

but must be regarded as an early twig in a bush-like radiation of birds. □

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Cultures in chimpanzees

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As an increasing number of field studies of chimpanzees (*Pan troglodytes*) have achieved long-term status across Africa, differences in the behavioural repertoires described have become apparent that suggest there is significant cultural variation^{1–7}. Here we present a systematic synthesis of this information from the seven most long-term studies, which together have accumulated 151 years of chimpanzee observation. This comprehensive analysis reveals patterns of variation that are far more extensive than have previously been documented for any animal species except humans^{8–11}. We find that 39 different behaviour patterns, including tool usage, grooming and courtship behaviours, are

customary or habitual in some communities but are absent in others where ecological explanations have been discounted. Among mammalian and avian species, cultural variation has previously been identified only for single behaviour patterns, such as the local dialects of song-birds^{12,13}. The extensive, multiple variations now documented for chimpanzees are thus without parallel. Moreover, the combined repertoire of these behaviour patterns in each chimpanzee community is itself highly distinctive, a phenomenon characteristic of human cultures¹⁴ but previously unrecognised in non-human species.

Culture is defined in very different ways in different academic disciplines¹⁵. At one extreme, some cultural anthropologists insist on linguistic mediation, so that culture is constrained to be a uniquely human phenomenon¹⁶. In the biological sciences, a more inclusive definition is accepted, in which the significance of cultural transmission is recognized as one of only two important processes that can generate evolutionary change: inter-generation transmission of behaviour may occur either genetically or through social learning, with processes of variation and selection shaping biological evolution in the first case and cultural evolution in the second. From this perspective, a cultural behaviour is one that is transmitted repeatedly through social or observational learning to become a population-level characteristic¹⁷. By this definition, cultural differences (often known as 'traditions' in ethology) are well established phenomena in the animal kingdom and are maintained through a variety of social transmission mechanisms¹⁸. Well documented examples include dialects in song-birds^{12,13}, sweet-potato washing by Japanese macaques (*Macaca fuscata*) at Koshima¹⁹, and stone handling by Japanese macaques at Arashiyama²⁰. However, each case refers to variation in only a single behaviour pattern.

Tabulations of population differences amongst chimpanzees have indicated that multiple behavioural variants may exist^{2–7}. However, these tabulations have been based on published reports, which, although they record the presence of behaviours, remain problematic in three respects: they are incomplete; they frequently do not clarify the extent to which each behaviour pattern is habitual in the community; and they do not systematically document the absence of behaviour patterns present elsewhere. We therefore adopted a different strategy in our attempt to provide a definitive assessment of what is now known of chimpanzee cultural variation.

Phase 1 of the study established a comprehensive list of candidate cultural variants, which are behaviours suspected by research workers to be specific to particular chimpanzee populations. Beginning with a list drawn from literature review by A.W. and C.B., the research directors of the major chimpanzee field projects (Table 1) added and defined unpublished candidate patterns. The patterns were then split and lumped as appropriate. This complex, collaborative and iterative process produced a listing of candidate cultural variants that were fully and consensually defined (see Supplementary Information; Table 1 gives abridged descriptions). The scope of this list, differentiating 65 categories of behaviour, represents a unique record of the inventiveness of wild chimpanzees.

In phase 2, the research directors assigned to each of these behaviour categories one of the following six codes, as applicable at their site: (1) customary, for which the behaviour occurs in all or most able-bodied members of at least one age-sex class (such as adult males); (2) habitual, for which the behaviour is not customary but has occurred repeatedly in several individuals, consistent with some degree of social transmission; (3) present, for which the behaviour is neither customary nor habitual but is clearly identified; (4) absent, for which the behaviour has not been recorded and no ecological explanation is apparent; (5) ecological explanation, for which absence is explicable because of a local ecological feature; and (6) unknown, for which the behaviour has not been recorded, but this may be due to inadequacy of relevant observational opportunities. These codings were cross-checked and confirmed by senior colleagues at each site. Our results are for the seven chimpanzee

groups with the most long-term observation record, so the 'unknown' code was seldom applicable (Table 1). These studies bring together a total of 151 years of direct observation (range 8–38 years), so our data summarize the enormous increase in our knowledge of chimpanzee behaviour achieved in the latter half of this century.

