Current Biology *17*, 1–6, June 19, 2007 ©2007 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2007.05.031

Report

Transmission of Multiple Traditions within and between Chimpanzee Groups

Andrew Whiten,[1,*] Antoine Spiteri,[1] Victoria Horner,[1,2] Kristin E. Bonnie,[2] Susan P. Lambeth,[3] Steven J. Schapiro,[3] and Frans B.M. de Waal[2]

[1] Centre for Social Learning and Cognitive Evolution and Scottish Primate Research Group
School of Psychology
University of St Andrews
St Andrews KY16 9JP
United Kingdom

[2] Living Links
Yerkes National Primate Research Center
Emory University
Atlanta, Georgia 30329

[3] Department of Veterinary Sciences
The University of Texas M. D. Anderson Cancer Center
Bastrop, Texas 78602

Summary

Field reports provide increasing evidence for local behavioral traditions among fish, birds, and mammals [1–7]. These findings are significant for evolutionary biology because social learning affords faster adaptation than genetic change and has generated new (cultural) forms of evolution [8–10]. Orangutan and chimpanzee field studies [3, 4, 11–13] suggest that like humans [14, 15], these apes are distinctive among animals in each exhibiting over 30 local traditions. However, direct evidence is lacking in apes and, with the exception of vocal dialects [16, 17], in animals generally for the intergroup transmission that would allow innovations to spread widely and become evolutionarily significant phenomena. Here, we provide robust experimental evidence that alternative foraging techniques seeded in different groups of chimpanzees spread differentially not only within groups but serially across two further groups with substantial fidelity. Combining these results with those from recent social-diffusion studies in two larger groups [18–20] offers the first experimental evidence that a nonhuman species can sustain unique local cultures, each constituted by multiple traditions. The convergence of these results with those from the wild implies a richness in chimpanzees' capacity for culture, a richness that parsimony suggests was shared with our common ancestor.

Results and Discussion

Numerous local variations in the behavior patterns of wild chimpanzees and orangutans have been inferred to be cultural variants, transmitted through observational learning [3, 4, 11–13]. However, this inference relies heavily on circumstantial evidence that alternative genetic or environmental explanations are implausible. Field experiments could in principle provide a more robust test that putative traditions are truly socially learned, but logistic and ethical considerations have prevented exploratory interventions from employing controls to clearly discriminate the effects of social from individual learning [21, 22]. We have instead investigated chimpanzees' cultural capacities by conducting large-scale, controlled social-diffusion experiments with captive groups.

To investigate between-group transmission, we used a unique chimpanzee population that includes six groups of 8–11 individuals at Bastrop, Texas (Table S1 in the Supplemental Data available online), where each group has visual access to its neighbors (Figure 1). Two complex tool-use problems ("probe task" and "turn-ip"), each designed to make solution through individual exploration unlikely but solvable by two quite different techniques (Figure 2), were presented separately to each group for a 2 hr baseline period. Most chimpanzees explored these objects in the baseline period (Table S2), but none successfully extracted the food items they had seen dropped inside.

For each task in turn, a single chimpanzee from group B1 was then trained to use one of the two techniques to extract food, out of sight of her group. An individual from group B4 was likewise trained to use the alternative technique. Each model was then returned to its compound, with the apparatus available to the whole group at location 1 (Figure 1). Interactions with the apparatus were recorded on video for analysis. A total of 1643 successful (food-gaining) operations of the probe task were watched by a median of six individuals sitting within 1 m (range one to nine individuals). For the turn-ip, a median of four individuals (range one to nine) watched 5360 successes. Thus, all members of a group sometimes formed a tightly packed cluster of observers within 1 m around an actively foraging chimpanzee.

