CHARTING CULTURAL VARIATION IN CHIMPANZEES

by

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Summary

Cultural variation among chimpanzee communities or unit-groups at nine long-term study sites was charted through a systematic, collaborative procedure in which the directors of the sites first agreed a candidate list of 65 behaviour patterns (here fully defined), then classified each pattern in relation to its local frequency of occurrence. Thirty-nine of the candidate behaviour patterns were discriminated as cultural variants, sufficiently frequent at

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one or more sites to be consistent with social transmission, yet absent at one or more others where environmental explanations were rejected. Each community exhibited a unique and substantial profile of such variants, far exceeding cultural variation reported before for any other non-human species. Evaluation of these pan-African distributions against three models for the diffusion of traditions identified multiple cases consistent with cultural evolution involving differentiation in form, function and targets of behaviour patterns.

Introduction

Research on animal culture and social learning has been conducted intermittently all through the twentieth century (Whiten & Ham, 1992; McGrew, 1998), but has accelerated in recent years. The accumulating results of this theoretical and empirical work are represented in a profusion of reviews, reappraisals and collections of papers in the last decade (Galef, 1990, 1992, 1998; Tomasello, 1990, 1994, 1996; Visalberghi & Fragaszy, 1990, in press; McGrew, 1992, 1998; Moore, 1992; Whiten & Ham, 1992; Heyes, 1993; Quiatt & Reynolds, 1993; Tomasello *et al.*, 1993; King, 1994; Thierry, 1994; Wrangham *et al.*, 1994b; Boesch, 1996a, b; Heyes & Galef, 1996; Parker & Russon, 1996; Sperber, 1996; Zentall, 1996, 2001; Russon, 1997; Tomasello & Call, 1997; Boesch & Tomasello, 1998; Byrne & Russon, 1998; Russon *et al.*, 1998; Box & Gibson, 1999; Miklosi, 1999; Aunger, 2000; Whiten, 2000; Myowa-Yamakoshi, 2001; Rendell & Whitehead, 2001; Fragaszy & Perry, in press; Meltzoff & Prinz, in press).

Much of the recent work has concerned transmission processes such as imitation, most often studied in minimal, dyadic configurations (what does individual A learn from observing individual B?). Although these social learning processes have typically been studied because of their putative role in the transmission of behavioural traditions, relatively few studies have sought to chart cultural variation itself, in wild populations. Amongst primates, for example, such studies are largely restricted to just two taxa; the chimpanzee (*Pan troglodytes*), and the Japanese macaque (*Macaca fuscata*) (McGrew, 1998; Whiten, 2000).

The evidence that does exist derives from studies that have typically focused on only a single type of behaviour that varies between populations. Birdsong dialects represent perhaps the most comprehensively documented example (Marler & Tamura, 1964; see Catchpole & Slater, 1995, for a review). Although inter-populational song variation has been well-documented for some species, and complemented by experimental, laboratory studies establishing the kind of social learning process at work, we still do not know the extent to which variations in other patterns of behaviour, such as foraging and courtship patterns, map onto the dialect-groups. Whether such multiple cultural variations exist, and if so, what mechanisms underlie them, are important question for at least two reasons. One is that however much we would wish to eschew anthropomorphism in the study of animal behaviour, the phenomenon of culture is best known in our own species, thus inevitably providing patterns against which putative animal cultures can be compared. Since it is a matter of common observation that any two human cultures vary in multiple ways (eating habits, courtship rituals, forms of greeting *etc.*), the extent to which this is true of other species is an inescapable question of interest. In the present paper we present what may be the richest patterns of such variation documented in a non-human species to date.

A second reason to analyse multiple traditions appeals to the very much broader goal of understanding the nature of cultural processes in biological systems, including, eventually, their interaction with genetically-based processes of behavioural evolution (Boyd & Richerson, 1985; Feldman & Laland, 1996). One important empirical step towards this lies in analysing the spatial patterning of multiple cultural variations. In the present paper we assess whether the observed patternings of putative cultural variations amongst chimpanzees are consistent with specific alternative models of the diffusion process.

Models of cultural processes

As a first step in this enterprise we consider just three basic cultural models (Fig. 1). In the first, Diffusion from Unitary Origin (Fig. 1a), a single behavioural innovation originates in one community (or ‘unit-group’) and the behaviour then spreads (diffuses) outwards to other communities through social learning (probably in turn resting upon cross-community migration). A putative cultural behaviour found to be both widespread in, and restricted to, a population that includes multiple communities within one geographic region, would be consistent with this model. The second model involves Diffusion from Multiple Origins (Fig. 1b), a scenario that would be predicted to occur for types of behaviour that are easier for the species to invent than in the case of a unitary origin. This model would be supported by

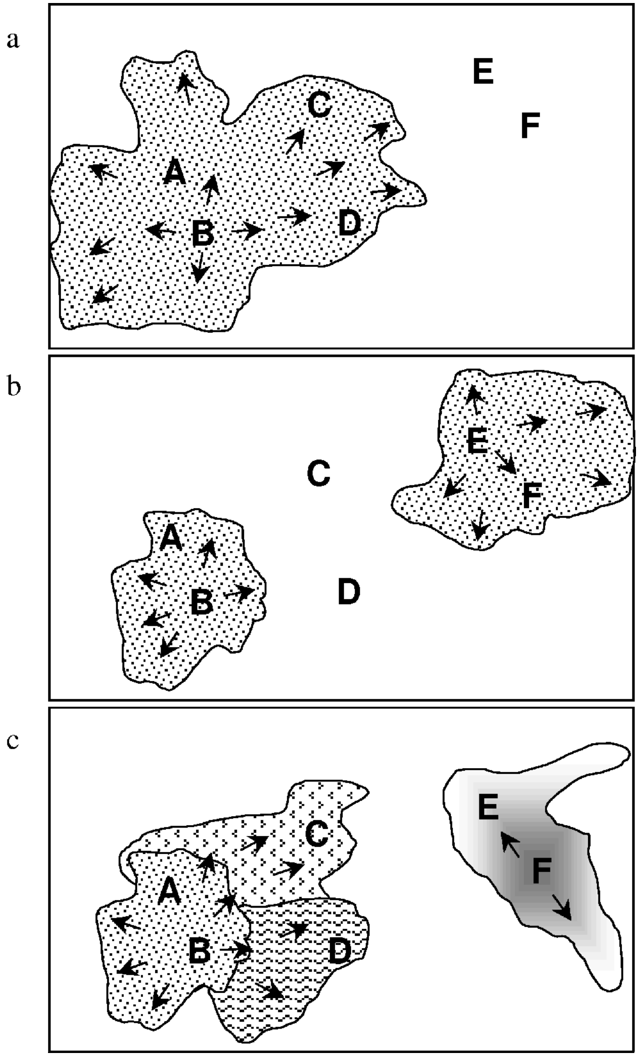

Fig. 1. Three models of cultural diffusion, illustrated in relation to hypothetical chimpanzee study sites/communities A-F. (a) Diffusion of a behaviour pattern (shading) from a unitary origin (community B) to neighbouring populations including communities A, C, D; (b) Diffusion from multiple initial sources (B, E) to neighbouring communities; (c) Diffusion together with differentiation, creating variants. On the left a qualitative differentiation occurs as a behaviour pattern diffuses from B to C, and another as it passes from B to D. On the right, the possibility of more graded differentiation (*e.g.* in aspects of action intensity or tool dimensions) is recognised in diffusion of a behaviour pattern from F to others, including E.

finding two or more separate regional distributions for the behaviour in question, each indicating diffusion from a different original source. Third, is Diffusion with Differentiation (Fig. 1c), in which the behaviour is modified in some significant way during its spread (although its 'lineage' remains sufficiently identifiable). As we shall see, the change might be in the form of the behaviour, its functions or its targets. Boesch & Tomasello (1998, p. 602) envisaged such a process as the 'branching' of a tradition. Evidence consistent with this third model would be behavioural patterns in adjacent sub-populations that represent variants on a theme common to the larger region in which they are found, or variants of behaviour found in neighbouring sub-populations. Of course, this would mean that a behavioural distribution might be correctly considered as consistent with model 1 (or 2, if the relevant conditions are met) so long as the behaviour category is described at a relatively global or inclusive level, but as consistent with model 3 once differentiated subcategories are distinguished. In the words of Boyd *et al.* (1997), we might in this case witness hierarchically structured spatial patterns of behavioural distribution. In the present paper we begin to evaluate distributions of chimpanzee behavioural variation against the predictions of these models.

These distinctions concern each category of behaviour considered separately. As Boyd *et al.* (1997) also noted in surveying the fundamental questions of cultural analysis, a higher-level issue concerns whether variations in certain behaviours might cluster or covary with others, suggesting an underlying linkage. Boyd *et al.* added that any one community might also be differentiated from others by a distinctive suite of variations, which in the human case has sometimes been suggested to reflect a relatively resilient cultural 'core' of the community concerned. Multiple behavioural variations are sufficiently complex in chimpanzees that we can begin to address these higher-level issues also.

Charting cultural variation in chimpanzees

Chimpanzees have for some time been in the vanguard of non-human species for which such issues might be addressed. Attempts to chart multiple cultural variations have become more elaborate as data from long-term field studies have accumulated (Goodall, 1973, 1986; McGrew *et al.*, 1979; Baldwin *et al.*, 1981; Nishida *et al.*, 1983; McGrew, 1992; Wrangham *et al.*, 1994a; Boesch, 1996a; McGrew & Marchant, 1997; Boesch & Tomasello, 1998).