For any row in Table 1, the profile of codings of particular interest with respect to cultural variation is that in which behaviours are recorded as customary or habitual in some communities, yet absent at others. Three other classes of profile need to be recognized and discriminated from this.

First, seven behaviours proposed as potential cultural variants in

Table 1 Variation in occurrence of behaviour patterns across long-term study sites

			Site						
			Bs	Ta	Go	Ma	Mk	Kib	Bd
A	1	Investigatory probe (probe and sniff)	H	C	C	H	H	+	(-)
	2	Play start (invite play holding stem in mouth)	+	H	C	C	C	C	H
	3	Drag branch (drag large branch in display)	H	C	C	C	C	H	H
	4	Leaf-sponge (leaf mass used as sponge)	C	C	C	+	e	C	C
	5	Branch-clasp (clasp branch above, groom)	H	C	C	C	C	C	C
	6	Branch-shake (to attract attention, court)	C	C	C	C	C	H	C
	7	Buttress-beat (drum on buttress of tree)	C	C	C	C	C	C	C
B	8	Nasal probe (clear nasal passage with stick)	-	-	-	+	-	-	-
	9	Comb (stem used to comb through hair)	-	-	-	-	-	-	+
	10	Insect-pound (probe used to mash insect)	+	-	-	-	-	-	-
	11	Resin-pound (extract resin by pounding)	+	-	-	e?	e?	-	-
	12	Branch-hook (branch used to hook branch)	+	-	-	-	-	-	-
	13	Perforate (stout stick perforates termite nest)	-	e	-	-	-	e	e?
	14	Dig (stick used as spade to dig termite nest)	+	e	-	-	-	e	e?
	15	Brush-stick (probing stick with brush end)	-	-	-	-	-	-	-
	16	Seat-stick (stick protection from thorns)	-	-	e	e?	e?	e	e
	17	Stepping-stick (walking on sticks over thorns)	-	-	e	e?	e?	e	e
	18	Container (object used as container)	-	-	+	-	-	-	-
	19	Leaf-mop (leaves used to mop up insects)	-	-	+	-	+	e	e?
	20	Leaf-wipe (food wiped from skull etc.)	e?	+	+	-	-	-	-
	21	Leaf-brush (leaf used to brush away bees)	-	-	+	-	-	-	-
	22	Open and probe (perforate, then probe)	-	-	-	-	-	-	-
	23	Sponge push-pull (stick and sponge tool)	+	+	+	+	e	e	-
C	24	Algae-scoop (scoop algae using wand)	C	e	e	e	e	e	e
	25	Ground-night-nest (night-nests on ground)	(-)	e?	+	e?	e?	e?	+
	26	Anvil-prop (rock used to level anvil)	H	e	e	e	e	e	e
D	27	Food-pound onto wood (smash food)	C	C	C	-	-	e?	H
	28	Food-pound onto other (such as stone)	-	H	C	-	-	e?	-
	29	Nut-hammer, wood hammer on wood anvil	-	C	-	e	e	e?	e
	30	Nut-hammer, wood hammer on stone anvil	-	C	-	-	-	e?	e
	31	Nut-hammer, stone hammer on wood anvil	+	C	-	e	e	e?	e
	32	Nut-hammer, stone hammer on stone anvil	C	C	-	-	-	e?	e
	33	Nut-hammer, other (such as on ground)	-	H	-	-	-	e?	e
	34	Pestle-pound (mash palm crown with petiole)	C	-	-	e?	e?	e?	e?
	35	Club (strike forcefully with stick)	+	H	H	+	-	+	-
	36	Termite-fish using leaf midrib	+	e	-	-	C	e	e?
	37	Termite-fish using non-leaf materials	-	e	C	-	C	e	e?
	38	Ant-fish (probe used to extract ants)	+	-	+	C	C	-	-
	39	Ant-dip-wipe (manually wipe ants off wand)	+	-	C	-	-	-	-
	40	Ant-dip-single (mouth ants off stick)	C	C	+	-	-	-	-
	41	Fluid-dip (use of probe to extract fluids)	-	C	C	H	H	H	-
	42	Bee-probe (disable bees, flick with probe)	-	C	-	-	+	-	-
	43	Marrow-pick (pick bone marrow out)	-	C	-	-	-	-	-
	44	Lever open (stick used to enlarge entrance)	-	H	C	-	-	-	-
	45	Expel/stir (stick expels or stirs insects)	-	C	H	H	H	-	-
	46	Seat-vegetation (large leaves as seat)	+	H	-	-	-	+	-
	47	Fly-whisk (leafy stick used to fan flies)	-	H	+	-	-	-	H
	48	Self-tickle (tickle self using objects)	-	-	H	-	-	-	-
	49	Aimed-throw (throw object directionally)	C	C	C	C	-	+	+
	50	Leaf-napkin (leaves used to clean body)	-	+	C	+	-	C	C
	51	Leaf-dab (leaf dabbed on wound, examined)	-	+	+	-	-	C	-
	52	Leaf-groom (intense 'grooming' of leaves)	-	-	C	C	C	C	+
	53	Leaf-clip, mouth (rip parts off leaf, with mouth)	C	C	-	C	C	H	C
	54	Leaf-clip, fingers (rip leaf with fingers)	-	H	-	+	-	H	C
	55	Leaf-strip (rip leaves off stem, as threat)	+	-	H	+	-	H	-
	56	Leaf-squash (squash ectoparasite on leaf)	-	-	H	?	?	-	-
	57	Leaf-inspect (inspect ectoparasite on hand)	-	+	?	?	?	-	C
	58	Index-hit (squash ectoparasite on arm)	-	C	+	-	-	-	-
	59	Hand-clasp (clasp arms overhead, groom)	-	H	-	C	C	C	-
	60	Knuckle-knock (knock to attract attention)	+	C	H	C	C	-	-
	61	Branch din (bend, release saplings to warn)	-	-	-	-	-	-	-
62	Branch-slap (slap branch, for attention)	C	C	-	+	-	-	C	
63	Stem pull-through (pull stems noisily)	C	-	+	H	-	H	-	
64	Shrub-bend (squash stems underfoot)	H	-	-	C	-	-	C	
65	Rain dance (slow display at start of rain)	-	H	C	C	C	C	H	

