



Innovation in Wild Chimpanzees {*Pan troglodytes*}

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Innovations of behavior have major implications for the concept of culture in animals. Innovation has rarely been documented in wild animal populations. The chimpanzees of the Tai National Park, Cote d'Ivoire, spontaneously included new patterns of behavior in their repertoire during our study. Some innovations were incorporated into a minority of the group members' repertoire, whereas others, such as building day nests in trees and on the ground more frequently, became general behaviors. Similarly, new contexts for use of leaf-clipping behavior and novel ways of feeding on some leaves appeared and rapidly became part of the behavior of most group members. The environmental parameters were too stable to explain these new forms of behavior, as most of them took place within 1 month during the same dry season. In a similar way, leaf-grooming acquired a new function in Gombe chimpanzees. A process similar to social conventions could explain the emergence of these new functions for an existing behavior in a way rather similar to human "fashion." Three major characteristics of human culture — the absence of individual variations in the performance of the behavior, the general use of the behavior by group members, and the ability to modify the function of a behavior — characterize leaf-clipping in Tai chimpanzees and leaf-grooming in Gombe chimpanzees.

KEY WORDS: chimpanzee; culture; innovation; tool-use; cross-population comparisons.

INTRODUCTION

Innovation is the introduction of a new behavior in the repertoire of one or more individuals that may be, for example, a solution to a new

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problem, an ecological discovery, or an existing signal used for a new purpose (Kummer and Goodall, 1985). Most innovations are expected to be adaptations to environmental conditions, which tend to be stable during the lifetime of an individual, and we would expect such innovations to be rare. However, other innovations might develop independently of any ecological influence and, if so, to disseminate within the social group. This would per definition involve a cultural process (Kummer, 1971; Kummer and Goodall, 1985; McGrew, 1992). Among humans, not all cultural behavior is independent of environmental factors, but because adaptations to environmental conditions are common in animals, a nonhuman behavior can be labeled as cultural only if its existence cannot be explained by genetic or ecological factors (Nishida, 1987; Galef, 1990; Tomasello *et al.*, 1993).

The most widely cited example of innovation came from a community of Japanese macaques that invented and purportedly copied potato-washing and wheat-throwing (Kawai, 1965) with foodstuffs provided to them by humans. A recent and critical look at these examples led some to doubt their cultural component; Galef, (1990), Tomasello (1990), and Visalberghi and Fragasy (1990) argue that imitation was not at work due to the slow dissemination rate of the behavior within group members. This argument, based solely on the process underlying the dissemination of a behavior, rests on the distinction made in psychology between different social learning processes; e.g., in a tool-use activity, the simplest process results in the naive individual having its attention focused on the tool used by the model ("stimulus enhancement"), but it may also simply try to achieve the goal and try any possible way to achieve it ("emulation") or it copies the behavior itself ("true imitation") (Thorpe, 1956; Tomasello, 1990; Whiten and Ham, 1992). For some psychologists, only behaviors that are learned by true imitation can be cultural (Tomasello 1990; Tomasello *et al.*, 1993; Visalberghi and Fragasy, 1990), and experiments performed with captive animals failed to show imitation within the capacities of nonhuman primates (Beck, 1980; Cheney and Seyfarth, 1990; Tomasello, 1990; Tomasello *et al.*, 1993; Visalberghi and Fragasy, 1990). However, this argument may miss the point since in humans too the acquisition of new behaviors might be possible via social facilitation, stimulus enhancement, or emulation, and human and nonhuman culture may be based on more than one transmission mechanism (Boesch, 1993; McGrew, 1992; Wynn, 1992). In addition, the fact that sand-throwing and using sticks for reaching were not imitated in some captive chimpanzees (Tomasello, 1990; Tomasello *et al.*, 1987) does not tell us much about the mechanism of acquisition of nut-cracking or termite-fishing in wild chimpanzees and does not mean that the capacity to imitate does not exist at all in this species (Boesch, 1993; McGrew, 1992).

New examples show that wild chimpanzees might learn some aspects of an artificial language (Fouts *et al.*, 1982; Tomasello *et al.*, 1994) or of nut-cracking (Boesch, 1991) by imitation.

