
Social Conventions in Wild White-faced Capuchin Monkeys

Evidence for Traditions in a Neotropical Primate¹

by Susan Perry, Mary Baker,
Linda Fedigan, Julie Gros-Louis,
Katherine Jack,
Katherine C. MacKinnon,
Joseph H. Manson,
Melissa Panger, Kendra Pyle, and
Lisa Rose

Ten researchers collaborated in a long-term study of social conventions in wild white-faced capuchin monkeys, involving examination of a 19,000-hour combined data set collected on 13 social groups at four study sites in Costa Rica over a 13-year period. Five behavior patterns qualified as social traditions, according to the study's criteria: handsniffing, sucking of body parts, and three types of "games." Some conventions were independently invented in virtually identical form at multiple sites. The extinction of several conventions was observed during the course of the study; it appears that they rarely last longer than ten years. It is hypothesized that the monkeys are using these group- or clique-specific social conventions to test the quality of their social relationships.

SUSAN PERRY is Director of the Independent Junior Research Group in Cultural Phylogeny at the Max Planck Institute for Evolutionary Anthropology (Inselstrasse 22, D-04103 Leipzig, Germany [perry@eva.mpg.de]) and Assistant Professor of Anthropology at the University of California, Los Angeles. MARY BAKER is Visiting Assistant Professor of Anthropology at Whitier College. LINDA FEDIGAN is Professor and Canada Research Chair in the Department of Anthropology, University of Calgary. JULIE GROS-LOUIS is a postdoctoral fellow in psychology at Indiana University. KATHARINE JACK is Assistant Professor of Anthropology at Appalachian State University. KATHERINE C. MACKINNON is Assistant Professor of Anthropology in the De-

1. We are grateful to the Costa Rican National Park Service, the Area de Conservación Guanacaste (especially Roger Blanco Segura), the Area de Conservación Tempisque, the community of San Ramón de Bagaces, Hacienda Pelón, Rancho Joboba/Brin D'Amor, and the Schutt family for permission to work in the areas occupied by these monkeys. Assistance in data collection was provided by Laura Sirot, Todd Bishop, Kathryn Atkins, Marvin Cedillos Amaya, Sarah

partment of Sociology and Criminal Justice, Saint Louis University. JOSEPH H. MANSON is a scientist in the Cultural Phylogeny Group of the Max Planck Institute for Evolutionary Anthropology in Leipzig and Associate Professor of Anthropology at the University of California, Los Angeles. MELISSA PANGER is a researcher in the Department of Anthropology at George Washington University. KENDRA PYLE is a graduate student in biology at the University of Pennsylvania. LISA ROSE is Assistant Professor in the Department of Anthropology and Sociology, University of British Columbia. The present paper was submitted 10 IX 01 and accepted 30 V 02.

Social learning has become a topic of intense research interest for anthropologists, psychologists, and behavioral ecologists (McGrew 2001:325). Behavioral ecologists are primarily interested in determining the relative costs and benefits of acquiring behaviors via social learning, asocial learning, and/or genetic transmission under various sets of conditions and in modeling the population dynamics of social transmission (see, e.g., Boyd and Richerson 1985; Giraldeau and Caraco 2000; Laland 1996, 1999; Lefebvre and Giraldeau 1996; Dewar n.d.). Psychologists generally focus on the proximate mechanisms and developmental processes by which animals engage in socially biased learning and are interested in the cognitive aspects of social learning (e.g., Whiten 2000, Whiten and Ham 1992, Custance, Whiten, and Fredman 1999, Byrne 1995; see also chapters in Russon, Bard, and Parker 1996, Heyes and Huber 2000, and Heyes and Galef 1996). Anthropologists are interested in social learning and social traditions (one of the possible outcomes of social learning) because of what they can tell us about the origin of culture in humans (King 1991, 1994; McGrew 1992; Boesch and Tomasello 1998; Boyd and Richerson 1996). When anthropologists turn to the comparative method for aid in constructing models of human evolution, they generally take one of two approaches: argument by homology or argument by analogy. In an argument by homology, the researchers investigate the qualities of those organisms that are shared by humans and their closest living relatives (i.e., chimpanzees and the other great apes) and infer that these traits were present in their recent common ancestors. Given the tremendous variation in social organization, diet, and cognitive abilities among the apes, however, it is difficult to use the behavioral data from the extant apes to reconstruct ancestral traits. In an argument by analogy, the researcher searches the zoological record more broadly, seeking instances in which taxa have been confronted by similar adaptive problems and asking whether they solved them in the same way. For example, Harcourt (1995), in seeking to test whether males of species having promiscuous mating systems engage in sperm compe-