A, Patterns absent at no site; B, patterns not achieving habitual frequencies at any site; C, patterns for which any absence can be explained by local ecological factors; D, patterns customary or habitual at some sites yet absent at others, with no ecological explanation. To facilitate comparison, behaviours are listed so that adjacent categories share broad functions; in Band D these are: 27–35, pounding actions; 36–40, fishing; 41–43, probing; 44 and 45, forcing; 46 and 47, comfort behaviour; 48 and 49, miscellaneous exploitation of vegetation properties; 50–57, exploitation of leaf properties; 58–59, grooming; 60–64, attention-getting. Sites (with subspecies, observation period in years by September 1998, site director): Bs, Bossou, Guinea (*verus*, 23, Y.S.); Ta, Tai Forest, Ivory Coast (*verus*, 23, C.B.); Go, Gombe, Tanzania (*schweinfurthii*, 38, J.G.); Ma, Mahale M-group, Tanzania (*schweinfurthii*, 30, T.N.); Mk, Mahale K-group (*schweinfurthii*, 18, T.N.); Kib, Kibale Forest, Uganda (*schweinfurthii*, 11, R.W.W.); Bd, Budongo Forest, Uganda (*schweinfurthii*, 8, V.R.). C, customary; H, habitual; +, present; -, absent; e, absent with ecological explanation; e?, ecological explanation suspected; (-), absent possibly because of inadequate observation; ?, answer uncertain (see text for full definitions). Branch din (behaviour 61) is allocated to band D because it is known to be customary at Lopé, Gabon (C.E.G.T.); behaviours 13, 15–17 and 22 are allocated to band B because they have been recorded at shorter-term sites (see Supplementary Information). For full definitions of all behaviours, see Supplementary Information.



Figure 1 Distribution of behaviour patterns from band D in Table 1 across six African study sites. Behaviours are arranged in the 5 × 8 arrays to cluster those behaviours customary or habitual at each site, with clusters for westerly sites on the left of the array and clusters for easterly sites on the right. The secondary

Mahale site (K) is omitted. Colour icons, customary; circular icons, habitual; monochrome icons, present; clear, absent; horizontal bar, absent with ecological explanation; question mark, answer uncertain.

phase 1 were shown instead to be either customary or habitual in all communities (band A in Table 1). Second, 16 patterns failed to achieve habitual status in any community (band B in Table 1). The third class includes profiles in which all cases of absence are explicable by local conditions (band C in Table 1); just three cases were identified. Absence of algae-fishing can be explained by the rarity of algae, and any absence of ground night-nesting by high predator risk. Use of an additional stone to balance an anvil (anvil-prop) occurs only at Bossou, but it is not expected elsewhere because stone anvils are either not used or (at Tai) are embedded in the ground.