However, to achieve the most definitive analysis we took an approach different to these earlier analyses, which were based upon published records from field studies. Relying on published data poses at least three problems in arriving at an accurate picture. One is that the literature is incomplete; fieldworkers may steadily accumulate records of the repertoire of behaviour at their sites, but there is always a backlog of unpublished findings, sometimes substantial (field researchers naturally vary in what they consider to have high priority for publication). Secondly, even when records are published, it is not necessarily a priority of the author to describe how common in the community is the behaviour in question; yet for cultural analysis it is vital to know where a behaviour lies on the continuum from unique, or anecdotal, to customary. Thirdly, to identify cultural variation it is vital to know which behaviour patterns, common at some sites, remain absent at others; yet such 'negative' data will naturally tend to be under-reported.

We instead approached the problem through a systematic survey, first defining a set of candidate cultural variants, then having the key researchers at each of nine major field sites classify the level of occurrence recorded for the communities of chimpanzee studied. The method is described fully further below.

A brief account of the behavioural distributions identified in this study has been published for the seven most long-term sites (Whiten *et al.*, 1999). In the present, companion paper we offer a comprehensive report of the information collated in our collaborative study, including the data for all nine sites. The resulting charts of cultural variation are by far the most extensive for any species but our own, encouraging us to begin to explore their fit to the alternative models of cultural processes outlined above. We note that despite an impressive set of pioneering explorations (*e.g.* Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985; Durham, 1991), Richerson & Boyd (1997, p. 342) were led to lament that 'to date, the use of Darwinian ideas to study cultural evolution has been mostly a conceptual and theoretical exercise'. Our data set is perhaps the first to permit an empirical investigation of substantial cultural patterning in any non-human species.

Methods

Communities studied

Nine communities that have been the subject of long-term fieldwork were assessed (Fig. 2). Sites (noting respectively the sub-species, observation period in years before our 'final census

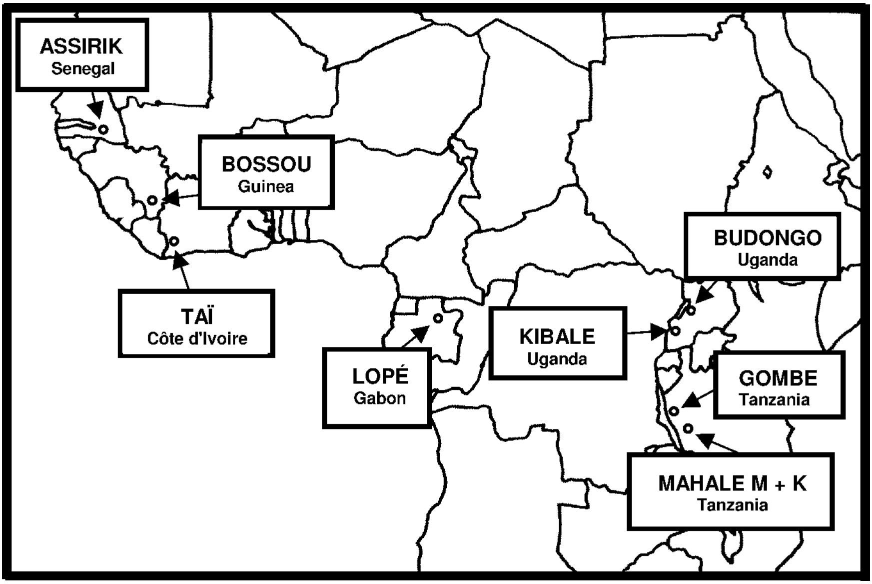

Fig. 2. Locations of long-term study sites in Africa.

date' of September 1998, and site director) were: Assirik, Senegal (*verus*, 4, McGrew); Bossou, Guinea (*verus*, 23, Sugiyama); Taï Forest, Côte d'Ivoire (*verus*, 23, Boesch); Lopé, Gabon (*troglodytes*, 14, Tutin); Gombe, Tanzania (*schweinfurthii*, 38, Goodall); Mahale M-group, Tanzania (*schweinfurthii*, 30, Nishida); Mahale K-group (*schweinfurthii*, 18, Nishida); Kibale Forest Kanyawara community, Uganda (*schweinfurthii*, 11, Wrangham); Budongo Forest, Uganda (*schweinfurthii*, 8, Reynolds). All field studies continue at these sites except for Mahale-K (terminated 1983) but we restrict the present analysis to the data we collated up to the end of 1998.

The study proceeded in two phases

Phase 1

The aim of Phase 1 was to generate a list of candidate cultural variations for input to a second phase in which occurrence at each site would be systematically established. Phase 1 was thus intended to be inclusive, logging any candidate behavioural pattern that we suspected might lead to the identification of cultural variants in Phase 2. Over-inclusion of inappropriate candidates in Phase 1 was expected to be unproblematic insofar as these would be weeded out in Phase 2. Directors of nine long-term chimpanzee field studies (the coauthors of this paper; see Table 1) received an initial list of defined behaviour patterns drawn up by A.W. and C.B. on the basis of existing published material. Together with their key co-workers, directors were asked to name and define any further behavioural patterns they suspected might vary culturally across sites.

On this basis a new, extended list was drawn up and circulated to all collaborators to check for clarity and negotiate issues of lumping or splitting of behavioural categories.

Collaborators found it relatively easy to achieve a consensus on the latter, although it is important to acknowledge that it is difficult to establish objective rules for deciding such matters. For example, it was agreed to lump 'dip a stick in a bee's nest to get honey', and 'dip a stick in a hole to get water', as 'fluid dip', because the action patterns appear so similar. In principle, the two categories could have been kept separate (one can always split a category into the different ways of doing it, or alternatively, lump categories together that share a common feature). Thus, the precise number of cultural variants we eventually came to identify should not be over-reified; it is a number dependent on the outcome of the process common to all ethology, of splitting or lumping categories of behaviour in a way appropriate to the study in hand. Objectivity in this aim was pursued in the present study through the systematic procedures specified by Phases 1 and 2, with Phase 1 requiring agreement between highly experienced chimpanzee researchers on what they regard as a usefully discriminable set of candidate behaviour patterns in the first place. It is likely that further insights will be gained in future through more refined and comprehensive versions of our procedure, of which the present study is merely a first, and exploratory, application.

Phase 1 generated a list of 65 fully defined behaviour patterns (Table 1). Appropriate references are included in Table 1 where the behaviour has been described well in existing literature. Particularly with regard to any future attempts to apply our approach to other species, it cannot be emphasised too strongly how important for Phase 2 we found these full, written definitions. Indeed, once directors proceeded to further discussion with their team in Phase 2, it became necessary to specify some definitions even more closely before the frequency of the behaviour could be properly coded by the respective field researchers.

Phase 2

In consultation with their key collaborators, the field-site directors assigned a code appropriate for the chimpanzee community they studied to each of the 65 candidate behavioural patterns, as follows:

- Customary — pattern occurs in all or most able-bodied members of at least one age-sex class (*e.g.* adult males).
- Habitual — pattern is not customary but has been seen repeatedly in several individuals, consistent with some degree of social transmission.
- Present — pattern is clearly identified but neither customary nor habitual.
- Absent — pattern is not recorded and no ecological explanation for absence is apparent.
- Ecological explanation — absence of pattern is explicable because of a local environmental or ecological constraint.
- Unknown — pattern is not recorded, but we cannot be sure of absence because of inadequacy of relevant observational opportunities.

As might be expected, the distinction that respondents on occasion found difficult to make was whether a pattern absent at any particular site could be ascribed to an ecological explanation or not. In most cases the answer appeared clear. For example, 'ecological explanation' for absence could be confidently coded when a species of tree essential to the act was known to be unavailable; conversely, 'absent' could be coded when such a tree species was present yet no sign of the behaviour pattern had ever been seen. In other cases the decision was more difficult, an issue we return to in the discussion section. Respondents at each camp

TABLE 1. *Definitions of candidate behaviour patterns (Phase 1)*

1 Investigatory probe: Probe used to examine location (usually a hole/recess), then sniffed (Goodall, 1968, p. 206). [PRB — see table foot text]

2 Play-start: Initiate play, incorporating an object. 'when initiating social play or during an ongoing session, one of the youngsters will break off a leafy twig or pick up some other objects such as a piece of palm-frond; with this in mouth or hand he approaches, then runs from, the chosen playmate' (Goodall, 1986, p. 560). [*cf* PSO]

3 Drag branch: Dragging a large branch while running, as part of aggressive display. [DRB]

4 Leaf-sponge: Wad of leaves/vegetation chewed and used to collect water, then squeezed in mouth (Goodall, 1964).

5 Branch-clasp: Grasping overhead branch whilst grooming (see McGrew, 1992, p. 69). [GNH]

6 Branch-shake: A branch is shaken to attract another's attention, as in courtship ('branching' — Goodall, 1968, p. 217). [SHR, SHB]

7 Buttress-beat: Beating/drumming with hands or feet on the buttress or trunk of a tree. [DRM, SLB]

8 Nasal probe: Use of a small stick to clear the chimpanzee's own blocked nasal passage (Nishida & Nakamura, 1993). [SNS]

9 Comb: A (leaf) stem is used to comb through body hair (Reynolds, Assersohn, unpubl.).

10 Insect-pound: Probe used to retrieve insect by prodding it ('take a small twig. . . , remove the side branches and leaves, and so make a small stick. Next, they would beat and pound the bottom of the hole several times. On pulling the stick out a few termites would be attached to it, mostly broken and adherent. The chimpanzee would lick them off and again try to pound the bottom of the hollow': Sugiyama & Koman, 1979).

