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Socioecological Influences on Tool Use in Captive Chimpanzees

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Some tool use in wild chimpanzees is seasonal because they follow the patterns of availability of resources. The type and abundance of vegetation affect the selection of materials used for tools. Besides triggering, does seasonality also shape tool use? We tested the tool performance of 2 chimpanzee groups in a large outdoor compound, enriched with hundreds of plants. We conducted the experiments in 4 seasons to test their behavioural adaptation to the environmental changes. Initially the groups showed preference for different tool materials, one group using grass, abundant in summer, the other using twigs. While twigs were constant through the year, the availability of grass fluctuated greatly, affecting the number of insertions and success of the individuals that used it. Therefore, seasonality did not affect the performance of the group that preferred twigs (less abundant but constant) as it affected the performance of the group that preferred grass (plentiful in certain seasons and scarce in others). We recorded several cases of observation, which may have biased the choices of material. Analysis of the episodes and first insertions of some subjects suggests social transmission, which might explain the initial intergroup difference in tool preference.

KEY WORDS: chimpanzees; honey-fishing; *Pan troglodytes*; seasonality; tool use.

INTRODUCTION

Field primatologists acknowledge the importance of seasonality in many aspects of primate ecology and behavior (Watts, 1998; White, 1998).

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The feeding habits, range, activity and grouping patterns of wild chimpanzees have been shown to be linked with seasonal food availability (Doran, 1997; Wrangham *et al.*, 1992). Some tool use in the wild are seasonal, due to availability of the resources that require the application of tools to process them (Boesch and Boesch, 1994; McGrew, 1992; Uehara, 1982) or scarcity of preferred food items (Yamakoshi, 1998).

Different kinds and the relative abundance of vegetation across an area might affect which species and classes of raw materials are used for tools (McBeath and McGrew, 1982; Nishida, 1973). So, in places where the occurrence and abundance of plants is weather controlled, does seasonality not only trigger but also shape tool use?

In captivity, due to the constancy of conditions, the importance of abiotic factors has been discarded. However, in naturalistic compounds vegetation can vary with changes in temperature and rainfall in which case seasonality might influence patterns of enclosure occupancy and behaviors such as tool use.

There have been many tool use studies in captivity, but the majority has provided the subjects with materials, either artifactual (Celli *et al.*, 2001; Hirata and Morimura, 2000; Paquette, 1992) or cut sticks and branches (Maki *et al.*, 1989; Nash, 1982). By restricting the availability of raw materials (or providing already selected ones), the researchers influenced the selection of tools and avoided the issue of flexibility in problem-solving skills. In this experiment, we set the task, but subjects were left to choose their own tools within a naturalistic enclosure. We aimed to test behavioral adaptation of the subjects to the climate-induced changes in the vegetation.

Long-term research revealed that communities of wild chimpanzees have developed unique sets of cultural traditions (McGrew, 1992; Whiten *et al.*, 1999), not explained by ecological and physical differences in their habitats (Boesch-Archermann and Boesch, 1994; McGrew, 1998). The traditions are transmitted nongenetically across generations (Matsuzawa *et al.*, 2001), therefore an individual's knowledge may affect the behavior of others in the community. Besides determining the role played by ecological constraints, we aimed to verify social influences on tool use.

METHODS

Subjects and Housing Conditions

Eleven adult chimpanzees (*Pan troglodytes*) served as subjects (Table I) at the Primate Research Institute (PRI) in Inuyama, Japan. They fed 3 times per day on a variety of fruits and vegetables and chow. Water was freely available. The subjects were routinely separated in 2 groups with

Table I. Group compositions and subjects main choice of tools for fishing/drinking tasks in previous experiments