The remaining behaviours are absent at some sites but are customary or habitual at others (band D in Table 1). We have found 39 such behavioural variants, significantly more than previously suspected for chimpanzees¹⁻⁶. We know of no comparable variation in other non-human species, although no systematic study of this kind appears to have been attempted.

We arrive at a similar comparative conclusion when we examine the overall profiles of cultural variants in the different communities (Fig. 1). Some customary and habitual patterns are unique to certain communities, but others are shared between two or more communities (Table 2), so the clusters of variants that characterize each community are not mutually exclusive. Nevertheless, the profiles of each community (Fig. 1) are distinctively different, each with a pattern comprising many behavioural variants. These patterns vary as much between sites associated with the same subspecies (*verus* at Bossou and Tai in the west, and *schweinfurthii* at the four eastern sites) as between subspecies themselves. The only major difference between the western and eastern populations is that nut-cracking occurs only in the west, although the fact that this behaviour terminates abruptly at the Sassandra-N'Zo river within the range of the *verus* subspecies²¹ shows that it is culturally, rather than genetically, transmitted. The patterns in Fig. 1 can thus be seen to resemble those in human societies, in which differences between cultures are constituted by a multiplicity of variations in technology and social customs¹⁴. It remains to be shown whether chimpanzees are unique in this respect, or whether any other animal species, if studied in the same way, would reveal qualitatively similar patterns.

Other comparisons between human and non-human animal cultures have focused on the cognitive processes involved, arguing that if processes of human cultural transmission, such as imitative learning and teaching, are not found in animals, then culture in animals is merely an analogue of that in humans, rather than homologous with it^{22,23}. Our data agree with experimental studies that have shown that chimpanzees copy the methods used by others to manipulate and open artificial 'fruits' designed as analogues of wild foods^{24,25}. These experimental designs show differential copying of each of two quite different methods used to process the foods. Similarly, some of the differences between communities described here represent not only the contrast between habitual versus absent, but also the contrast between different versions of an otherwise similar pattern. Examples include cases of tool use, such as the two different methods of ant-dip (Table 1, items 39 and 40); in the first of these, a long wand is held in one hand and a ball of ants is wiped off with the other, whereas in the second method a short stick is held in one hand and used to collect a smaller number of ants, which are transferred directly to the mouth. Other examples occur in social behaviour, such as the variants used to deal with ectoparasites discovered during grooming, with leaf-squash, leaf-inspect and index-hit occurring in different communities (Table 1, items 56-58). It is difficult to see how such behaviour patterns could be perpetuated by social learning processes simpler than imitation, the most commonly suggested alternative to which is stimulus enhancement²⁶, in which the attention of an observer is merely drawn to a relevant item such as a stick. But this does not mean that imitation is the only mechanism at work. Experimental studies on the acquisition of tool-use and food-processing skills by both children and captive chimpanzees indicate that there is a complex

Table 2 Number of unique versus shared patterns that are either customary or habitual

	Site						
	Bs	Ta	Go	Ma	Mk	Kib	Bd
Unique	1	8	3	0	1	1	1
Shared	8	16	13	11	9	9	8

Sites are abbreviated as in Table 1. Unique refers to customary or habitual patterns unique to the sites; shared refers to customary or habitual patterns shared with other sites. Frequencies exclude 'universal' behaviour patterns identified in band A of Table 1.

mix of imitation, other forms of social learning, and individual learning^{24,25,27-30}.

Our results show that chimpanzees, our closest sister-species, have rich behavioural complexity. However, although this study represents the definitive state of knowledge at present, we must expect that more extended study will elaborate on this picture. Every long-term study of wild chimpanzees has identified new behavioural variants. □

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Supplementary information is available on Nature's World-Web site (<http://www.nature.com>) or as paper copy from the London editorial office of Nature. An extended graphical database (unrefereed) of this material is also available (<http://chimp.st-and.ac.uk/cultures>).

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