11 Resin-pound: Probe used to obtain resin by pounding it. ('took a somewhat longer stick than that used for [insect-pound] . . . they repeatedly pounded and mixed by stirring the bottom of the hollow of a tree. On pulling the stick up, a brown-colored resin was seen to be conglutinated stickily on it': Sugiyama & Koman, 1979).

12 Branch-hook: Branch with twig(s) used to catch and pull closer another branch ('branch-haul' of Sugiyama & Koman, 1979: named differently here to avoid confusion with drag branch).

13 Perforate: Stout stick used to make probing holes in termite nests (termites then extracted with smaller probes) (Jones & Sabater Pi, 1969; McGrew *et al.*, 1979; Suzuki *et al.*, 1995).

14 Dig: Use of a stick as spade to dig away part of a (termite) nest mound (*cf* perforate) (Jones & Sabater Pi, 1969; McGrew *et al.*, 1979; Suzuki *et al.*, 1995). [*cf* DGS]

15 Brush-stick: Use of a stick for digging, making the end brush-like (tools identified but behaviour not observed; probably for termite digging and/or termite catching; 'brush' end 2-10 cm wide: Sugiyama, 1985).

16 Seat-stick: Branch broken from tree and sat upon, *e.g.* as protection on thorny branch (Alp, 1997, p. 50). [*cf* MCU]

17 Stepping-stick: Branch broken from tree and placed under sole of foot as protection on thorny branch ('by placing it under one or both feet, gripping the tool between the greater and lesser toes': Alp, 1997, p. 48).

TABLE 1. *(Continued)*

18 Container: Leaves used to catch/hold material ('picked a couple of large leaves, placed them on his hand, and defecated onto them': Goodall, 1986, p. 546)

19 Leaf-mop: Leaves used to mop up insects ('make a kind of handkerchief by crumpling them by both hands, with which she wiped many ants away with one hand and brought it to her mouth to lick': Nishida, 1973, p. 364) See also Goodall, 1986, p. 537.) [*cf* WIP]

20 Leaf-wipe: Leaves used to wipe out food from skulls, fruits (Boesch & Boesch, 1990). [*cf* WIP]

21 Leaf-brush: Leaves used to brush bees *etc*. away from an entrance or surface (*cf* fly-whisk) (Goodall, 1986).

22 Open-and-probe: Use of strong tools to open up a food site (*e.g.* by chiseling, digging) followed by fine tools to probe and harvest food (chiseling and gouging followed by dipping; Brewer & McGrew, 1990: perforating followed by fishing; Suzuki *et al.* 1995; see also Sugiyama, 1997).

23 Sponge push-pull: Use of a stick to push leaf-sponge into hole and withdraw it (Matsuzawa, 1991, cited by Sugiyama, 1997).

24 Algae-scoop: Use of a stem, stripped of leaves, to scoop surface vegetation like algae from water surface.

25 Ground-night-nest: Night-nesting on ground. (at Nimba, >1/3 of night-nests are on ground: Matsuzawa and Yamakoshi, 1996, p. 224)

26 Anvil-prop: Putting a small stone under one end of an anvil stone to keep it more level (Matsuzawa, 1994).

27 Food-pound onto wood: Food item smashed open by beating it on a hard wooden surface, like the base of a tree. (Goodall, 1968, p. 185)

28 Food-pound onto other: Food item smashed open by beating it on a surface other than wood, such as stone or hard earth. (Goodall, 1968, p. 185)

29 Nut-hammer, wood hammer on wood anvil: Use of piece of wood to crack nuts on wooden anvil (*e.g.* tree root) (Boesch & Boesch, 1983).

30 Nut-hammer, wood hammer on stone anvil: as 29 but using stone anvil.

31 Nut-hammer, stone hammer on wood anvil: as 29 but using a stone hammer.

32 Nut-hammer, stone hammer on stone anvil: as 31 but using stone anvil.

33 Nut-hammer, other: as 29-32 but using alternative materials, *e.g.* hard ground as anvil.

34 Pestle-pound: Palm petiole used to pound and deepen hole in crown of palm tree (Yamakoshi & Sugiyama, 1995).

35 Club: Striking forcefully with one end of stick, the other end held in hand (Kortlandt & Kooij, 1963). [CLB]

36 Termite-fish using leaf midrib: Leaf midrib used to extract termites from tunnels (Goodall, 1964; McGrew *et al.*, 1979). [FIT]

37 Termite-fish using non-leaf materials: Probing instrument, sometimes modified, used to extract termites from tunnels (Goodall, 1964). [FIT]

38 Ant-fish: Probes used to extract arboreal ants from tunnels ('selects and strips the grass or vine stem or scrapes the bark of wood vine with fingers and teeth. Then the rod is poked down into the ants' hole and withdrawn laden with ants, which are picked off with the lips': Nishida, 1973, p. 362.) See also Nishida & Hiraiwa (1982). [FIA]

39 Ant-dip-wipe: Use of wand to collect safari ants that swarm up it, ants then manually wiped off in a cluster and eaten (McGrew, 1974). See also Goodall (1968). [*cf* PTH]

TABLE 1. *(Continued)*

40 Ant-dip: Use of stick to collect safari ants that swarm up it, ants then picked off with lips and eaten (Boesch, 1996.) See also Sugiyama *et al.* (1988); Alp (1993).

41 Fluid-dip: Use of probe to extract fluid, including honey ('chimpanzees fish with sticks for the honey after trying to take out what they can with their hands': Boesch & Boesch, 1990, p. 89) and water ('A stem (*e.g.* Afromomum) is lightly chewed and inserted into a narrow hole to extract water: Wrangham, unpubl.).

42 Bee probe: ('First tests for the presence of adults by probing the nest entrance with a stick. If present, adult bees block the entrance with their abdomens, ready to sting. The chimpanzee then disables them with the stick to make them fall out and eats them rapidly': Boesch & Boesch, 1990, p. 89). [*cf* PRB]

43 Marrow-pick: Use of probe to extract contents of bone/skull. 'Taï chimpanzees regularly eat the marrow of long bones . . . with the help of small sticks': Boesch & Boesch, 1990, p. 90).

44 Lever open: Stout stick is used in levering fashion to enlarge insect or bird nest entrance (Goodall, 1968, p. 207; 1986, p. 540).

45 Expel/stir: Vigorous insertion, probing and removal of stick used in attempt to expel or stir up insects or other animals in hole (*e.g.* 'dead branch 118 cm in length and 400 g in weight . . . repeatedly and violently inserted and withdrew it with 'power-grip': Nishida, 1973, p. 364.) See also Huffman & Kalunde (1993).

46 Seat-vegetation: A few large, detached leaves placed on the ground for sitting on, *e.g.* as apparent protection from wet ground (Hirata *et al.*, 1998). [*cf* MCU]

47 Fly-whisk: Leafy twig used to fan away flies ('to take a twig with leaves from a tree and to fan away flies': Sugiyama 1969, p. 216 — he continued 'which were swarming about the genital area after copulation' but this need not be part of basic definition).

48 Self-tickle: An object is used to probe ticklish areas on self. 'sometimes a large stone or a stout stick is used . . . the object is pushed and rubbed into those especially ticklish areas between neck and shoulder and in the groin' (Goodall, 1986, p. 559).

49 Aimed-throw: Throwing of object with clear (even if inaccurate) tendency to aim (Goodall, 1964; Sugiyama & Koman, 1979). [THA]

50 Leaf-napkin: Leaves used to clean body surfaces (Goodall, 1964). [WIP]

51 Leaf-dab: 'Wound inspected by touching leaves to it, then examining leaves (leaves may be chewed)': Wrangham, unpubl.

52 Leaf-groom: 'Grooming' of leaves. ('the chimpanzee picks one or more leaves and, peering at them closely, grooms them most intently, sometimes lip-smacking at the same time' Goodall, 1986, p. 391; see also Goodall, 1968; Nishida, 1980). [GRL]

53 Leaf-clip, mouth: Noisy ripping of leaf, to gain attention for various functions ('A chimpanzee picks off 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-blade, a ripping sound is conspicuously and distinctly produced' Nishida, 1980, p. 117) Clipping may also be done with the lips. [GLL]

54 Leaf-clip, fingers: As 53 but using the fingers, rather than mouth. [*cf* CLL]

55 Leaf-strip: 'Leaves torn off stem by fingers, generally by thumb and fingers encircled around stem and swept off end of stem in violent move that tears at several or many leaves simultaneously' Wrangham, unpubl.) [*cf* PTH]

TABLE 1. *(Continued)*

56 Leaf-squash: Squashing of ectoparasites on leaves used in leaf-groom (Boesch, 1995).

57 Leaf-inspect: Ectoparasite placed on leaf on palm of hand, visually inspected, then eaten or discarded (Assersohn, unpubl.) [*cf* INS]

58 Index-hit: Finger used to squash ectoparasite on forearm. ('they place it on one forearm and hit it with the tip of the forefinger until it is squashed, and then eat it': Boesch, 1996).

59 Hand-clasp: Two chimpanzees clasp hands overhead, grooming each other with the other hand (McGrew & Tutin, 1978; see also de Waal & Seres, 1997). [GHC]

60 Knuckle-knock: Knuckles knocked on hard vegetation or other hard surface to attract another's' attention, as in courtship (Boesch, 1996) (see also Nishida, 1997, p. 385 — 'thump'). [RAP]

61 Branch-din: Saplings, shrubs and similar vegetation pulled down then released to make considerable noise (Tutin, unpubl.). At Lopé this is done when entering dense herb areas where elephants or gorillas may be encountered, or before crossing savannahs.