By contrast with the absence of task solutions in the baseline phase, after observing the initial model, a second individual successfully solved the probe task after 28 min in group B1 and after 15 min in group B4. During 8 hr of exposure spread over 3 days, all but three individuals mastered the probe task. To test for preferential adoption of the model's technique, we computed a "%stab" index (%stab = 100 × stab/[stab + slide]). The %stab index was significantly greater in group B1 (median 100%), seeded with the stab technique, than in B4, seeded with the alternative slide technique (median 0.0%; Mann-Whitney U test, $U = 2$, $p = 0.016$: Figure 3A; Table S3 lists sample sizes). For the two-step turn-ip task, an individual other than the model was successful after 87 min in group B1 and 36 min in group B4. During 24 hr of exposure spread over 8 days, all but two individuals gained food from the turn-ip, although four completed only the second of the two required actions after a group mate had performed the first (Figure 3). To test for social transmission, we

*Correspondence: a.whiten@st-andrews.ac.uk

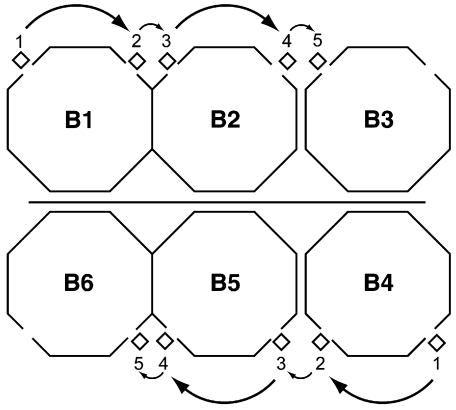

Figure 1. Compound Configuration

Each external compound, diameter 21 m, accommodates 8–11 chimpanzees. Successive presentation locations of foraging tasks next to barred windows are marked 1–5. Chimpanzees in B2 and B5 were able to watch foraging techniques applied by their neighbors at location 2 before attempting the task themselves at location 3; the same was later true for chimpanzees in B3 and B6 with respect to locations 4 and 5, respectively.

computed "%ratchet" (%ratchet = 100 × [ratchet then slide]/[ratchet then slide] + [turn then press]). This index was significantly greater in group B1, seeded with the ratchet-then-slide technique (median 100%) than in B4, seeded with the turn-then-press technique (median 0%; Mann-Whitney U test, U = 0, $p < 0.001$; Figure 3B).

Once half of a group's members were successful, each foraging task was presented to the same group at a second location where the neighboring group could observe work on it through their windows at a distance of approximately 3 m (B1 and B2) or 5 m (B4 and B5; Figure 1), for six 30 min sessions. This procedure was later repeated for a third group in each case (B3 and B6, respectively). Operations of the probe task in one group were watched by a median of four individuals (range 1–11), and operations of the turn-ip were watched by a median of three individuals (range 1–11) in the neighboring group (see Table S3 for details). Each of these observing groups in turn was then given access to the foraging device at its own window (locations 3 and 5 in Figure 1). Each technique was transmitted with high fidelity across these groups (Figure 3). Both measures of differential use of techniques, %stab and %ratchet, were significantly greater in B2 than in B5 and greater in B3 than in B6 (p always < 0.02; Table S3).

This is the first evidence in a nonhuman species for the between-group diffusion of socially learned behavior patterns necessary for significant spreading of traditions. As in prior within-group diffusion experiments (18–20), individual corruption events occurred in each group, raising the prospect that the contrasts between traditions would progressively erode; yet instead, each seeded variant remained clearly dominant in the corresponding final group, suggesting a conformity effect (Figure 3). The social diffusion of experimentally seeded, alternative foraging techniques across over 20 individuals in each case is unprecedented in the literature on animal social learning (reviewed in [19]). These results hold substantial import for recent debates concerning the inherent weaknesses of nonexperimental evidence