Group	Subjects: Name	Sex	Birth date	Juice drinking[a]: Outdoor compound	Honey fishing: Social context[b]	Single context[c]
A	Pan	F	83/12/07	Leaves	Plastic string	Plastic string
	Ai	F	76/10/—	Hand[d]	No preference[d]	No preference[d]
	Akira	M	76/06/—	Hand[d]	No preference[d]	No preference[d]
	Mari	F	76/06/—	Not tested	Rubber tube	Rubber tube
	Petite	F	66/—/—	Leaves	Rubber tube	Rubber tube
	Reiko	F	66/12/—	Leaves	Not tested	Not tested
B	Pendesa	F	77/02/02	Hand	Plastic string	Plastic string
	Chloe	F	80/12/13	Hand/leaves	Rubber tube	Rubber tube
	Popo	F	82/03/07	Hand	No preference[d]	No preference[d]
	Gon	M	66/—/—	Hand[d]	Rubber tube	No preference
	Reo	M	82/05/18	Not tested	Not tested	Not tested

[a]Tonooka *et al.*, 1997.
[b]Hirata and Morimura, 2000.
[c]Celli, unpublished.
[d]Apparently low skills and/or lack of motivation.

random composition and alternately spent the day in a large outdoor compound. For the experiment we determined the group compositions based on mutual affinities among subjects, and they remained stable in all sessions of the experiment. The compound is a 770-m^2 area (Fig. 1), enriched with artificial streams containing fish, unprotected trees and plants ($\geq$400 trees of 63 different species, some edible), ropes and climbing structures (Ochiai and Matsuzawa, 1997). At night the groups remained separate in smaller compounds and 8 interconnected concrete walled residential rooms.

Many of the individuals had been subjects in cognitive studies (Biro and Matsuzawa, 1999; Fujita and Matsuzawa, 1990; Kojima, 1990; Myowa-Yamakoshi and Matsuzawa, 1999; Tanaka, 1995; Tomonaga, 1998; among others). With regard to tool use experience, some of the subjects had participated in honey fishing experiments indoors, where artifactual materials were provided (Celli, unpublished; Hirata and Morimura, 2000) and experiments in the outdoor compound, using leaves to drink juice (Tonooka *et al.*, 1997). Table I is a summary of the subjects' tool abilities and preferences. Although the task was not novel for 9 of the 11 subjects, this was the first time that the chimpanzees encountered the honey fishing task outdoors, and in which no artifactual tool was provided for them to fish for honey.

Task and Materials

The experimental task was honey fishing (Celli *et al.*, 2001; Hirata and Morimura, 2000). We placed 2 transparent polyethylene bottles

Fig. 1. The large outdoor compound with trees and climbing structures. Note the outdoor booth at the bottom of the figure (Photo Courtesy: Akihiro Hirata, The Mainichi Newspapers Co.).

($4 \times 2.5 \times 6$ cm), each containing 30 g of honey in polycarbonate boxes attached to the walls of an outdoor booth (Fig. 5). The 2 fishing sites were 1 m apart. The bottles had a 3-cm^2 opening on the upper part of, which was connected with a 5 mm hole in the center of each panel, *ca.* 45 cm from the floor, where the tools had to be inserted in order to obtain honey.

We provided the chimpanzees with no artifactual materials, but they had access to the compound where they could select branches, twigs, vines, or leaves from several species of grass, shrubs and trees. We recorded the sessions with 4 video cameras to record the interactions between the chimpanzees around the outdoor booth, tool selection and the individual performances at each of the 2 fishing sites.

Procedure

We conducted the experiments at the large outdoor compound (Fig. 1) in 4 phases—Summer, Autumn, Winter and Spring—distributed uniformly across the experimental year. We conducted 10 sessions per group for each phase, everyday, alternately with each group. Each session lasted 30 min even if no individual arrived at the fishing site. During the initial phases—Summer and Autumn—we conducted sessions in the morning, from 08:00 to 08:30, after the first feeding. During Winter and Spring, we conducted experiments around midday, from 12:30 to 13:00 h, after the second feeding. This change was necessary to avoid low levels of activity in mornings of cold months.