62 Branch-slap: Sitting on and slapping a branch with a hand to attract another's attention. This may be used in courtship (Reynolds, pers. com).

63 Stem pull-through: ('Sitting while pulling a leafy branch or a shrub or clump of grass through the hand, producing a conspicuous sound. The stem is immediately released': Nishida, 1997, p. 385). [PTS]

64 Shrub-bend: Putting stem(s) under foot and squashing, to attract attention of potential mating partner ('sitting while pushing down the stem of a shrub, grass or herb such as ginger, putting one of the feet on the plant, and repeating the same series of actions again and again, thus apparently making a crude ground cushion or bed. Usually followed by stamping or thumping the ground': (Nishida, 1997, p. 385). [BES]

65 Rain-dance: At the start of heavy rain, several adult males perform vigorous charging displays. Displays tend to return the males to their starting position, to be coordinated or in parallel, may include slow charges as well as rapid and may involve a variety of display patterns (*e.g.* ground slap, buttress-beat, branch drag, pant-hoots). (Goodall, 1971; Wrangham, unpubl., Boesch, unpubl.). [DSR]

Where categories are similar to those in a comprehensive ethogram ($N = 515$ behaviour patterns) published for the Mahale chimpanzees (Nishida *et al.*, 1999) since our data collation exercise, we indicate the appropriate code in square brackets to facilitate cross-referencing by researchers. Those where the linkage between categories entails more contrast are denoted [*cf*]. Such contrasts suggest that the potential for harmonisation of such developing taxonomies as these should be considered in future comparative projects updating that reported here.

agreed their consensual best judgment on each coding, adding a query mark to express any reservations in specific cases. Returns were collated and tabulated (Tables 2 and 3).

We note that chimpanzees have been studied for different periods of time at each site. Two devices were used to ensure that the codings across sites were comparably reliable. First, the 'unknown' code gave researchers the option of recording when a reliable judgement could not yet be made about a specific behaviour pattern at their site. In the event, as is evident in Tables 2 and 3, use of this code divided the sample into two quite different groups. In one fall two sites where the 'unknown' code had to be applied extensively; these are Assirik, where study had to be halted after four years of intensive work, and Lopé, where research priorities did not include intensive chimpanzee habituation. The codings for such sites are nevertheless important overall, because they include valuable records ranging from 'customary' to 'absent' for the more ostentatious behaviour patterns (including those leaving obvious material traces, such as certain forms of tool use) that will quickly be apparent to observers if they are being performed. Such codings, in conjunction with those from other sites, can be used to identify cultural variants at least for the behaviour patterns concerned. For the other seven sites, all studied intensively for eight years or more, the unknown code was rarely used. This gives a good indication of the scale of study ideally required for the kind of analysis we offer here.

The second device we used in recognising observational limitations was the query code. As indicated above, the principal cause of the (still relatively infrequent) use of this code (see tables) was a difficulty in being confident that an ecological explanation for absence could be discounted.

These safeguards have been implemented with the intention of making it unlikely that 'absent' is prematurely coded. Note also that even if the latter error were made, it is unlikely that a behaviour pattern that was truly habitual or customary (as opposed to merely present) would have been recorded as absent; yet re-classification of putative cultural variants (shifting them from Table 3 to 2: see Results) would be necessitated only if correction on this scale became necessary. The bias in our procedures instead leans to conservatism in the number of variants identified. Given that identification of cultural variants rests on contrasts we identify in this paper between (minimally) any two sites (customary/habitual at one, absent at another), it is logically more likely that those behaviour categories which have so far not been coded as differing between sites in this way (Table 2) may come to be so as further observation permits confident codings to be made.

Respondents were finally invited to add to their formal questionnaire returns supplementary comments about the nature of each behavioural pattern at their site. Certain of these comments provided useful and unexpected information reported in the results section below, but clearly the unsystematic nature of this component of the study constrains the kinds of conclusions that can be drawn, in contrast with the formal collation exercise.

Results and discussion

1. Identifying cultural variants

We identified as putative cultural variants those behavioural patterns that are absent without ecological explanation in at least one community, yet achieve habitual or customary status in at least one other (Table 3). Behavioural patterns fail to meet this criterion for three different kinds of reason and we consider these patterns first (Table 2).

In category A fell seven behavioural patterns that were not recorded as 'absent without ecological explanation' at any site, and thus cannot be classed as cultural variants by our criteria. Instead, these patterns are better

TABLE 2. *Behaviour patterns failing criteria for cultural variants*

a) 'Universals'	As	Bs	Tai	Lo	Ma	Mk	Go	Kib	Bd
Buttress-beat (drum on base of tree)	C	C	C	C	C	C	C	C	C
Branch-shake (to attract attention, court)	H	C	C	H	C	C	C	H	C
Branch-clasp (clasp branch above, groom)	H	H	C	H	C	C	C	C	C
Play start (invite play using stems in mouth)	+	+	H	H	C	C	C	C	H
Drag branch (drag large branch in display)	(--)	H	C	H	C	C	C	H	H
Leaf-sponge (leaf mass used as sponge)	(--)	C	C	+	+	e	C	C	C
Investigatory probe (probe and sniff)	(--)	H	C	(--)	H	H	C	+	(--)
b) 'Rarities'									
Sponge push-pull (stick and sponge tool)	(--)	+	+	(--)	+	e	+	e	--
Dig (stick used as spade to dig termite nest)	(--)	+	e	--	--	--	--	e	e?
Insect-pound (probe used to mash insect)	(--)	+	--	(--)	--	--	--	--	--
Resin-pound (extract resin by pounding)	(--)	+	--	(--)	e?	e?	--	--	--
Branch-hook (branch used to hook branch)	(--)	+	--	(--)	--	--	--	--	--
Leaf-wipe (food wiped from skull etc.)	(--)	e?	+	(--)	--	--	+	--	--
Leaf-brush (leaf used to brush away bees)	(--)	--	--	(--)	--	--	+	--	--
Container (object used as container)	(--)	--	--	(--)	--	--	+	--	--
Leaf-mop (leaves used to mop up insects)	(--)	--	--	(--)	--	+	+	e	e?
Nasal probe (clear nasal passage with stick)	(--)	--	--	(--)	+	--	--	--	--
Comb (stem used to comb through hair)	(--)	--	--	(--)	--	--	--	--	+
Perforate (stout stick perforates termite nest)	(--)	--	e	--	--	--	--	e	e?
Brush-stick (probing stick with brush end)	(--)	--	--	--	--	--	--	--	--
Seat-stick (stick protection from thorns)	(--)	--	--	(--)	e?	e?	e	e	e
Stepping-stick (walking on sticks over thorns)	(--)	--	--	(--)	e?	e?	e	e	e
Open and probe (perforate, then probe)	(--)	--	--	--	--	--	--	--	--
c) 'Environmentally explicable'									
Ground-night-nest (>10% nests on ground)	(--)	(--)	e?	--	e?	e?	+	e?	+
Anvil prop (rock used to level anvil)	(--)	H	e	e	e	e	e	e	e
Algae-scoop (scoop algae using wand)	(--)	C	e	(--)	e	e	e	e	e

(a) 'Universals', behaviours recorded as absent at no sites studied; (b) 'Rarities', behaviours not attaining habitual frequencies; (c) 'Environmentally explicable', behaviours whose absence appears always explicable by environmental factors. Study sites: West Africa — As, Assirik, Senegal; Bs, Bossou, Guinea; Taï, Taï Forest, Côte d'Ivoire; Central Africa — Lo, Lopé, Gabon; East Africa — Ma, Mahale M community, Tanzania; Mk, Mahale K community, Tanzania; Go, Gombe, Tanzania; Kib, Kibale Kanyawara community, Uganda; Bd, Budongo, Uganda. Behaviour occurrence codes: C, Customary; H, Habitual; +, present; –, absent with no environmental explanation; e, absence explained by environmental factors; (–), status not yet established (see text for full definitions).

thought of as putative chimpanzee universals, at least in relation to the communities studied here. Discovering these patterns at this stage of our analysis reflects our rule to lean towards being over-inclusive in Phase 1, given it would be followed by the 'sieving' function of Phase 2. In fact this vindicates the two-phase approach, because before we conducted this analysis, there was simply no way of knowing that a pattern like leaf-sponging is a chimpanzee 'universal' rather than a cultural variant. Of course, this does not mean such behaviours are not culturally acquired by a