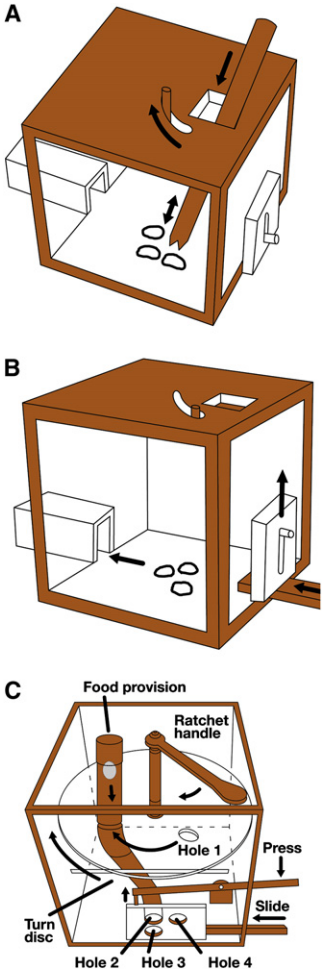

Figure 2. Probing and Turn-Ip Foraging Tasks

(A) Probing task, stab technique. By pushing to one side a small button, chimpanzees can open a doorway in the top surface and insert a tool to stab food items.

(B) Probing task, slide technique. Once a hatch door is raised, a flat tool can be inserted, pushing food items along the floor and out of a tunnel on the opposite side, with the food then rolling to chimpanzees down a ramp (not shown) beneath.

(C) Turn-ip task. Food items dropped into the pipe are trapped until the disc is rotated to align hole 1 with the pipe. This can be achieved either by directly turning the front edge of the disc protruding through a slit (method "turn") or by repeatedly pulling a ratchet handle on the top surface (method "ratchet"). Once the food drops, it can be released either by pressing down a handle to lift plate aligning holes 2 and 3 (method "press") or pushing a sliding handle that aligns holes 2 and 4 (method "slide").

for cultural variations among wild apes [23–25]. We conclude that chimpanzees have a demonstrable capacity for fidelity in social learning across multiple groups, consistent with the hypothesis that regional behavior patterns in Africa have spread through cultural transmission [4, 12]. In the wild, the context for intergroup transmission would be unlikely to directly mirror that of our experiments because of intergroup antagonism, but opportunities for the observational learning we have documented arise naturally through the transfer of females between groups [4, 22, 26]. Indeed, our results suggest that investigating intergroup transmission by translocation of skilled individuals into naive groups

Please cite this article in press as: Whiten et al., Transmission of Multiple Traditions within and between Chimpanzee Groups, Current Biology (2007), doi:10.1016/j.cub.2007.05.031