Habitat Data

Because the chimpanzees tended to select tools from vegetation near the fishing sites we measured and identified vegetation within a 2-m range around the outdoor booth. Within the area we identified all vegetation specifically when possible, or per plant type: grass or woody plant. We also estimated the abundance of each plant within the area—percentage of coverage—around the middle of each experimental phase, to assess changes in species and density of the vegetation across seasons. We analyzed information on temperature and rainfall to illustrate climatic changes. The data was measured by the meteorological observatory of Nagoya City, located 24 km south of PRI.

Data Analysis

We analyzed the performance of each individual that engaged in honey fishing, counting all the attempts to insert tools into the honey bottle and the insertions that resulted in success. An attempt is any insertion of a tool into the hole, regardless of the result—all successes and failures—and success is when the inserted tool reaches the honey. For each attempt, we identified the type of tool to the specific level when possible. Due to different tool use experience, ability, and motivation of the individuals, for the final analysis we established a criterion that excluded subjects that had performed <100 attempts within all sessions (Summer, Autumn, Winter and Spring). In group A ($n = 6$), we excluded Ai. In group B ($n = 5$), we excluded Popo, Gon and Reo.

In group A, we used all year data to analyze the type of tool used and result of attempts with Wilcoxon Matched Pairs test. For the subjects that met the criterion in each group, we compared the number of attempts and successful insertions via a Mann Whitney U test. Furthermore, we used a Page's test (Page, 1963) to assess the relationship between attempts with each type of tool by the groups and available vegetation around the honey fishing sites.

We recorded all ≤2 m of the sites, the tool used by the focal individual, and the outcome of the insertion.

RESULTS

Seasonality in Climate

In Japan seasonality is marked and involves variation of both rainfall and temperature. Monthly rainfall over 12 consecutive months from August 1998 to July 1999, when the study was conducted, averaged 138.1 mm ± 103.6 mm. The distribution for the period (Fig. 2) showed 2 rainy seasons—September-October and May-July—a dry season in November-April, and a less dry period in August. Seasonal variation in temperatures was also pronounced, with daily maximum and minimum temperatures varying markedly across the months. For example, the mean monthly maximum temperature over the 12-mo period varied from 33.3° to 9.3°C ($\chi = 21.1$°C; SD = 8.3°C), while the mean minimum varied from 24.8° to 1.2°C ($\chi = 12.7$°C; SD = 8.2°C).

Seasonality of Vegetation

The vegetation around the fishing sites, changed considerably within the year (Fig. 3). In Summer a notable part of the area was covered by grass. However, its density decreased in subsequent seasons, from 51.5% in Summer to 21.2% in Autumn and only 2.5% in Winter. In Spring, the percentage of grass coverage increased to 21%, but consisted mostly of leaves and no stem. The percentage of woody plant—shrub and tree—coverage was lower but more stable, ranging from 6.8% in Spring to 4.7% in Winter.

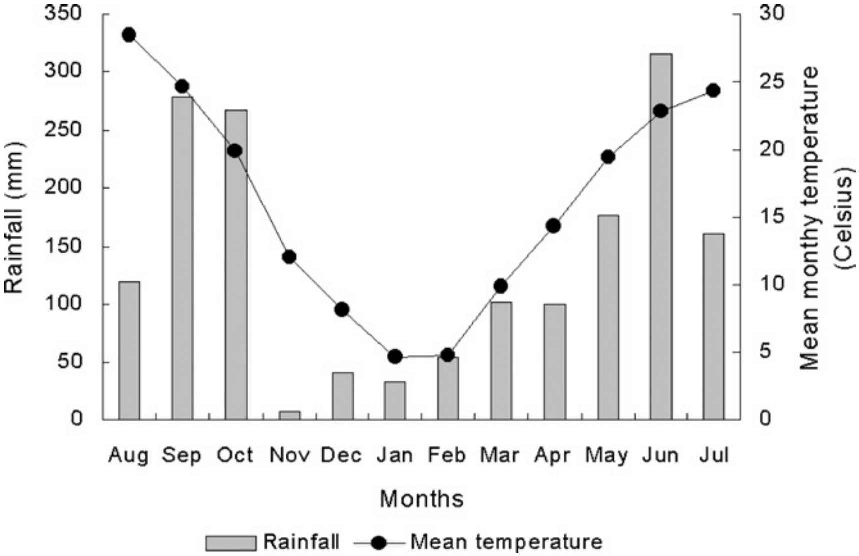

Fig. 2. Monthly temperature and rainfall variations in Nagoya City over the period of study.