In chimpanzees, examples of innovation are reported from Gombe, where, for example, a juvenile female, Fifi, performed a new gesture, "wrist-shaking," in an aggressive context for a period of 10 months. Another young female used the same movement within a week of the first performance by Fifi. But the gesture disappeared progressively from the repertoire of both individuals (Goodall, 1973; Kummer and Goodall, 1985). In Mahale, a newly acquired behavior was transmitted to a larger number of individuals: A new style of courtship display, the "cushion-making," has been used by 10 immature males of the M-group (Nishida, 1987). These "incipient" cultures (Nishida, 1987) in the social sphere were acquired by a limited number of group members and gradually disappeared without disseminating to other individuals. This raises the question about the conditions necessary for an innovation to be taken up by other group members and to become established.

If innovation is followed by social transmission (which would constitute a cultural diffusion), we should expect to find variations in behavior in populations that cannot be explained by variations in the habitat. These variations in behavior should be found either within a group for different periods of time or at one time in two neighboring groups in a same habitat. I shall test the first possibility in this paper, whereas the second is analyzed elsewhere (Boesch *et al.*, 1994).

Novelty of the behavior will be judged by its new appearance or by variation in context or both factors and in the frequency of its use. I present new observations made on tool use and changes in frequency and context of use of three precise sets of behavior: day-nest building, leaf-clipping, and leaf-cutting,

METHODS

Since 1979, we have studied wild chimpanzees in the tropical rain forest of the Tai National Park, Cote d'Ivoire by following individuals during their daily ranging. No artificial provisioning occurred (Boesch and Boesch, 1983, 1989). The rainy seasons occur in May-June and September-November. In December, a cold and very dry wind, the Harmattan, starts blowing southward from the Sahara. It can last for several weeks and brings the mean temperature of 25°C during the day in this season down to 22°C with extreme lows of 15°C at night.

I use chi-square tests to compare the different frequencies of behavior patterns because independence is guaranteed by the large number of individuals that contributed to the data for leaf-clipping (Table III). If, however, data were not independent within individuals between the different periods, this would bias the comparison toward nonsignificance, that is, toward the conservative side of the analysis.

RESULTS

New Tool Use

Table I lists the new tool-use types that we observed since Boesch and Boesch (1990). Some tool uses are rare or unique observations in common contexts and are not new in the sense that they were probably not invented recently. For instance, Tai chimpanzees frequently eat *Cerambycidae* that develop inside the trunks of small saplings. To do so, they open the sapling with their teeth at the beetle's tunnel entrance, halve the sapling by pulling it apart with both hands, and remove the grubs with their fingers. Only once I saw an adult male make a stick to extract a grub that he could not reach with his fingers because it was protected within the underground part of the trunk. Similarly, mushrooms growing inside the termite mounds of *Thoracotermes* sp. are regularly eaten by the chimpanzees, which scrape them partly off with the tip of a fingernail. Once I saw an adolescent female use a stick twice to extract more of the mushroom than she was able to reach with her fingernail. This situation typified all chimpanzee feeding on these mushrooms, so it is puzzling that they do not use tools more often.

Other tool use is performed in rare contexts. This is the case vis-a-vis the use of a weapon. Several times chimpanzees held or threw branches during interactions with leopards (Boesch and Boesch, 1989). However, once I observed the chimpanzees with a leopard that they had cornered under a fallen tree. This gave them the opportunity and the time to try to hurt it with branches (Boesch, 1991). Weapon use was performed on this occasion by seven different individuals. They used big branches that they transported from the vicinity to the place where the leopard was trapped. Individuals repeatedly hit and stabbed ≤ 11 times each despite the aggressive growls of the leopard. Four of the seven chimpanzees threw its branch at the leopard at the ends of their attacks (Boesch, 1991).

Still other tool use seems to constitute genuine invention. The larvae of the beetle, *Pterognatha gigos*, live under the bark of large fallen trees, and groups of chimpanzees regularly search for them and eat them for ≤ 40 min at a time. They expose the shells of the eggs in which the pupae

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Table I. List of New Types of Tool-Use in Tai Chimpanzees Observed During a 3-Year Period from 1988 to 1991^a

Tool-use activity	Tool-use aim	No. of observations	Tool material	Tool size: length (range), thickness (range)	No. tools used (No. tools made)
Insert	Grub eating ^b	1	Twigs (<i>n</i> = 4)	10.5 cm (8-13) 6.25 mm (6-7)	4(4)
	Larva eating ^c	6	Twigs (<i>n</i> = 4)	27.2 cm (20-35) 4.75 mm (4-5)	6(6)
	Mushroom eating	1	Twigs (<i>n</i> = 2)	26.5 cm (21-32) 3.5 mm (3-4)	2(2)
Probe	Trunk hole	1	Twigs		1(1)
Clean	Wond	2	Twigs (<i>n</i> = 2)	10.0 cm 4.0 mm	2(2)
Display	Hitting insect				
	Away ^d	1	Sapling		1
	Play ^e	15	Sapling		20 (20)
	Weapon ^f	7	Branches		7(2)
	Leaf-clipping	315	Leaves		315 (315)