TABLE 3. *Putative cultural variation amongst chimpanzees: behavioural patterns absent in at least one location yet habitual or customary in at least one other*

site:	As	Bs	Tai	Lo	Ma	Mk	Go	Kib	Bd
Pestle-pound (mash palm crown with petiole)	e	C	--	--	e?	e?	--	e?	e?
Nut-hammer, stone hammer on stone anvil	e	C	C	--	--	--	--	e?	e
Ant-dip-single (one handed dip stick on ants)	--	C	C	--	--	--	+	--	--
Aimed-throw (throw object directionally)	+	C	C	(--)	C	--	C	+	+
Food-pound onto wood (smash food)	C	C	C	(--)	--	--	C	e?	H
Bee-probe (disable bees, flick with probe)	(--)	--	C	(--)	--	+	--	--	--
Index-hit (squash ecto-parasite on arm)	(--)	--	C	(--)	--	--	+	--	--
Nut-hammer, stone hammer on wood anvil	e	+	C	--	e	e	--	e?	e
Nut-hammer, wood hammer on wood anvil	e	--	C	--	e	e	--	e?	e
Nut-hammer, wood hammer on stone anvil	e	--	C	--	--	--	--	e?	e
Nut-hammer, other (e.g. on ground)	e	--	H	--	--	--	--	e?	e
Seat-vegetation (large leaves as seat)	(--)	+	H	--	--	--	--	+	--
Marrow-pick (pick bone marrow out)	(--)	--	C	(--)	--	--	--	--	--
Food-pound onto other (e.g. stone)	H	--	H	(--)	--	--	C	e?	--
Club (strike forcefully with stick)	(--)	+	H	(--)	+	--	H	--	--
Ant-dip-wipe (manually wipe ants off wand)	H	+	--	--	--	--	C	--	--
Fluid-dip (use of probe to extract fluids)	H	--	C	C	H	H	C	H	--
Lever open (stick used to enlarge entrance)	(--)	--	H	C	--	--	C	--	--
Expel/stir (stick expels or stirs insects)	(--)	--	C	(--)	H	H	C	e?	--
Self-tickle (tickle self using objects)	(--)	--	--	(--)	--	--	H	--	--
Leaf-clip, fingers (rip single leaf with fingers)	(--)	--	H	--	+	--	--	H	C
Leaf-squash (squash ecto-parasite on leaf)	(--)	--	--	(--)	(--)	(--)	H	--	--
Leaf-clip,mouth (rip parts off leaf, with mouth)	(--)	C	C	--	C	C	--	H	C
Knuckle-knock (knock to attract attention)	(--)	+	C	(--)	C	C	H	--	--
Branch-slap (slap branch, for attention)	(--)	C	C	(--)	+	--	--	--	C
Leaf-groom (intense 'grooming' of leaves)	(--)	--	--	--	C	C	C	C	+
Ant-fish (probe used to extract ants)	H	+	--	C	C	C	+	--	--
Hand-clasp (clasp arms overhead, groom)	(--)	--	H	H	C	C	--	C	--
Shrub-bend (squash stems underfoot)	(--)	H	--	(--)	C	--	--	--	C
Stem pull-through (pull stems noisily)	(--)	C	--	(--)	H	--	+	H	--
Rain dance (slow display at start of rain)	(--)	--	H	(--)	C	C	C	C	H
Termite-fish using leaf midrib	H	+	e	e?	--	C	--	e	e?
Termite-fish using non-leaf materials	H	--	e	e?	--	C	C	e	e?
Leaf-napkin (leaves used to clean body)	+	--	+	(--)	+	--	C	C	C
Leaf-strip (rip leaves off stem, as threat)	(--)	+	--	--	+	--	H	H	--
Leaf-dab (leaf dabbed on wound, examined)	(--)	--	+	(--)	--	--	+	C	--
Fly-whisk (leafy stick used to fan flies)	(--)	--	H	(--)	--	--	+	e	H
Leaf-inspect (inspect ecto-parasite on hand)	(--)	--	--	(--)	(--)	(--)	+	--	C
Branch din (bend, release saplings to warn)	(--)	--	--	H	e?	e?	--	--?	--

Behavioural patterns are organised in rows such that high frequency occurrences (customary, habitual) occurring in the same regions of Africa are as far as possible clustered, forming a ragged, shaded diagonal band from top-left to bottom right (the nature of the distributions means this can be achieved only approximately). Key: as for Table 2. 'H' for Ant-dip-wipe at Assirik is based upon the nature of recovered tools.

process of social learning; just that if chimpanzees do acquire them by social learning, they do so in all communities studied. Nevertheless, behavioural patterns in category A do not offer circumstantial evidence for cultural *variation* in the way that those in Table 3 do.

A further 16 patterns of behaviour that failed to exhibit habitual or customary status in any community made up Category B. These 'rarities' cannot count as cultural variants since nowhere do they achieve a frequency consistent with being socially transmitted. The patterns in this category provide a different vindication of the two-phase approach; without it, there was no way to know whether some of the behavioural patterns might somewhere have achieved the cultural status mooted for them in Phase 1.

Category C contains just three behavioural patterns that reach at least habitual status in one community (including 'ground-night-nest', known to be habitual at Nimba, a relatively new site not yet appropriate for full inclusion in our survey; Matsuzawa & Yamakoshi, 1996) and are absent elsewhere, yet these absences were all explicable by local ecological factors. For example, where 'algae fishing' was absent, there appeared to be either no opportunity (no algae) or no need for it (available without need of fishing). That only three such behaviour patterns needed to be excluded in this way may on first sight appear surprising. However, it must be remembered that the initial list of candidate cultural variants generated in Phase 1 began with proposals from experienced field researchers, who likely filtered from their potential suggestions those judged certain to fail on this criterion.

No less than 39 behavioural patterns remain that meet our criteria for cultural variants, being absent in at least one community and habitual or customary in at least one other (Table 3). This central finding of the survey is remarkable in two ways. First, as will be apparent from the brief review introducing this paper, this number far exceeds that known to date for any species except our own. Second, inspection of Table 3 shows that each community has its own unique suite of cultural (*i.e.* habitual or customary) behavioural patterns. We discuss these findings further in the concluding section of the paper.

2. The fit with alternative cultural models

The richness of the patterns charted in Table 3 encourages us to begin to examine their fit to the models of cultural processes outlined in the introduction. Dispersal over distances up to about 900 km is detectable in maternally transmitted chimpanzee genotypes (Morin *et al.*, 1994), underlining the potential for cultural diffusion over even larger distances. Accordingly, we have to entertain the possibility that the behaviour patterns of interest here may have achieved their present distributions across Africa by cultural diffusion between the populations that exhibit them.

A. Consistency with diffusion from unitary *versus* multiple origins

Some behavioural patterns were found to achieve customary or habitual status in more than one community. These distributions are drawn together in Table 4, for clarity, in order to examine whether they are consistent with diffusion from unitary or multiple origins. If there were a common origin, the habitual and customary cases for behavioural pattern of interest should tend to occur in the communities that are closest together; they should tend not to be separated by communities in which the pattern is absent. To facilitate inspecting the distributions in this respect, in Tables 2-4 the three West African sites are in the first three, adjacent columns; the one Central African

TABLE 4. *Behaviour patterns habitual or customary in two or more communities*

site:	As	Bs	Tai		Lo		Ma	Mk	Go	Kib	Bd
Nut-hammer, stone hammer on stone anvil	e	C	C		--		--	--	--	e?	e
Leaf-groom (intense 'grooming' of leaves)	(--)	--	--		--		C	C	C	C	+
Leaf-napkin (leaves used to clean body)	+	--	+		(--)		+	--	C	C	C
Knuckle-knock (knock to attract attention)	(--)	+	C		(--)		C	C	H	--	--
Leaf-strip (rip leaves off stem, as threat)	(--)	+	--		--		+	--	H	H	--
Ant-fish (probe used to extract ants)	H	+	--		C		C	C	+	--	--
Expel/stir (stick expels or stirs insects)	(--)	--	C		(--)		H	H	C	e?	--
Fluid-dip (use of probe to extract fluids)	H	--	C		C		H	H	C	H	--
Rain dance (slow display at start of rain)	(--)	--	H		(--)		C	C	C	C	H
Aimed-throw (throw object directionally)	+	C	C		(--)		C	--	C	+	+
Hand-clasp (clasp arms overhead, groom)	(--)	--	H		H		C	C	--	C	--
Leaf-clip,mouth (rip parts off leaf, with mouth)	(--)	C	C		--		C	C	--	H	C
Ant-dip (dip stick on ants to harvest)	(--)	C	C		--		--	--	C	--	--
Food-pound onto wood (smash food)	C	C	C		(--)		--	--	C	e?	H
Food-pound onto other (e.g. stone)	H	--	H		(--)		--	--	C	e?	--
Club (strike forcefully with stick)	(--)	+	H		(--)		+	--	H	--	--
Lever open (stick used to enlarge entrance)	(--)	--	H		C		--	--	C	--	--
Termite-fish using non-leaf materials	H	--	e		e?		--	C	C	e	e?
Fly-whisk (leafy stick used to fan flies)	(--)	--	H		(--)		--	--	+	e	H
Leaf-clip, fingers (rip single leaf with fingers)	(--)	--	H		--		+	--	--	H	C
Branch-slap (slap branch, for attention)	(--)	C	C		(--)		+	--	--	--	C
Shrub-bend (squash stems underfoot)	(--)	H	--		(--)		C	--	--	--	C
Stem pull-through (pull stems noisily)	(--)	C	--		(--)		H	--	+	H	--

Columns (study sites) are arranged by region as in Table 2 and 3. For organisation of rows, see text. Key: as for Table 2.

site of Lopé comes next; and the remaining columns, reading left to right, correspond to adjacent East African sites from the most southerly, Mahale, to the most northerly, Budongo.

Of course, a gap could correspond not to the absence of diffusion, but to diffusion followed by localised loss of the pattern from the repertoire. We interpret cases where patterns are widely and continuously distributed with only a single gap as the most likely to be consistent with this latter scenario. Conversely, regional occurrences separated by several records of absence are more consistent with multiple regional origins.