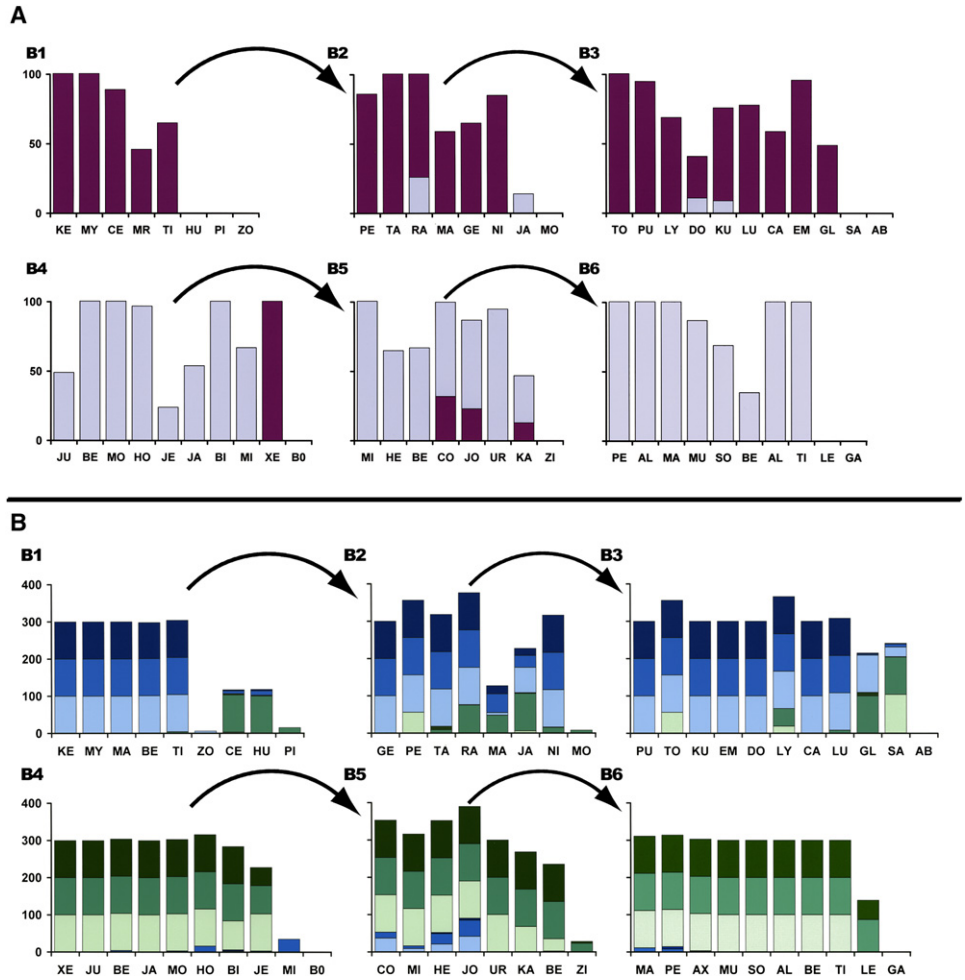

Figure 3. Spread of Alternative Traditions across Two Series of Three Groups

Arrows indicate direction of between-groups information transfer.

(A) Probing task, initiated by trained models KE in group B1 (stab method) and JU in group B4 (slide technique). Chimpanzees in group B2 were able to observe techniques employed by group B1 and in turn were observed by group B3. Groups B4, B5, and B6 had parallel observational opportunities. Individual chimpanzees are labeled with two-character codes and arranged by order of successful task solution. Each bar shows the number of stab (dark) and slide (light) actions by each chimpanzee, capped at their first 100 successes.

(B) Turn-ip task, initiated by trained models KE in group B1 (ratchet-then-slide technique) and XE in group B4 (turn-then-press technique). Between-group observation opportunities were as for the probing task. Each bar shows the number of successful ratchet (light green), slide (midgreen), ratchet-then-slide (dark green), turn (light blue), press (midblue), and turn-then-press (dark blue) actions by each chimpanzee. Each category is capped at the first 100 successes (for overall statistics, see Table S2 in the Supplemental Data). Slide could exceed ratchet, and press could exceed spin, where one individual exploited the prior performance by another individual of the first of the two actions necessary to attain food.

would be a valuable further step, even if a much more difficult one to arrange in practice.

Combining these results with those recently obtained in three separate diffusion experiments with two larger groups of chimpanzees now allows us to address the controversial hypothesis that chimpanzees are able to sustain multiple, diverse behavioral traditions aptly described as local cultures, by analogy with the human case [9, 10, 14, 15]. These data are illustrated in Figure 4, which collates the results of three experiments conducted at the Field Station of the Yerkes National Primate Research Center (respectively labeled "Doorian," "panpipes," and "token" experiments after the manipulanda involved [18–20] with those from the intergroup experiments (turn-ip and probe task) conducted at Bastrop and reported in detail above. Each of these studies has separately demonstrated a new aspect of cultural transmission in animals. Here, we integrate them to document local cultures defined by multiple behavioral variations, to our knowledge the first demonstration of this capacity in a nonhuman species. Thus, the Yerkes FS1 culture is characterized by lifting open the Doorian, poking a tool in the panpipes to gain food, and using a bucket for depositing tokens, whereas the Yerkes FS2 culture typically involves sliding open the Doorian, lifting an obstacle to release food from the panpipes, and posting tokens down a pipe. Similarly, the Bastrop-West culture (groups B1–B3) is defined by stabbing in the probe task and applying the ratchet-then-slide technique to the turn-ip, whereas in Bastrop-East (B4–B6), chimpanzees typically use two different techniques for these tasks. In addition, the spontaneous emergence