^aTypes of tool-use newly observed in Tai follow the classification system of Boesch and Boesch (1990). I use the term insert for tools introduced into a cavity in order to extract food and the term probe for tools introduced into a cavity in order to investigate what might be inside, but not followed by feeding.

^bA larva eating the wood of a buried root was extracted with a twig. The chimpanzee could not reach it directly.

^cNumerous pupae embedded in the dead wood of large fallen trees were extracted with a twig after the bark had been stripped away.

^din one instance, an adult female swayed a sapling so that it hit leaves on a nearby sapling where a tse-tse fly rested.

^e After reading McGrew's (1993) comparisons of tool use in apes, I realized that playing youngsters that stole leafy branches from one another could be described as a tool-use behavior. These figures are for the last 7 years of study.

^f Weapon use includes repeatedly hitting or stabbing an enemy with a tool without releasing one's grip. Chimpanzees used branches thus during an encounter with a leopard (Boesch, 1991). I differentiate weapon-use from aimed-throwing that occurs also in interspecific encounters, viz., toward leopards and colobus monkeys (Boesch and Boesch, 1989).

mature by removing the bark of the tree. This occurred nine times before November 1989. However, in November 1989, I saw for the first time chimpanzees inserting sticks into the hole where the larva lives in order to remove it from its envelope that is tightly embedded in the wood. This occurred 6 times in the 11 observations made between November 1989 and November 1991. In addition, abundant traces, including probes and the remains of their fabrication on the ground, showed that other chimpanzees had used tools in my absence. This change was not dependent upon the

identities of the chimpanzees; two of the three adults that used tools had previously taken pupae with their fingers only. This change might be cultural. However, unknown subtle ecological factors might be involved, like the depth at which the eggs were laid in the wood (I did not measure this before the use of tools) or the species of grubs (identification of cerambycid grubs is very difficult).

These new observations (Table I) add 9 tool-use types to the 19 already known for Tai chimpanzee (Boesch and Boesch, 1990). The proficiency of tool use by Tai chimpanzees is confirmed by these additional observations.

Changes in Frequency and Context of a Behavior

Day-Nest Building

Weaned chimpanzees build a new, arboreal nest every day for overnight sleeping. Tai chimpanzees sometimes also make day-nests in trees during long rest periods. In addition, on the very cold days in December when the Harmattan blows, Tai chimpanzees built day nests on the ground. We hypothesize this to be an adaptation to protect the body from the unusually cold ground. Day nests on the ground are more crudely made than nests in trees are, often by bending (but not breaking) a small sapling to sit on the leafy branches that touch the ground, sometimes with more branches or big leaves from nearby laid on this simple bed. We rarely observed branches to be broken or interwoven into these nests, which is the rule for tree nests.

Since January 1991, I have noticed that the chimpanzees started to build day nests in the trees more frequently than before (Table II). For the first time, groups of chimpanzees started to build nests together in the same (group of) tree(s) during day-resting periods. In addition, they seemed to build them for shorter resting periods. This was not correlated with particularly tiring activities, since they sometimes started to build day nests <30 min after leaving the night nest, and it was observed throughout the year over periods of differing activity levels. Sick individuals will rest in day nests, but our subjects were apparently healthy. Day nests in trees were the same composition, at the same height, and in similar trees before and after January 1991.

Likewise, concurrently they began to build day nests on the ground much more frequently than before (Table II). The first two ground nests after January 1991 were built during the Harmattan wind as had happened previously during cold days. However, the chimpanzees continued to build

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Table II. Day-Nest Building Behavior of the Tai Chimpanzees⁰

	Nests in trees		Nests on the ground	
	PI	PH	PI	PII
Number of individuals	15	30	1	23
Number of nests built	19	74	1	80
	<i>U</i> 1 = 0, <i>p</i> = 0,02		<i>U</i> 1 = 3, <i>p</i> = 0.015	

"Data for the first period (PI) were collected during 6 months in fall 1989 and 1990 and winter 1990, whereas for the second period (PII), they were collected during 5 months in fall and winter 1991. For the statistical test, the monthly frequencies of nest-building were compared between period I and period II with a Mann-Whitney Utest (*N*1 = 6, *N*2 = 5).

day nests on the ground for the next 10 months. More than 25 individuals did so, including juveniles and adults of both sexes. The Harmattan in January 1991 was shorter and less cold than in previous years, and temperatures were at normal levels for the next 10 months.