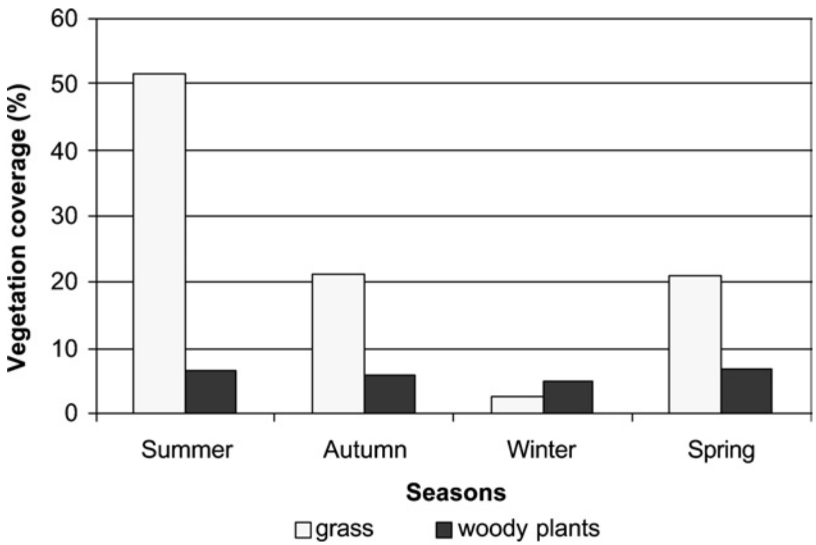

Fig. 3. Variation of the vegetation around the honey fishing sites by season.

Table II. Plants most commonly used as tools, available at the outdoor compound around the honey fishing sites

Family	Scientific name	Life form	Tool type
Gramineae	*Digitalia ciliares*	Grass	Grass
”	*Setaria* sp.	”	”
”	*Echinochloa* sp.	”	”
Cyperaceae	*Cyperus microiria*	”	”
Asteraceae	*Artemisia* sp.	Shrub	Twig
Saxifragaceae	*Hydrangea macrophylla*	”	”
Cupressaceae	*Juniperus chinensis*	”	”
Rosaceae	*Spiraea thunbergii*	”	”
Cupressaceae	*Thuja ocidentalis*	”	”
Caprifoliaceae	*Abelia grandiflora*	”	”
Oleaceae	*Osmanthus fragrans*	Tree	”
Theaceae	*Camellia* sp.	”	”
Aquitoliaceae	*Buxus microphylla*	”	”
Podocarpaceae	*Podocarpus macrophyllus*	”	”
Pineceae	*Pinus* sp.	”	”

Choice of Materials for Tool Use

Despite the fact that groups A and B were tested in the same outdoor compound and had equal access to the surrounding vegetation, they showed different choices of tools (Table II). The extent to which they used the 2 kinds of tools differed: the average number of attempts for the subjects of A, over the phases, showed that they significantly used more twigs ($\chi = 1368$) than grass ($\chi = 72.2$) (Wilcoxon Matched Pairs test, N $= 5$; T $= 0$; Z $= 2.02$; P < 0.05). The amount of successful twig insertions ($\chi = 798.4$) is significantly higher than grass insertions ($\chi = 38$) (Wilcoxon Matched Pairs test, N $= 5$; T $= 0$; Z $= 2.02$; P < 0.05) (Top panel in Fig. 4).