Please cite this article in press as: Whiten et al., Transmission of Multiple Traditions within and between Chimpanzee Groups, Current Biology (2007), doi:10.1016/j.cub.2007.05.031

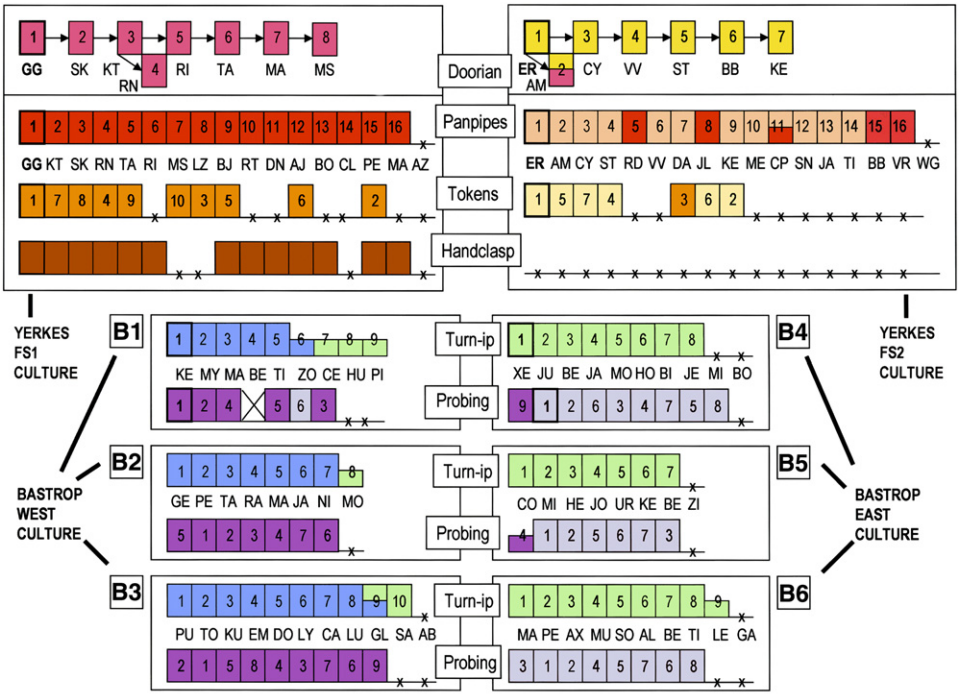

Figure 4. Four "Cultures" Each Defined by Multiple Different Traditions

Yerkes-FS1 culture (Doorian-lift, token-to-bucket, panpipe-poke, and handclasp traditions) is shown on the upper left; Yerkes-FS2 culture (Doorian-slide, token-to-pipe, panpipe-lift, and no-handclasp traditions) is shown on the upper right; Bastrop-West (B1–B3) culture (probe-by-stab, turn-ip ratchet-then-slide traditions) is shown on the lower left; and Bastrop-East (B4–B6) culture (probe-by-slide, turn-ip turn-then-press traditions) is shown on the lower right. Each rectangle denotes a chimpanzee, identified by a two-character label in the corresponding column. Initial, trained models are denoted by thick borders. Numbers represent order of successful acquisition of each task. Order was not reliably known for handclasp grooming and was predetermined in the transmission-chain Doorian-task study charted in the upper Yerkes frame. In the lower Yerkes and Bastrop frames, acquisition order in the first task (panpipe at Yerkes, turn-ip at Bastrop) is numbered serially left to right, with order for other tasks labeled for the same chimpanzees. Color boxes indicate the following: Doorian task [19]: red = lift, yellow = slide; panpipe task [18]: red = poke, pink = lift; token study [20]: orange = bucket, cream = pipe; handclasp [27]: brown = handclasp; probing: purple = stab, lilac = slide; and turn-ip: blue = ratchet-then-slide, green = turn-then-press. For each chimpanzee, the dominant response is shown, with those performing one of the alternatives at between 25%–75% of the total indicated here as 50%. Individuals performing only half the turn-ip task are indicated by a half bar. A cross indicates those individuals who never performed a task.