Table 4 has been constructed to illustrate such continuities and discontinuities. First are shown 11 behavioural patterns for which any habitual or customary occurrences together form a continuous distribution, consistent with cultural diffusion from a unitary origin. Only two point strongly to such a unitary origin, however. The first is 'nut-hammer', found at two adjacent West African sites (and also known to occur elsewhere in West Africa: McGrew, 1992; Joulian 1996), but at none of the other sites examined here. Boesch *et al.* (1994) showed that nut-hammer is not found in an area inhabited by *P. t. verus* to the west of the large Sassandra river in Côte d'Ivoire. As noted by McGrew (1992), nut-hammering is perhaps the best supported case for cultural diffusion of a behaviour pattern amongst chimpanzees, starting from a unitary source and extending to a quite large yet circumscribed region of West Africa.

'Leaf-groom' is confined to East Africa and is widespread there, highly consistent with a unitary origin, mirroring the case for nut-hammering in the West. But the other eight cases are less clear. Use of 'leaf-napkin', for example, shows a continuous customary distribution at one pole of the Eastern sites, yet has also been observed in the West, perhaps reflecting a potential for multiple origins. 'Knuckle-knock' occurs customarily at some locations in both east and west, with no evidence of absence between them. Since these populations were once continuous with each other it is possible that such a behavioural distribution reflects ancient and far-reaching diffusion from a single source. However this inference is weakened by the observation that the pattern is absent in communities that are much closer geographically than those that share it. The same can be said of the other six behavioral patterns with continuous distributions ('leaf-strip' to 'aimed throw' in Table 4), for although these occur habitually in two to five communities in East Africa and are thus consistent with diffusion from a unitary source, they also occur in some communities in the west, in six cases reaching habitual or customary levels.

The next two behaviour patterns, ‘hand-clasp grooming’ and ‘leaf-clip with mouth’, show widespread, continuous distributions but for a single, well-documented gap in their midst (Gombe, in both cases). As noted above, the most parsimonious explanation for such a distribution is diffusion from a unitary source, followed by loss of the behaviour in a single community. Such a scenario is given plausibility insofar as functional alternatives at Gombe exist that might reduce the intrinsic value of such customs; branch-clasp grooming (an apparent ‘universal’ — Table 2) as an alternative to hand-clasp grooming, and branch-shaking as an alternative to leaf-clipping to attract attention.

The remaining eleven distributions in Table 4 are more obviously discontinuous and consistent with multiple origins. Four of these (‘food pound’ to ‘lever open’), are common at Gombe and Taï, in one case at Bossou too. Although this could in principle reflect a much earlier diffusion from a unitary source, this seems unlikely given the overall spatial pattern. We suggest it is more plausible that the distribution results from multiple, independent innovations of relatively simple behavioural patterns — food pound, club, and lever. It would not be surprising if these had been invented more than once by wild chimpanzees, especially since the communities concerned, Gombe and Taï, possess a rich repertoire of other forms of tool use.

Of the last four patterns in the table, two occur in three quite separate communities. All four behavioural patterns are attention-getting acts used particularly by males during courtship; they appear to be the most capricious in their occurrence, although each achieves customary frequencies in at least one community. Unlike tool use that is constrained by its fit to external requirements, these social gestures may be more labile, expressing local innovations on the basic tendency to use vegetation for attracting others’ attention. To be more speculative, it could be that such acts express local fashions (recurring in many communities from time to time), with males expressing their fitness by their ability to track them. Miller (2000) suggested that various aspects of human courtship may act as sexually-selected displays of intelligence; in an intelligent non-human species a similar if less extreme process might operate. This speculation leads to the testable prediction that these behaviour patterns will be found to be socially transmitted, yet changeable, over relatively short periods (*i.e.* fashions). A parellel is possible here with recently reported changes in humpback whale songs thought to function as sexual displays, which showed a rapid acquisition of the forms introduced by a small number of immigrant males (Noad *et al.*, 2000).

B. Consistency with diffusion plus differentiation

Results consistent with differentiation come from two sources: first, the systematic questionnaire returns; and second, from the supplementary information submitted. The questionnaire information is quite circumscribed, perhaps because our focus was on defining discrete behavioural patterns and charting their distribution. Nevertheless, the two sources together suggest that differentiation may be a more pervasive phenomenon than expected, meriting more formal investigation in future phases of this project.

(i) Questionnaire data: Table 5 brings together data for three kinds of case relevant to this question. The first includes behavioural patterns for dealing with ectoparasites, each of which occurs in one specific community, and also the category 'leaf-groom'. These show a hierarchical distribution consistent with a differentiation model. 'Index-hit', the technique found at Taï in West Africa, does not incorporate leaves. The two other methods, 'leaf-squash' at Gombe and 'leaf-inspect' at Budongo, do incorporate leaves; moreover, they (particularly leaf-squash) utilise actions quite like those involved in leaf-grooming, a behavioural pattern that occurs at all East African but no western sites. Parsimonious explanations for this pattern of distribution are that either (a) the three eastern leaf-using patterns are derived from the same ancestral pattern, or (b) leaf-squash and leaf-inspect are divergent techniques derived from the leaf-grooming behaviour that still occurs throughout their range (Fig. 3).

TABLE 5. *Three distributions consistent with diffusion plus differentiation*

site:	As	Bs	Tai		Lo		Ma	Mk	Go	Kib	Bd
Index-hit (squash ecto-parasite on arm)	(--)	--	C		(--)		--	--	+	--	--
Leaf-squash (squash ecto-parasite on leaf)	(--)	--	--		(--)		?	?	H	--	--
Leaf-inspect (inspect ecto-parasite on hand)	(--)	--	--		(--)		?	?	+	--	C
Leaf-groom (intense 'grooming' of leaves)	(--)	--	--		--		C	C	C	C	+
Leaf-clip,mouth (rip parts off leaf, with mouth)	(--)	C	C		--		C	C	--	H	C
Leaf-clip, fingers (rip single leaf with fingers)	(--)	--	H		--		+	--	--	H	C
Ant-dip-single (one handed dip stick on ants)	(--)	C	C		--		--	--	+	--	--
Ant-dip-wipe (manually wipe ants off wand)	H	+	--		--		--	--	C	--	--

For explanation, see text. Key: as for Table 2.

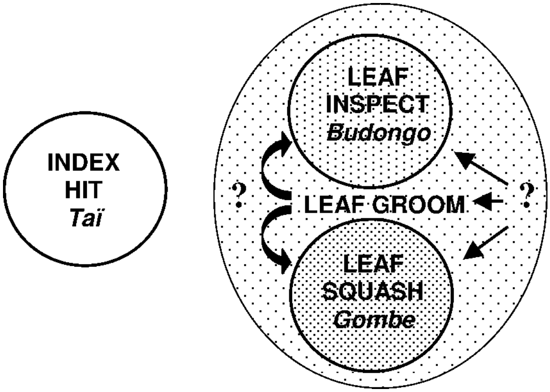

Fig. 3. An example consistent with a differentiation model: distribution of three techniques (shown schematically) for dealing with ectoparasites. The occurrence of 'leaf inspect' at Budongo and 'leaf squash' at Gombe is consistent with either (a) differentiation from 'leaf groom', that occurs throughout their range; or (b) differentation of all three of these leaf-using patterns from a common origin. At Taï in the west, an index finger is used instead of leaves.

Table 5 also shows that 'Leaf-clip with fingers' occurs at least habitually in only three of the six communities that habitually show 'leaf-clip with mouth'. This hierarchical nesting of the distributions suggest that the less frequent variation has been derived from the more common one.

Finally, 'ant-dip-single' is habitual or customary in two West African populations but not elsewhere. At Gombe the more complex technique of 'ant-dip-wipe' is customary, and at Assirik is suspected to be so on the basis of recovered tools (McGrew *et al.*, unpubl. data). In this method, a longer stick is used together with a deft bimanual wiping action that is much more productive than the simple method used at Taï (McGrew, 1974; Boesch, 1996a). It seems likely that the complex Gombe (and perhaps Assirik) method differentiated from earlier application of the simpler kind of technique, rather than being generated in one step.

These cases (Table 5) illustrate three different kinds of differentiation: change in form and function (leaf-groom to leaf-squash and inspect), shift in bodily use (clip with mouth *versus* fingers) and elaboration in tool technique (simple dip to complex dip).

Of course, it is possible that other forms of tool use reflect differentiation, but that the relevant 'lineage' is simply lost in the past. One might expect this effect in types of tool use sharing a core functional element, such as 'pounding', but 'pounding-like' behaviours including hammer-nut, food-pound and pestle-pound do not appear to evidence the hierarchical distributions that would be consistent with this. The same conclusion is suggested by inspection of the distribution of behaviour patterns exploiting stick-use, although the near-universality of fluid-dip and investigatory probe indicate that these would be the kind of simple usages from which the rarer and more sophisticated forms of stick use may have evolved.

(ii) Supplementary information: Together with responses gathered in the course of correspondence to clarify definitions and other matters, this information indicates further ways in which behavioural patterns have come to be performed differently at different sites. Three different kinds of differentiation appear worth distinguishing.

(a) Variations on a common behavioural theme

Rain dance. Several respondents agreed that ‘rain dance’ contrasts with normal charging displays in omitting intimidation of other chimpanzees, but differences between sites emerged. At Taï a rain dance is said to be totally silent and like a slow-motion version of a normal display, whereas at all East African sites, noisy pant-hoots were described, and for Gombe, Kamenya (pers. comm.) described rain dance as ‘mainly fast’. At Mahale, Nishida discriminated two versions, a ‘noisy, vigorous type’ involving several adult males and a ‘silent, slow type’ involving a single male. Such details suggest that further cultural variation still awaits systematic examination, and they highlight specific aspects of behaviour that may repay attention.