Leaf-Clipping

Nishida (1987, p. 466) first described leaf-clipping by the Mahale chimpanzees in Tanzania as follows: "A chimpanzee picks one to five stiff leaves, grasps the petiole between the thumb and the index finger, repeatedly pulls it from side to side while removing the leaf blade with the incisors, and thus bites the leaf to pieces. In removing the leaf blades, a ripping sound is conspicuously and distinctly produced. When only the midrib with tiny pieces of the leaf blade remains, it is dropped and another sequence of ripping a new leaf is often repeated." Note that none of the leaf is eaten. This also occurs regularly at Bossou (Sugiyama, 1981), but only twice at Gombe (Nishida, 1987). Such leaf-clipping is regularly observed among Tai chimpanzees as well. However, the form of the behavior differs slightly, so that, unlike Mahale chimpanzees, Tai chimpanzees take the leaf blades together from both sides of the petiole between their lips and remove them in one movement, instead of repeatedly nipping small pieces.

The function of this behavior seems arbitrary. In Mahale, chimpanzees most often show it as a herding or courtship activity in sexual contexts [23 of 41 observations (Nishida, 1987)]. Young adult males and adult estrous females apparently perform it to attract the attention of group members of the other sex (Huffman, personal communication). In Bossou,

it occurs mostly in apparent frustration or in play [41 of 44 observations (Sugiyama, 1981, personal communication)]. During the habituation period, some individuals surprised in trees leaf-clipped while looking at the observer. Once habituation was more advanced, this context of leaf-clipping disappeared; now it occurs only among youngsters at play.

In Tai, leaf-clipping is part of the drumming sequence of adult males. All males use it at the onset of the drumming display before they start to pant-hoot (129 of 132 observations). Given that only adult males display drum, no other age-sex class performed the behavior. Individual males, however, differed in the rate of its use (for period I, $\chi^2 = 95.43$, $df = 6$, $p < 0.001$) (Table III). Since the beginning of our study, this was the usual use of this behavior. It is possible that leaf-clipping is a kind of displacement behavior to release tension. We ascribed three leaf-clipping episodes to frustration when several males competed for an estrous female and they did not succeed in mating.

In late December 1990, a new context for leaf-clipping appeared. Individuals started to leaf-clip while resting on the ground, interrupting a nap (32 of the 183 observations made since January 1990 in Table III). All age-sex classes started to perform it, and there was no apparent reason for frustration. Conditions for sexual frustration as described above were not fulfilled either, since no estrous female was present and the role of leaf-clipping during these resting periods is unclear. In a few cases, mostly due to one male, the behavior differed in form from the leaf-clipping used by drumming males, i.e., ripping the leaf directly with the fingers instead of the teeth while it was attached to the sapling. Leaf-clipping during drumming remained constant in form (120 of the 183 observations made since December 1990) and was equally frequent (comparing monthly rate: $\chi^2 = 0.28$, $df = 2$, $p > 0.05$), but leaf-clipping due to frustration in sexual conflict situations became more frequent ($\chi^2 = 8.0$, $p < 0.01$) after December 1990.

Leaf-Cutting

Tai chimpanzees sometimes carefully take a leaf between their incisors and bite out a crescent-shaped piece of the leaf-blade, which they swallow without chewing. Between 1984 and 1991 we saw this cutting applied to only the very hairy leaves of a vine, *Macrophyton fulvum*, and only in the early mornings, before 0700. All 7 adult males, 11 of 15 adult females, and 5 subadults ingested *Macrophyton* by leaf-cutting. Wrangham and Nishida (1983) propose that leaves eaten by chimpanzees without being chewed may have a medical function, but at Tai there is no indication that

Table III Leaf-Clipping Occurrences in Tai Chimpanzees Over a 2-Year Period"