and spread of handclasp grooming, a locally varying custom known in the wild in which grooming partners clasp hands overhead [27], has been documented in detail in FS1 yet has not occurred in FS2 [28]. This provides a fourth tradition discriminating the Yerkes cultures (Figure 4).

The transmission of these different traditions in multiple groups offers the unique opportunity to investigate whether general principles apply to the diffusion process. We begin such investigation here by examining whether consistencies exist in the order in which techniques diffused through groups. The order in which individuals in each group mastered the probe and turn-ip tasks was significantly correlated in groups B2 ($r = 0.74$, $n = 7$, and $p = 0.037$), B3 ($r = 0.84$, $n = 9$, and $p = 0.001$), and B6 ($r = 0.95$, $n = 8$, and $p < 0.001$), and the correlation was high and positive for all six groups (Table S4) (binomial test, $p = 0.04$). By contrast, the correlation between order of acquisition in the panpipes and token tasks at Yerkes was negative and nonsignificant (FS1, $r = -0.50$, $n = 9$, NS; FS2, $r = -0.54$ $n = 6$, NS; such correlations cannot be tested for the Doorian study, because this required direct experimental control over order of acquisition, nor for the handclasp study, which spanned several years involving significant demographic changes). Together, the Bastrop and Yerkes results suggest that similar general principles govern tasks of the same kind (tool-based foraging in the case of the probe task and turn-ip) but different factors come into play for tasks as different as the panpipes (tool-based foraging) and tokens (arbitrary conventions of object use). The consistency between similar tasks and variations between different ones suggest there is much scope for future investigation of the social dynamics and other factors determining the spread of experimentally seeded traditions.

Our Bastrop experiments are the first to demonstrate the spread of alternative traditions from group to group in a nonhuman species. Whether the underlying social-learning mechanism is imitation or some other process is a separate question requiring different kinds of experiment. In a recent study [29], we found that chimpanzees did not learn from a "ghost" condition in which our panpipes task was operated remotely with no chimpanzee involved, challenging a current view that chimpanzees learn by "emulation," in which they focus only on the results of actions, as opposed to imitating the actions themselves [23]. Our ghost experiments indicate that chimpanzees are instead motivated to learn specifically from a conspecific doing the action of interest [29].

Please cite this article in press as: Whiten et al., Transmission of Multiple Traditions within and between Chimpanzee Groups, Current Biology (2007), doi:10.1016/j.cub.2007.05.031

Whatever the social-learning mechanisms involved in the studies reported here, our findings demonstrate a capacity for within-group and between-group transmission of the fidelity required to explain the spread of putative chimpanzee traditions across regions of Africa [4, 12]. In addition, we have shown that these animals can sustain local cultures constituted by multiple behavior patterns of different kinds, as apes have been hypothesized to do in the wild [3, 4, 7, 11–13]. These results suggest that humans' prodigious capacity for culture is likely to have evolved from a foundation in the common ancestor we share with chimpanzees that in these respects already represented the most developed cultural abilities among animals. Our seeding of alternative behavioral techniques in different groups has proven to be a powerful method in investigating such phenomena; extending it in future comparative studies with other species opens the prospect of a comprehensive picture of the evolutionary foundations of culture in the animal kingdom.