The number of individuals that met the criterion in B is too low ($n = 2$) for statistical analyses, nevertheless the bottom panel in Fig. 4 shows their preference for grass as tools in the first 3 phases, especially Summer, when we saw no twig use. Pendesa was responsible for twig use in Winter and Spring. Comparing both groups in Summer, individuals of B used grass significantly more ($\chi = 1336.5$) than individuals of A did ($\chi = 44.4$) (Mann Whitney's U test, $U = -2.01$; P < 0.05), and they were more successful ($\chi = 1121$) than individuals of A ($\chi = 28$) (Mann Whitney's U test, $U = -2.01$; P < 0.05).

Tool Use and Ecological Variables

To test the relationship between tool choice and availability of tool materials, we conducted Page's tests for ordered hypotheses (Page, 1963).

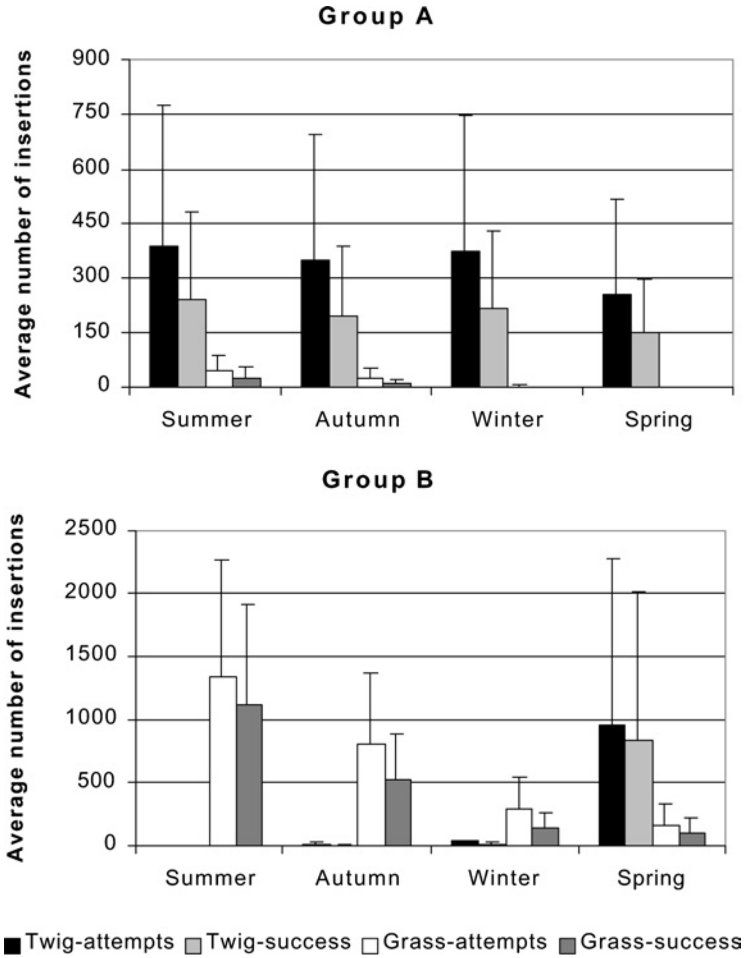

Fig. 4. Average number of attempted and successful insertions of twigs and grass by subjects in A and B across seasons. Error bars are standard deviations.

The null hypothesis is that the number of attempts with each type of tool material—grass or twigs—is independent of the availability of tool materials, whereas the alternative hypotheses are that 1) the number of attempts with each material increased as the availability of it increased, or 2) attempts with one material decreased as the availability of the other increased. Grass availability increased Winter < Autumn < Spring < Summer, and twig availability Winter < Autumn < Summer < Spring (Fig. 3).