Hand-clasp grooming. At Kibale, a hand-to-foot clasp is also used. Interestingly, the occurrence of the hand-clasp itself appears to fluctuate on a relatively local basis; it is customary at Mahale yet absent at the other Tanzanian site, Gombe; and it is customary at Kibale yet absent at the other Ugandan site, Budongo.

(b) Variation in the targets of an action

Leaf sponge. Although leaf-sponging is universally used to obtain water from out-of-reach locations like holes in trees, at Gombe it is reported as happening frequently at streams, where the chimpanzee could drink without help from a tool. At Taï, this never occurs. Thus although leaf-sponge appears in Table 2 rather than Table 3, a future, finer systematic analysis seems destined to identify cultural variants in how it is done.

Nut-hammer. This behaviour is absent from sites such as Gombe and Lopé, where nuts (including oil palm nuts) are present together with suitable materials for hammers, such as stone. At Taï, where nut-cracking is extensive, we find the opposite extreme; materials used for hammers and anvils not only include all four combinations of wood and stone but may extend to materials such as hard fruits and pieces of hard termite mounds. Bossou is intermediate, with stone hammers on stone anvils being much preferred, despite the availability of other materials. Possible explanations of the more differentiated Taï repertoire include the availability of surface roots as anvils at Taï (Boesch & Boesch, 1990); a relative abundance of stones at Bossou (Sugiyama, pers. obs.); or the fact that at Bossou only oil-palm nuts are cracked, whereas at Taï five different nuts are cracked, ranging from the abundant, soft *Coula edulis* that can be cracked using wooden hammers, to the very hard *Panda oleosa* that requires a heavy stone hammer (Boesch & Boesch, 1990). As noted earlier, the behaviour of the Taï chimpanzees is suggestive of a generalized push to innovation with materials beyond those used in nut-hammering, perhaps contrasting with more customary conservatism at Bossou.

Aimed throw. The targets of thrown objects also vary. At Taï throwing is reported as a component of threats towards leopards, other chimpanzees, and prey, notably monkeys. Clearly the identities of some of such potential targets may vary because they are constrained by the local environment. However at Mahale (M) and Gombe, throwing of stones into water is reported (commonly and elaborately, at Mahale) and this appears to be a distinctive pattern that could occur at several other sites, yet does not.

Food-pound. Pounding is linked to different foods at different locations: *Strychnos* and *Conopharyngea* at Gombe, *Balsamocitrus* at Budongo, *Adansonia* and *Strychnos* at Assirik. At Taï *Strychnos aculeata* is pounded terrestrially, *Landolphia* spp. arboreally and *Treculia africana* in both contexts. *Strychnos* is available also at Mahale but not pounded open, and at Kibale *Conopharyngia* is reported to be bitten open.

Club. Clubbing was reported to be directed at other chimpanzees at several sites (Taï, Gombe, Mahale), but also at leopards at Taï, and baboons and snakes at Gombe. At Mahale clubbing was also reported to be used for striking the ground in the context of courtship, which was not reported elsewhere, although use in aggressive displays was noted for Gombe. By contrast Kortlandt & Kooij's (1963) experimental provocation of chimpanzees using a stuffed leopard, which had elicited clubbing, has been performed at Kibale where it failed to elicit this response.

(c) Similar behaviour serving different functions

Leaf-clip with teeth. This pattern appears to be used in quite different contexts. At Mahale and Budongo it is used in courtship and prior to copulation. In West Africa, however, it precedes buttress drumming and signals frustration at Taï, and is seen in both frustration and play at Bossou, where the action is performed with upper and lower lips.

C. Independent *versus* clustered distributions

We find no significant evidence that any pair of behavioural patterns shows a correlated distribution across the various communities. Only two behavioural patterns have the same distribution pattern (expel/stir and knuckle-knock, both of which reach at least habitual levels only at Taï, Mahale and Gombe) but the proposition that this reflects a causal linkage makes no functional sense for this pair of patterns; it is more likely they co-occur by chance.

What of the possibility that the distinctive suite of behavioural patterns — some of them unique — that distinguishes each individual community, is explained by some distinctive 'functional core'? The most suggestive evidence of this comes from the distribution of tool use. Taï chimpanzees show 20 habitual or customary types of tool use, including nut-hammering, which requires a long apprenticeship (Boesch & Boesch, 1990, 2000); at the other end of the scale, Budongo and Kibale chimpanzees show respectively only six and five kinds of simple customary or habitual tool use. Although it remains possible that this contrast reflects a greater need for technology in the Taï Forest, for ten of the Taï tools the corresponding classification at Budongo is 'absent without ecological explanation'. Accordingly, it may be hypothesised that the cluster of tool use behaviours at Taï reflects an underlying 'core cultural orientation' towards technology, manifested in a disposition to innovate and to learn socially about a variety of forms of tool use.

A different kind of association is suggested by results for ant-fish. This pattern is customary at Mahale (M and K) and Assirik, where a small probe is used to extract arboreal ants. At Lope ants are also collected, but from terrestrial (subterranean) nests, and the brush-tools used for this are more similar to those described under 'brush-stick', assumed to be used to collect termites (Tutin *et al.*, 1995). It may be that in central Africa brush tools are applied to harvesting both ants and termites, whereas in other regions finer probes are used to fish for both ants and termites. If this is so, it raises a question about whether chimpanzees generalise customary local techniques to several contexts, such that what differs between communities are suites of functionally-related approaches, rather than individual patterns alone.

General discussion

1. Methodology

We believe that our general approach is vindicated by the results of this study (see also de Waal, 1999). The first point to emphasise about this is that the analysis presented here and in Whiten *et al.* (1999) would not have been possible without the willingness of fieldworkers to pool their long-term data, gathered through extended labour over decades, across Africa. This collaborative enterprise seems to be unprecedented in the study of traditions in any animal, but the comprehensiveness of the picture it has produced should encourage scientists studying other candidate taxa that the approach is worthwhile.

Second, the two-phase method (a first phase of drawing up a consensual and well-defined list of candidate cultural variants, followed by a second phase to code the frequency of each) merits further application. The next step required in this chimpanzee study is an updating round of data collection following this model. Lessons learned in the course of our first attempt are of two kinds. At a general level applicable to other studies of this kind, experience shows that extended efforts to agree the content and definitions of the list of behavioural patterns in Phase 1 are required. In our study, some of these required re-visiting and clarification once coders began to attempt the task of Phase 2. Accordingly, it may be more efficient to ask contributors to attempt a provisional coding for their site even during Phase 1, so as to sharpen the definitional effort that is crucial to this phase. At the more specific level of studying chimpanzee cultural variation, we discovered that the informal, additional comments that were a supplementary part of Phase 2 indicated several unsuspected behavioural variations that beg formal analysis in further studies of this kind. Accordingly, we can now begin a second, updating round of this project that will incorporate a list of putative cultural variants more refined and probably substantially longer than that used here. Recent published reports document variants not included in the pre-1999 corpus described here (Nakamura *et al.*, 2000; McGrew *et al.*, 2001; Nakamura, in press).

Finally, written definitions of behavioural categories can suffer obvious limitations, that are highlighted when researchers attempt to identify what may be subtle behavioural differences between communities, most of which the researchers have not directly observed (*e.g.* see Nakamura, Table 1, in press). We have therefore embarked upon an associated, ongoing project to build an illustrated archive of examples of the behavioural patterns identified, available on the internet (http://chimp/st-and.ac.uk/cultures). Nishida *et al.* (1999) have published a comprehensive ‘ethogram’ of the Mahale chimpanzees, that should in a complementary way assist future comparative studies.

2. Conclusions

(i) Multiple cultural variants

It was noted above that most evidence for traditional patterns in animals concern only a single type of behaviour. Accordingly two findings of the present project are striking. The first is the discovery that as many as 39 behaviour patterns meet our criteria for cultural variants. The second is that each community exhibits in own profile of occurrence amongst these 39 possibilities, visualised in the 'bar-code' columns of Table 3, each of which is unique. Qualitatively at least, these findings appear to correspond to the phenomenon of multiple cultural variations amongst humans.

Similarly, although quantitatively the variation we describe for chimpanzees appears unmatched in other non-human species, it is already evident that chimpanzees are not qualitatively distinctive in expressing multiple cultural variations. For example, van Schaik, *et al.* (1996; see also van Schaik & Knott, 2001) identified two kinds of tool use in the same community of Sumatran orangutans, that have never been observed in long term studies in Borneo. Rendell & Whitehead (2001) present evidence that transient populations of killer whales on the Pacific coast of North America differ culturally from residents not only in vocal dialects but also in social structure and hunting behaviour. Finally, we note that fieldworkers studying capuchin monkeys at different sites are now also beginning to collate data indicating multiple behavioural variations (Fragaszy & Perry, in press). Accordingly, such taxa as these may be excellent candidates for the systematic, two-phase approach we have implemented for chimpanzees.

Even for chimpanzees, however, our analysis is likely to under-represent the cultural complexity that may exist. We intentionally omitted three main classes of behaviour. The first concerns auditory communication, because specialist, technical analysis is necessary to undertake the required comparisons. This remains to be pursued at the majority of the sites included in our study. Nevertheless, there is some evidence from both the wild (Mitani *et al.*, 1992; Marshall *et al.*, 1999; but see Mitani & Gros-Luis, 1999) and captivity (Marshall *et al.*, 1999) for cultural variation in vocalisations, creating dialects. The second omission concerns ingestion, including both nutritional intake and consumption of items with medicinal effects. There is already published evidence indicating some cultural variation in these respects (McGrew, 1983; Nishida *et al.*, 1983; Huffman, 1997). However, scrutinising each case of a failure to ingest an item habitually consumed at another site was too challenging a task for the scale of our initial collaborative project. The third omission concerns the more specific behaviour of bed or nest-building, which like vocalisation appears to require a more sustained technical investigation — surprisingly perhaps, yet to be undertaken in any comprehensive way (*cf* Baldwin *et al.*, 1981). Taking all these considerations together, it seems likely that the extent of chimpanzee cultural variation demonstrated in the present paper may be only a part (perhaps even a relatively small part) of the whole.