Experimental Procedures

Subjects

"Bastrop" chimpanzees were housed at the University of Texas M.D. Anderson Cancer Center near Bastrop, Texas, and are described in Table S1. Yerkes subjects are fully described in [18] and [19]. High-ranking females were selected as the first two trained models so that they would maintain control of the task and initially perform a high level of competent demonstrations.

Materials

Foraging devices and alternative foraging techniques are described in Figure 2 and in detail in the Supplemental Data.

Procedures

Once each initial model in B1 and B4 was reunited with her group, an observation phase was maintained in which the apparatus was withdrawn if chimpanzees other than the model took the tool, until all in the group had witnessed five or more successful uses of the tool. In the subsequent open diffusion phase, all chimpanzees were allowed access to tools and foraging tasks. The first such trial was 30 min, and this was followed by five 5 hr trials. For the between-groups transfer phase that began once half the first group were successful, six 30 min observation periods were each followed by a 30 min trial with the inexperienced group. Alternation of 30 min periods between groups then continued until a new model appeared in the inexperienced group, at which point 5 hr sessions continued with this group. A detailed account of procedures is included in the Supplemental Data.

Interobserver Reliability

Reliability for each of the critical six behavior patterns (Figure 3) is shown in the Supplemental Data. Given the gross differences in technique, reliability was high, with a median of 99% agreement between coders.

Statistics

Choice of statistical procedures is described in the Supplemental Data.

Ethical Treatment of Animals

Both the Yerkes and Bastrop facilities are fully accredited by the Association for Assessment and Accreditation of Laboratory Animal Care—International. Training of chimpanzees as models was through human demonstration followed by positive-reward shaping as necessary.

Supplemental Data

Additional Experimental Procedures, Author Contributions, and five tables are available at http://www.current-biology.com/cgi/content/full/17/12/■■■/DC1/.

Acknowledgments

Studies reported here were supported by the Biotechnology and Biological Sciences Research Council and Leverhulme Trust (UK), National Institutes of Health (NIH) grants to the Yerkes National Primate Research Center, and the Living Links Center of Emory University. A.W. was supported by a Royal Society Leverhulme Trust Senior Fellowship. The Bastrop colony is supported by NIH/NCRR through cooperative agreement with the NIH National Center for Research Resources. We thank L. Hopper for interobserver-agreement coding, A. Burnley and E. Thiele for expert help in construction of foraging devices, and M. Dindo, T. Fitch, L. Hopper, R. Kendal, and W.C. McGrew for comments on the manuscript.

Received: April 6, 2007
Revised: May 9, 2007
Accepted: May 10, 2007
Published online: June 7, 2007