We used the trends of availability as alternative hypotheses for the tests. For A, wherein the individuals predominantly used twigs, the number of attempts with grass or twig is independent of these availabilities (all Ls < 131, 4 seasons, 5 subjects, all ns). In contrast, for B, wherein the individuals predominantly used grass, the number of attempts with grass significantly increased as the availability of grass increased ($L = 58.0$, 4 seasons, 2 subjects, $p < 0.05$, two-tailed), but independently of the availability of twigs ($L = 52.0$, ns). Furthermore, the number of attempts with twigs marginally increased as the availability of grass decreased ($L = 57.0$, $p = 0.0864$, two-tailed), yet was independent of twig availability ($L = 48.0$, ns), though the use of twigs increased in the final season.

Tool Use and Social Variables

In several instances subjects approached group members and observed them performing the task (Table III). We recorded the amount of time subjects spent observing others, before and after their first success for the 2 tool types. Individuals of group A exclusively observed the use of twigs while B individuals mainly observed the use of grass.

In group A, Pan successfully inserted twigs from the start of the first session of Summer without observing others. She had experience with the task indoors and discovered an effective tool in an outdoor juice drinking experiment (Tonooka *et al.*, 1997) (Table I). Petite observed Pan using a twig for 13 sec before her first success with a twig on the second Summer session. However, most of her observation time was in the 10th session of Summer (211 sec of twig use by Pan and Mari). She had used artificial materials to fish for honey and also used leaves to drink juice. Mari observed Pan using twigs for 193 sec before she tried for the first time in session 3 of Summer. She had experience with the task indoors but was never tested in a setting without provision of materials. Akira observed Pan and Petite (Fig. 5) using twigs for 104 sec in sessions 2 and 4 before his first attempt with a twig in session 5 of Summer. He had experience with the task indoors but was not proficient at it, and was unable to use leaves in the juice drinking task. Reiko was totally naïve at honey fishing and only attempted it in session 4 of Autumn. She observed Pan, Petite and Mari using twigs for 376 sec in Autumn sessions 4, 6 and 10, before using twigs in the Winter session 1.

In B, Pendesa started fishing successfully 10 sec from the start of the session, using a grass tool, while Chloe took 28 sec to make a grass tool and get honey. Both subjects experienced the task and performed well in a setting with artifactual materials. They did not observe others before using

Table III. First attempt, success and tool type used by each individual of groups A and B and the amount of time the observed others before and after their first success

					Observation (sec)			
		1st attempt	1st success		Before 1st success[a]		After 1st success	
Group	Subjects	Session/season	Session/season	Tool type	Grass	Twig	Grass	Twig
A	Pan	1/Summer	1/Summer	twig	—	—	—	13
	Ai	1/Autumn	—	—	—	27	—	—
	Akira	5/Summer	5/Summer	twig	—	104	—	32
	Mari	3/Summer	3/Summer	grass	—	193	—	346
	Petite	2/Summer	2/Summer	twig	—	13	—	435
	Reiko	4/Autumn	1/Winter	twig	—	376	—	137
B	Pendesa	1/Summer	1/Summer	grass	—	—	139	—
	Chloe	1/Summer	1/Summer	grass	—	—	25	—
	Popo	2/Summer	2/Summer	twig	—	—	—	—
	Gon	10/Autumn	9/Spring	twig	82	56	27	—
	Reo	—	—	—	30	—	—	—

[a]Subjects Ai and Reo had no success during the experiment. While Ai attempted to use tools, Reo never did so, despite the fact that they observed others.