Name of individual	First period			Second period				
	Number of drumming withLC	% of all drum.	Frustration	Number of drumming withLC	% of all drum.	Frustration		Rest
						For female	For other	
Adult mles								
Brutus	13	50	0	16	31	10	2	3
Darwin	9	45	1	18	51	1	1	3
Fitz	1	14	0	20	26		3	0
Kendo	18	45	0	16	39	4	1	8
Macho	77	69	0	50	67	6	—	4
Rousseau	1	8	0	0	0	2	—	2
Ulysse*	10	10	2	-	-	-	-	-
Adult emales								
Bijou	-	-	-	-	-	-	-	1
Castor	-	-	-	-	-	-	-	1
Goma	-	-	-	-	-	-	-	1
Loukoum	-	-	-	-	-	-	-	1
Xeres	-	-	-	-	-	-	-	1
Juvenile males								
Ali	-	-	-	-	-	-	-	1
Gerald	-	-	-	-	-	-	-	1
Marius	-	-	-	-	-	-	-	1
Nino	-	-	-	-	-	-	-	2
Sartre	-	-	-	-	-	-	-	1
Lychee	-	-	-	—	—	—	—	1

Table III Continued

Name of individual	First period			Second period			
	Number of drumming withLC	Frustration	Number of drumming withLC	Frustration		Rest	
				For female	For other		
Total number of leaf-clippings	129	3	120	23	8	32	
Number of months	9		4				
Frequency per month	14.33	0.33	30.0	5.7	2.0	8.0	

"The first period includes months between September 1989 and November 1990, whereas the second period includes December 1990 to November 1991. For drumming I give the number of drumming bouts preceded by leaf-clipping for each individual and the proportion of all drumming bouts that these represent. For leaf-clipping occurring in the frustration or resting context, I give the number of observations for each individual. *Ulysse disappeared in early December 1990.

the consumption of these leaves is linked to illness or other physical weakness.

In September 1991, I saw the chimpanzees for the first time eating leaves of two other species — *Tristemma coronatum* and *Sakersia africana* — via leaf-cutting. They bit out half-moons of leaves and directly swallowed them only very early in the morning. None of them was hairy or spiny. I occasionally saw chimpanzees eat *Tristemma coronatum* before 1991, at any time of the day, but they simply chewed and swallowed the leaves. This new way of eating *Tristemma* was exhibited 25 times within the first 2 months by 5 of the 7 males and 11 other group members. Three adult males ate *Sakersia africana* by leaf-cutting. We had not seen them eat it before. It is unknown why this behavior suddenly started during late 1991.

DISCUSSION

Tai chimpanzees exhibited innovation in tool use as well as in day-nest building, leaf-clipping, and leaf-cutting. Dissemination of the new habits within the community was quick, and no detectable environmental change explains their appearance. Accordingly, I propose that they are culturally transmitted fashions. Ecological explanations for day-nest building and the two leaf-processing behaviors can be excluded because they began at the start of the dry season, which was similar in terms of rainfall, fruit production, fruit distribution, and community composition to conditions in previous years. Only one adult male had disappeared just before the changes. Moreover, these changes did not imply any modification in the form of existing behavior, except for a nuance in leaf-clipping, but instead showed variations in the frequency and the context of use by the same individuals that had used it before.

As in human fashions, the transmission of a new fashion among Tai chimpanzees was extremely rapid. The changes occurred within about a month, between the end of November 1990 and the beginning of January 1991 for nest-building and leaf-clipping. Similarly the timing of the changes seemed to be arbitrary. Leaf-cutting must have changed between March and September 1991. I cannot define the exact duration of transmission because I was absent.

Why were the innovations of these particular behavior patterns acquired by group members, whereas others have not been copied? The adaptive value of using a stick to extract more of the mushroom within a *Thoracotermes* mound is more obvious than the value of leaf-clipping during a rest, but it is the second innovation that was adopted by group members, and not the first one. The status of the inventor may accelerate the acqui-

sition of a new behavior by other group members. The inventor of the new function of leaf-clipping might possibly be an adult male because they were the ones clipping before the change, whereas it was a low-ranking young female that used a stick to feed on mushrooms.

Leaf-clipping has been described in three chimpanzee populations (Bossou, Mahale, and Tai), and it is absent from Gombe chimpanzee's repertoire (Goodall, 1986). An ecological difference might explain why leaf-clipping is present in only three of four populations or why the form of leaf-clipping differs between Mahale and Tai chimpanzees. But it is very difficult to find ecological reasons to explain why each population uses leaf-clipping in another context. The changes in the context of use among Tai chimpanzees suggest that leaf-clipping is a cultural behavior for which the context of use is arbitrarily fixed by group members. A social convention imitated by group members seems the best explanation to account both for the different functions of this behavior in three chimpanzee populations and for the new function that it acquired in Tai chimpanzees.