It must be reiterated, however, that the number of cultural variants here identified — 39 — should not be seen as a rigorously-measured absolute number, easily comparable with equivalents in other taxa. This number depends in part on how categories are split or lumped. However, it is equally important to stress that this number is the outcome of two processes that make it far from arbitrary; first, our systematic two-phase procedure, which includes 'sieving' procedures in both phases; and second, iterative decision processes operating between a large number of highly experienced, long-term field researchers. We believe that if similar approaches are adopted by those studying other taxa, sensibly objective comparisons will be facilitated.

(ii) Comparisons with cultural diffusion models

We examined three models, which can be labeled as the 'unitary', 'multiple' and 'differentiation' alternatives. Eleven behaviour patterns were found to have quite continuous distributions of customary and habitual occurrences consistent with diffusion from a unitary source, but for all but two of these there were counter-indications to this interpretation, such as (minimal) occurrence at more distant locations. Only two behavioural patterns — 'nut-hammer' in the west and 'leaf-groom' in the east — showed a good fit to the kind of distribution expected of spread from a unitary source. Another 11 behavioural patterns showed discontinuous distributions more consistent with multiple origins, a possibility made more likely by the relative simplicity of several of these patterns, making them more plausibly invented at multiple locations. Much of the variation we recorded, both formally in the questionnaire returns and more informally in supplementary comments, is consistent with the third model that incorporates differentiation in concert with diffusion, a process more deserving of the term 'cultural evolution'. Our analysis indicates differentiation of several kinds, including the form of patterns (variations on an original common 'theme'), their functions, the part of the body used, the objects or targets of actions, and elaborations on tool use. The richness of these alternatives suggests this as a productive future topic of research in this area.

It can also be said that for many or most of the behavioural patterns examined, it is not yet possible to draw firm conclusions about which, if any, of the three models shows the best fit with the observed data. However, this is the first time that students of animal behaviour have assembled a corpus of data with respect to which such questions can even be framed. In the past some evidence has been offered for diffusion of traditions, such as the opening of milk bottles by birds (Fisher & Hinde, 1949; Hinde & Fisher, 1951). A recent re-analysis of these data supports a multiple-source diffusion model, including an accelerating function consistent with cultural transmission (Lefebvre, 1995). However, such evidence is rare and concerns only a single behavioural pattern rather than the multiple variations we are dealing with in the case of chimpanzees. A similar picture holds in relation to evidence from other species that fit the differentiation model. Birds again provide some of the clearest data, notably the evidence for dialect differentiation across populations of songbirds (Jenkins, 1978; Jenkins & Baker, 1984); but corresponding data sets are rare in mammals (see Noad *et al.*, 2000), as a recent comprehensive survey confirmed (Box & Gibson, 1999). Our treatment of these issues must therefore be recognised for what it is; a first exploration of the scope for large scale cultural analysis in a non-human primate.

(iii) The question of core cultural tendencies or themes

It has been suggested that each human culture tends to be characterised by a central cultural core or theme, that pervades a multitude of more peripheral manifestations of tradition (Boyd *et al.*, 1997). Does anything correspond to this in chimpanzees? We found little substantive evidence for this, but two trends are worth highlighting in relation to future research. One is that some communities appear to be strikingly more oriented to tool use than others, the largest contrast being between Taï, with 20 kinds of customary or habitual tool use (Table 3), and Kibale with only five. The second is that there may be general forms of tool use that affect the specific variants that differentiate there, as suggested by the use of brush tools to harvest both ants and termites in Central Africa, which in other regions is typically done using only finer probes. Both of these trends should best be thought of as hypotheses to be subjected to focused testing in future research.

3. Outstanding problems and solutions in charting natural cultural variation

The behaviour patterns of interest to us as cultural variants have been identified as those achieving at least habitual levels of occurrence at one or more sites, yet also absent at one or more sites, without an environmental explanation. In addition these differences in occurrence are inferred to occur through social rather than genetic transmission. Ruling out either environmental or genetic explanations is not always easy, however. Indeed, some experimentalists have argued that it is impossible ever to be sure that environmental differences are not responsible for any variation (Galef, 1990; Tomasello, 1990). For example, where one community eats a food or uses a tool that another does not, it could be argued that one can never check every potential chemical or physical difference that might by causing this variation through individual rather than social learning. How well can we deal with these difficulties? We can consider the problems of environmental and genetic differences in turn.

Different kinds of reasons are relevant to rejecting environmental explanations, according to the behavioural pattern concerned. One is the case where the ‘environment’ interacted with is other chimpanzees, so it is difficult to imagine how this could cause the systematic behavioural variations recorded. Hand-clasp grooming is the purest case of this; it could occur wherever there are chimpanzees, yet it does not.

For other patterns the environmental constraints are so broad that it remains highly implausible they could be determining factors. A good example of this is rain dance, which could in principle be performed in any environment with the shakable vegetation used to enhance the display. Many other patterns in our list require only basic and universal raw materials. Several, for example, depend on leaves or other simple configurations of vegetation, of which many different kinds appear suitable for the task: this is true for self-tickle, leaf-clip (with either fingers or mouth), leaf-squash, knuckle-knock, branch-slap, leaf-groom, shrub-bend, stem-pull-through, leaf-napkin, leaf-strip, leaf-dab, leaf-inspect and branch-din. A similar case can be made for the three different forms of handling ecto-parasities, for in principle it would seem the parasites could be squashed or inspected equally well against either leaf or forearm.

It is with the more complex use of tools and their targets that the question of environmental determinism may be most difficult to resolve. However in the case of nut-hammering, two studies have set out to explicitly test the environmental hypothesis by directly assessing the affordances of tools and nuts in non-hammering regions (Boesch *et al.*, 1994; McGrew *et al.*, 1997). Both studies confirmed that tools and nuts of appropriate kinds were available and functional, the strong inference being that what explains whether nut-hammering occurs must be the availability of social models. These studies demonstrate the most rigorous form that rejection of an environmental hypothesis can take and provide good models for future research. However, in several of the remaining set of tool usages in Table 3, strong inferences can be made even when formal measurements of the materials have not been made. For example, although marrow-pick occurs at only one site, marrow bones and the small kinds of stick used as picks are commonly in evidence at other sites where the pattern is absent. In this case and nine other forms of tool use, coders reported no problems in making the judgment that environmental explanations for occurrence *versus* absence were sufficiently implausible to set aside.

What remain are six other kinds of tool use where coders exercised the option to annotate their coding with a query (*i.e.* those showing ‘?’ in Table 2 and 3). This also occurred for nut-hammer at a site where formal studies like those cited above have not been performed. Such cases merit attention because they highlight the kinds of problems that beg eventual resolution if environmental reasons for a behaviour pattern’s absence are to be clearly ruled out. Illustrative reasons a query was thought necessary included the following. (1) Pestle-pound. Although oil palms are present at Mahale, lack of any feeding on the shoots may mean they are not so suitable a food as at Bossou; alternatively at Budongo oil palms were not present but caution was expressed about whether other palms might be suitable. (2) Nut-hammer. Nuts (*Parinari excelsa*) are available, although not cracked, at Kibale; this may be because the seed is small and may be low quality but this has not been confirmed. (3) Termite-fish. At Budongo some termite mounds are available on the forest fringe. Although this distribution may constitute an environmental reason for lack of termite fishing, it remains possible that chimpanzees’ neglect of this opportunity has a cultural explanation. Residual uncertainties like these should be resolvable through detailed studies of the kind noted above for nut-hammering. In the meantime, these behavioural patterns entered Table 3 as cultural variants in any case, because observers at other sites felt able to make the necessary judgments with reasonable confidence.

The reasons for rejecting genetic explanations of the behavioural diversity under scrutiny are different. One is that many of the variations occur within a single sub-species (in particular, the last five columns of Table 3 concern *P. t. schweinfurthii*), some even between neighbouring communities (Ma and Mk). Similarly the study by Boesch *et al.* (1994) showed that nut-hammering was absent on one side of a large river, yet was customary on the other. In addition, many of the behaviour patterns concern tool use, and particularly where this is complex, the evidence that chimpanzees readily and flexibly learn such object use (Byrne, 1995; McGrew, 1989) means that these are poor candidates for merely instinctual variations. The possibility of instinctive variations is perhaps of most concern in the case of patterns that appear to incorporate aspects of universal chimpanzee behaviour such as aggressive displays; these include rain dance and certain forms of aimed throw (lobbing large rocks into streams at Mahale); similarly leaf-clip with fingers, shrub-bend, stem-pull-through and leaf-strip can be seen as variants on a common male tendency to attract fertile females' attention by noisily deforming vegetation.

Some difficulties of interpretation thus remain in our attempt to chart cultural variation and these merit special attention in the increasing efforts to pursue such studies in other species. For *Pan troglodytes*, however, an overall picture of rich cultural complexity is becoming apparent. In anthropologists' terms, cultural primatology has begun to achieve both systematic ethnography and ethnology.

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