 1982; van Zinderen Bakker & Coetzee, 1972). The last expansion of Sub-Saharan forests is thought to have peaked around 12,500 years ago (Haffer, 1982;

Hamilton, 1976, 1988; Mayr & O'Hara, 1986). At this time, Budongo and Kibale were part of a continuous forest, which had originated from a core area in northeastern DR Congo (Grubb, 1982; Hamilton, 1976; Howard, 1991). Since then, the forests have generally retracted, in recent times mainly because of anthropogenic activities (Hamilton, 1984; Hamilton, Taylor, & Vogel, 1986; Howard, 1991; Philipson, 1977). It is estimated that the western forests, including Budongo and Kibale, became separated from one another between 8,000 and 10,000 years ago (Reynolds, 2005). The genetic diversity of Eastern African chimpanzees is low, suggesting that they are the descendants of a small population of no more than 6,000 individuals (Goldberg, 1996). During the last Ice Age, rather than retracting into forested refugia, this population is thought to have occupied woodland habitats during arid, colder, and less forested episodes, which may have kept their population size low (Goldberg, 1996; Goldberg & Ruvolo, 1997a, 1997b). As mentioned earlier, the small genetic diversity of this subspecies suggests that any observed behavioral differences between communities are unlikely to have genetic reasons, but that social or ecological factors provide a better explanation.

Many chimpanzee communities in Uganda and elsewhere in Africa use sticks as tools (Whiten et al., 2001). The behavior appears to develop easily under laboratory conditions (Tennie et al., 2009) but, for unknown reasons, not so easily under natural conditions (Gruber et al., 2011). Among the Ugandan chimpanzees, the Sonso community has the smallest number of extractive tool-using behaviors of all communities. In particular, stick use is nearly absent, in striking contrast to all other main chimpanzee long-term study sites (Whiten et al., 2001). Although sticks are sometimes manipulated during nest building or as part of play behavior, they are not used during food acquisition. The situation in Sonso may be representative for the whole of Budongo Forest. Our preliminary experimental results from Kaniyo Pabidi and Busingiro (1 week of experiments with five to 10 individuals at each site) using the honey-trap protocol did not result in any stick use in either of the two sites. These results are significant if compared with the behavior observed in the Kanyawara community, where chimpanzees started to use tools from the first day of the experiments. Although these results still demand further confirmation, they currently suggest that stick use is absent throughout Budongo Forest. It is also interesting that some of the communities living in fragmented, isolated forest patches adjacent to Budongo (some 25 km from the main block) are thought to use sticks during foraging (McLennan, 2011b; Reynolds, 2005; J. Wallis, personal communication, 2010). These sites are characterized by poor food availability for chimpanzees, especially if compared to the Sonso area (Reynolds, 2005).

In summary, the experimental and observational data presented here, in addition to our previous experimental work (Gruber et al., 2009, 2011), suggest the following for the emergence of fluid-dip. First, this type of tool use is not an obvious solution to naïve chimpanzees to extract food, suggesting that the behavior is not readily invented by wild chimpanzees confronted with this task. Second, the fact that stick use is absent in communities where food is reliably available throughout the year (Sonso), but present where food shortage are likely to occur, either because of the low item diversity (Ngogo) or low food quality (Kanyawara) or both (Kasokwa, Bulindi: forest fragments around Budongo), suggests that periodic food shortages lead to innovations in food acquisition techniques (Lee, 1991, 2003).

It is interesting that the history of the Ugandan forests and the geographical differences in tool use among their chimpanzee communities concur with these patterns. During the last Ice Age, the ancestral chimpanzee population may have been coping with a harsher environment in which food was potentially more difficult to access, and this may have favored various behavioral innovations, including the development of food extractive tool-using behaviors, as still found in many Eastern African communities. During the subsequent warmer periods of reforestation, the Budongo area gradually became a *Cynometra*-dominant forest (Howard, 1991; Plumptre, 1996), whose seeds are a major food source for chimpanzees (Reynolds et al., 1998). This tree species, along with a number of others, is absent at Kibale. Therefore, one plausible scenario is that the original colonizers of Budongo Forest were able to expand and diversify their diet, and tool-based food acquisition probably became less important throughout Budongo Forest and was gradually lost (see Wrangham, 2006, for a similar point regarding nut smashing).

Environment as a Selective Force Integrated in the Cultural Diversity Hypothesis

The scenario we have presented is speculative, as it is not possible to accurately reconstruct events that have taken place 8,000 years ago. Moreover, stick use may have disappeared and reappeared several times in different communities. Bearing this in mind, our main goal was to illustrate the key role that ecology appears to play in the emergence of behavioral variants that are usually interpreted as "cultural." In this final part, we summarize how environmental and social factors could act as cocontributors in the appearance and disappearance of cultural behaviors.

Ecological differences were present across sites, but they were not correlated with the currently observed differences in tool use. Ecological conditions may lead to cultural behaviors, not by triggering the development of these behaviors through individual plasticity in each group member independently, as predicted by the ontogenetic flexibility hypothesis, but rather through a more "temporal" effect by creating conditions that favor innovations of beneficial behaviors. Because chimpanzees are good social learners, one single innovation can be sufficient to lead to a novel tradition. Environmental changes thus act as a selective force that can render some behaviors more adaptive than others at a given time. Social learning then causes community-wide spread and maintenance. Similarly, the environmental pressure on the maintenance of a given behavior may disappear, resulting in the disappearance of this behavior through the same process. Adopting this view allows one to put the emphasis on the dynamic characteristic of this phenomenon: Food-related cultural behaviors appear and disappear in conjunction with ecological variations, not because each individual learns them independently (as predicted by the ontogenetic flexibility hypothesis), but because the environment alters the odds for new behavior to be invented and to subsequently spread throughout a group of individuals through social learning, making them cultural *in fine*.

Our experiments have shown that chimpanzees do not easily learn stick use individually, even when highly motivated (Gruber et al., 2011). Therefore, it seems unlikely that, under harsher ecological conditions, Budongo chimpanzees would all independently begin to use sticks. More likely, a few individuals will discover the behavior and start practicing it regularly to access difficult foods. These individuals, similar to the potato-washing Japanese macaque "Imo" (Hirata, Watanabe, & Kawai, 2001), may then cause the behavior to spread to other individuals with more or less social learning at work. Our own work suggests that this social exposure is mandatory. This scenario also has the advantage that it can be linked with environmental unpredictability: If ecological conditions become more favorable, individuals may be less likely to access more difficult foods with complex tool-using behaviors, which will lower the number of demonstrations, suppressing the social exposure necessary for the maintenance of the behavior. This may result in the loss of the behavior in family units and, eventually, its disappearance from the entire community knowledge pool.

In conclusion, rather than seeing "ecology" and "culture" as opposing forces, we should see them as complementary, acting in different ways on the innovation, spread, maintenance, and loss of behaviors in a community. Analyzing cultural behaviors as dynamic traits also may be useful when comparing species, notably apes. In highly social species, such as chimpanzees or humans, behavioral innovations may spread faster and last longer because of the numerous interactions between individuals. In less social species, such as orangutans, innovations may occur equally often, but then mainly linger within the family-level units (Jaeggi et al., 2010). Loss of innovations at the community level also may be more common because of lower rates of encounters between family units. Cultural differences between species may thus, in addition to differences in abilities to innovate or socially learn, also have to do with the structure of the social group.

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