Tomasello *et al.* (1993) propose that human cultures possess three characteristics: the absence of individual variations in the performance of the cultural traditions, virtually all group members' performing them, and the ability to accumulate modifications over generations in these traditions. With regard to this, in leaf-clipping, the form of the behavior remained constant for years among all of the males despite strong idiosyncrasy in the drumming sequence among them. For example, each adult male has his own way of preparing a drumming bout during the warming up phase. While silently expelling air before starting the pant-hoots, Macho would bend his head repeatedly low toward the ground, while Kendo would shake a sapling forward and backward violently and Brutus would rhythmically move his whole body forward and backward. Then each would run to a buttress to drum. Contrary to these individual differences in drumming, leaf-clipping remained constant for all males. Modification in the context or function of use — frustration in sexual competition, distraction while resting, drumming sequence — is observed as well. Thus, the three essential characteristics of human culture seem to be demonstrated by chimpanzees in leaf-clipping (Boesch, 1993).

Have other examples of modifications in cultural traditions been observed in another chimpanzee population? Innovations have been reported from Gombe, but they did not propagate to many group members. The only exception is the spread of sticks as levers to pry open banana boxes, which should be considered an adaptation to new environmental conditions (Kummer and Goodall, 1985; Goodall, 1986).

I proffer leaf-grooming in Gombe chimpanzees is another example of spontaneous cultural change. They were observed in the grooming context suddenly to pick up one or more leaves and, peering closely at them while holding them bimanually, to move both thumbs as if they were grooming them, often with great intensity (Goodall, 1986). After several minutes, they discarded the leaves on the ground.

The function of this behavior remained a puzzle, though it recurred for years (Goodall, 1986). When I visited Gombe in April 1990, I observed that the chimpanzees had developed a new function for this behavior: They placed ectoparasites that they found while allogrooming or autogrooming on these leaves. I confirmed the presence of an ectoparasite on the leaves in only nine cases, but this is not surprising because ectoparasites may be exceptionally small. For example, I had difficulty seeing small ticks sucking blood from my own forearms. Similarly, eggs of lice that Gombe chimpanzees regularly remove from each others' hairs with their teeth are impossible to see when only 1 m away.

The subjects apparently chewed the very small and presumably hard parasites while detaching leaves from a sapling. Then they placed them labially onto the leaves and tried to smash them with their thumbs. Repeatedly, they took the parasites labially, bit them, and placed them back on the leaves which they had flattened with their thumbs. Earlier observers of leaf-grooming at Gombe never saw the chimpanzee actually place anything labially onto the leaves or take anything from the leaves to chew (Goodall and McGrew, personal communication). I observed 24 individuals of the Kasakela community perform leaf-grooming. In only 10% of observations ($N = 42$) did a chimpanzee leaf-groom without placing and removing something on the leaves with its lips. In three cases, youngsters placed "objects" on the leaves: Once mucus from an eye and twice pus pressed from an infected foot. This new function was stable during the 2-year span between my visits to Gombe. Accordingly, generalization in use, stability in form, and the ability to modify are also shown by chimpanzees in leaf-grooming.

Intriguingly, this new function of leaf-grooming at Gombe — squashing ectoparasites — is performed by Ta'i chimpanzees, but in another way. Tai chimpanzees place ectoparasites on the forearm and squash them by tapping them with the tip of the index of the contralateral hand. After many blows, they take it back in the mouth and chew it further. Thus, the same ecological function — squashing small parasites — may elicit different behavior among chimpanzee populations.

Such analogous behavior occurs in other situations. For example, at Mahale, young male chimpanzees may attract the attention of estrous females by leaf-clipping, which is less conspicuous than the more common

sapling-waving that older males display. Similarly, in Tai, a male that may have wanted to be inconspicuous knocked against branches or tree trunks with his knuckles to attract the attention of an estrous female. Leaf-clipping at Mahale and knuckle-knocking in Tai are analogous behavior patterns for attracting the attention of sexual partners, while leaf-clipping at Mahale and in Tai would be homologous behavior with different functions. In all cases, a social convention decides on the function of the behavior that is learned by most group members. Thus, chimpanzees can respond to an ecological or social problem in different ways, following different social conventions. However, within a social group the solution seems to be the same and is stable for many years.

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