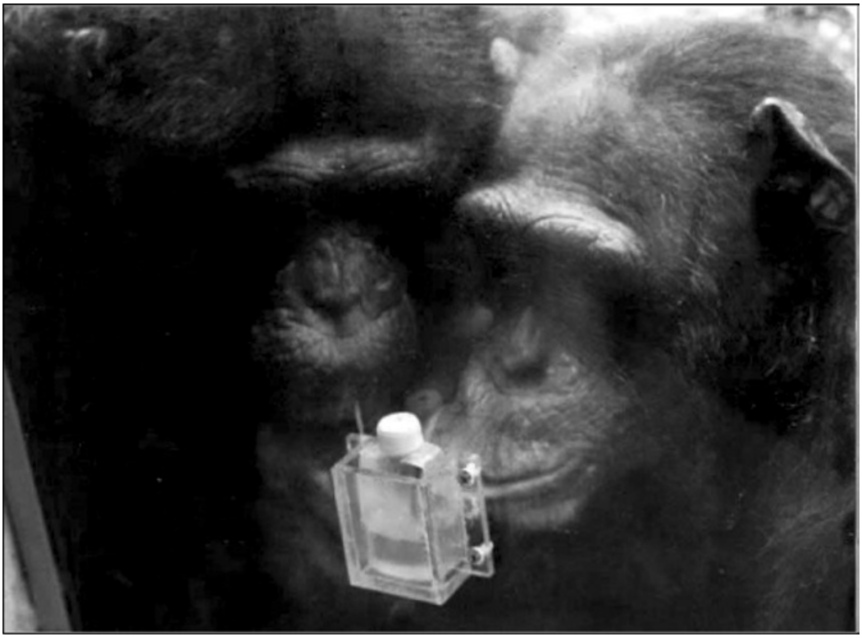

Fig. 5. One of the fishing sites available at the outdoor booth with a honey bottle attached to the polycarbonate panel. Note Akira (left) observing closely the performance of Petite (right).

tools for the first time therefore, we consider their use of grass tools is likely to be an independent invention.

DISCUSSION

Seasonal fluctuations of rainfall and temperature were related to variation in the density of some of the vegetation in the outdoor compound. Grass was plentiful during Summer but scarce in the Autumn and Winter, whereas woody plants, which provided twigs, were less abundant than grass but more constant through the year.

Most subjects could recognize the plants as tools, and their relation to the referent, i.e. honey, which could indicate flexibility (Sakura and Matsuzawa, 1991). Concerning group preferences, individuals of A showed a preference for the less prominent twigs. Their fishing performances were not influenced by seasonality once twigs were available throughout seasons.

Conversely, subjects in B, preferred to use grass as a tool to extract honey. Nevertheless, their use of grass and success with it are correlated with availability of the material, as in Autumn and Winter when grass coverage declined, as did the number of attempted and successful grass insertions. The results show that the tool use behavior of individuals that used grass as a material was influenced by ecological variables. The data also showed that one individual of B shifted preference from grass to twig (bottom panel, Fig. 4). The shift began during Winter when grass availability was lowest. Less predictably, the shift magnified in Spring, when grass coverage was returning. The fact that although grass leaves were present in Spring, stems—the only part used as a tool by the subject—remained absent, which might explain the shift. However we cannot rule out the possibility that the change simply indicates that the subject figured out a better way to access the reward.

When tested in a juice drinking task outdoors, the subjects converged to one kind of plant as a tool (Tonooka *et al.*, 1997). Tonooka (2001) suggested social transmission of tool selectivity, because Bossou chimpanzees select a particular kind of leaf to dip water. The use of a material or technique may be acquired by observation of skilled individuals and lead to local traditions (McGrew, 1992; Sugiyama, 1993; Matsuzawa *et al.*, 2001). However as Beck (1980) points out, although there is evidence that observational learning is operative in the acquisition of tool use in pongids, we must be careful about inferring social learning.

There was an initial group difference concerning tool choice that discounted ecological explanation because we tested both groups at the same site. For subjects of B and Pan of A, because they started inserting in the first session without observing others, we considered independent invention and not observational learning. However, for the subjects that spent time observing others, selection of materials was not as clear. Individuals of A were only exposed to the use of twigs and they may have biased the observers. Interestingly, subjects of the same group used the same tool, despite the fact that when tested indoors individuals had different material preferences. However, despite the fact that the subjects' histories are known and may have influenced selection, the possibility of response generalization or independent learning or both remains. As we were unable to precisely assess the impact of observations and prior experience, we cannot be certain of social transmission.

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