References

1. Fragaszy D.M. and Perry S., eds. (2003). The Biology of Traditions: Models and Evidence (Cambridge: Cambridge University Press).
2. Laland, K.N., and Hoppitt, W. (2003). Do animals have culture? Evol. Anthropol. *12*, 150–159.
3. van Schaik, C.P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C.D., Singleton, I., Suzuki, A., Utami, S.S., and Merrill, M. (2003). Orangutan cultures and the evolution of material culture. Science *299*, 102–105.
4. McGrew, W.C. (2004). The Cultured Chimpanzee: Reflections on Cultural Primatology (Cambridge: Cambridge University Press).
5. Emery, N.J., and Clayton, N.S. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. Science *306*, 1903–1907.
6. Krützen, M., Mann, J., Heithaus, M.R., Connor, R.C., Bejder, L., and Sherwin, W.B. (2005). Cultural transmission of tool use in bottlenose dolphins. Proc. Natl. Acad. Sci. USA *102*, 8939–8943.
7. Whiten, A. (2005). The second inheritance system of chimpanzees and humans. Nature *437*, 52–55.
8. Dawkins, R. (1976). The Selfish Gene (Oxford: Oxford University Press).
9. Richerson, P., and Boyd, R. (2005). Not by Genes Alone: How Culture Transformed Human Evolution (Chicago: Chicago Univ. Press).
10. Mesoudi, A., Whiten, A., and Laland, K.N. (2006). Towards a unified science of culture. Behav. Brain Sci. *29*, 329–383.
11. van Schaik, C.P. (in press). Geographic variation in the behaviour of wild great apes: Is it really cultural? In The Question of Animal Culture, K.N. Laland, and B.G. Galef, Jr., eds. (Cambridge, MA: Harvard University Press).
12. Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E.G., Wrangham, R.W., and Boesch, C. (1999). Cultures in chimpanzees. Nature *399*, 682–685.
13. Whiten, A., and van Schaik, C.P. (2007). The evolution of animal cultures and social intelligence. Philos. Trans. R. Soc. Lond. B Biol. Sci. *362*, 603–620.
14. Guglielmino, C.R., Viganotti, C., Hewlett, B., and Cavalli-Sforza, L.L. (1995). Cultural variation in Africa: Role of mechanisms of transmission and adaptation. Proc. Natl. Acad. Sci. USA *92*, 7585–7589.
15. Hewlett, B.S., de Silvestri, A., and Guglielmino, C.R. (2002). Semes and genes in Africa. Curr. Anthropol. *43*, 313–321.
16. Catchpole, C.K., and Slater, P.J.B. (1995). Bird Song: Biological Themes and Variations (Cambridge: Cambridge University Press).
17. Noad, M.J., Cato, D.H., and Bryden, M.M. (2000). Cultural revolution in whale songs. Nature *404*, 536.
18. Whiten, A., Horner, V., and de Waal, F.B.M. (2005). Conformity to cultural norms of tool use in chimpanzees. Nature *437*, 737–740.
19. Horner, V., Whiten, A., Flynn, E., and de Waal, F.B.M. (2006). Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. Proc. Natl. Acad. Sci. USA *103*, 13878–13883.

Please cite this article in press as: Whiten et al., Transmission of Multiple Traditions within and between Chimpanzee Groups, Current Biology (2007), doi:10.1016/j.cub.2007.05.031

20. Bonnie, K.E., Horner, V., Whiten, A., and de Waal, F.B.M. (2007). Spread of arbitrary customs among chimpanzees: A controlled experiment. Proc. R. Soc. B *274*, 367–372.
21. Matsuzawa, T., and Yamakoshi, G. (1996). Comparison of chimpanzee material culture between Bossou and Nimba, West Africa. In Reaching into Thought: the Minds of the Great Apes, A.E. Russon, K.A. Bard, and S.T. Parker, eds. (Cambridge: Cambridge University Press), pp. 211–232.
22. Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., and Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. Anim. Cogn. *6*, 213–223.
23. Tomasello, M. (1999). The Cultural Origins of Human Cognition (Cambridge, MA: Harvard University Press).
24. Galef, B.G., Jr. (2004). Approaches to the study of traditional behaviours of free-living animals. Learn. Behav. *32*, 53–61.
25. Laland, K.N., and Janik, V. (2006). The animal cultures debate. Trends Ecol Evol. *21*, 542–547.
26. Goodall, J. (1986). The Chimpanzees of Gombe: Patterns of Behaviour (Cambridge, MA: Harvard University Press).
27. McGrew, W.C., and Tutin, C.E.G. (1978). Evidence for a social custom in wild chimpanzees. Man *13*, 234–251.
28. Bonnie, K.E., and de Waal, F.B.M. (2006). Affiliation promotes the transmission of a social custom: Handclasp grooming among captive chimpanzees. Primates *47*, 27–34.
29. Hopper, L.M., Spiteri, A., Lambeth, S.P., Schapiro, S.J., Horner, V., and Whiten, A. (2007). Experimental studies of traditions and underlying transmission processes in chimpanzees. Anim. Behav. *73*, in press. Published online May 10, 2007. 10.1016/j.anbehav.2006.07.016.