Carnegie, Alisha Steele, Matthew Duffy, Maura Varley, Ryan Crocetto, Hannah Gilkenson, Jill Anderson, Craig Lamarsh, Sasha Gilmore, Dale Morris, Dusty Becker, three expeditions of Earthwatch volunteers, and seven groups of University Research Expedition Program volunteers. Susan Wofsy and Denise Alabart assisted in compiling the data. Barb Smuts, Joan Silk, Simon Reader, Mike Huffman, Dorothy Fragaszy, Bill McGrew, Andy Whiten, and two anonymous reviewers commented on the manuscript, providing many helpful comments. Members of the UCLA Behavior, Evolution, and Culture group and the contributors to the "Traditions

tion, used type of mating system as the independent variable (i.e., the adaptive challenge) and testes size as the dependent variable (i.e., the adaptive outcome), controlling for phylogeny to some extent by performing the analysis at the level of the genus. Although Japanese researchers working with Japanese macaques (*Macaca fuscata*) were the first to propose that social traditions (which they termed "pre-culture," "infrahuman culture," or "sub-human culture") were an important part of the behavioral biology of primates (Itani 1958, Itani and Nishimura 1973, Kawai 1965, Kawamura 1959), the majority of research in the field now known as "cultural primatology" (McGrew 1998, de Waal 1999) has focused on the great apes (e.g., McGrew 1992; McGrew and Tutin 1978; Whiten et al. 1999; Russon 1996; van Schaik, Fox, and Sitompul 1996; Boesch 1996a, b; Matsuzawa and Yamakoshi 1996). Social learning is by no means restricted to humans and their closest relatives; in fact, some of the best-documented examples of social learning and traditions are found outside the order Primates (e.g., feeding traditions in rats [Terkel 1996, Galef n.d.], social learning of courtship signals in cowbirds [West and King 1996], mate-choice copying in guppies and quail [Dugatkin 1996, White and Galef 1999], and vocal traditions

in birds and cetaceans [see review by Janik and Slater n.d.]. To understand the socioecological factors that promote social learning in an evolutionary perspective, it is necessary to look beyond the great apes.

The genus *Cebus* (capuchin monkeys, a type of New World primate) proves to be a particularly interesting source of data for researchers interested in explaining human origins because capuchins have independently evolved many traits that are present in humans and/or chimpanzees (Visalberghi and McGrew 1997). Capuchins have extraordinarily large brain sizes relative to their body sizes (Harvey, Martin, and Clutton-Brock 1987, Stephan, Baron, and Frahm 1988), they are omnivorous and rely heavily on extractive foraging (Freese 1976, Chapman and Fedigan 1990, Terborgh 1983), they hunt vertebrates (Terborgh 1983, Perry and Rose 1994, Fedigan 1990, Rose 1997), they are very tolerant during foraging and sometimes share food (de Waal 1997, 2000; Perry and Rose 1994), they are skilled tool users (Urbani 1999, Visalberghi 1990, Ottoni and Mannu 2001, Boinski 1988, Westergaard 1994, Westergaard and Suomi 1995), they engage in nonconceptive sex in all age-sex combinations (Manson, Perry, and Parish 1997), they exhibit frequent alloparenting (Manson 1999, O'Brien and Robinson 1991), they have high rates of intraspecific lethal aggression (unpublished data), and they have complex social relationships characterized by frequent cooperation and coalitionary aggression (Perry 1996, 1997, 1998a, b, n.d.; Manson et al. 1999; Rose 1992). The capuchin's generalist lifestyle, combined with its large brain size, tolerance, and intensely social nature, makes this taxon a likely candidate for prevalent social learning in a variety of behavioral domains (van Schaik, Deaner, and Merrill 1999, Reader n.d., Coussi-Korbel and Fragaszy 1995). Previous studies in captivity have demonstrated capuchins' abilities to engage in social learning in the behavioral domains of food choice and food processing (Custance, Whiten, and Fredman 1999, Fragaszy and Visalberghi 1996, Visalberghi and Addessi 2000), and these studies provide mixed results regarding the complexity of the social learning mechanisms used by capuchins. To date, there is no published literature on social learning or traditions in wild capuchins in any behavioral domain.

If you ask laypeople or even cultural anthropologists to describe the cultural differences between two cultures they have experienced, chances are they will not dwell upon the technological differences between the two populations but will tell you much about their social customs, perhaps detailing the various faux pas they made when attempting to interact with the locals properly. Human cultures are so rich in social conventions (i.e., dyadic social behaviors or communicative behaviors that are unique to particular groups or cliques) that it takes immigrants decades to become enculturated to the point that they know the subtle nuances of appropriate interaction patterns and cease to make social blunders. If social conventions are such an important aspect of human culture, then it is striking that so little of the literature to date on culture in nonhumans has dealt with this

in Nonhuman Primates" conference at the University of Georgia-Athens provided useful comments as well. Joan Silk wrote the data-collection program, FOCOBS, used by many of the researchers. Gayle Dower produced the line drawings.

The UCLA Council on Research provided SP with funding for this project during the data analysis stage, and the Max Planck Institute for Evolutionary Anthropology provided funding during the write-up stage. Numerous other granting agencies inadvertently funded the fieldwork that gave rise to this project as well: SP thanks the National Science Foundation (for a graduate fellowship, an NSF-NATO postdoctoral fellowship, and a POWRE grant #SBR-9870429), the L. S. B. Leakey Foundation (for three grants), the National Geographic Society, the University of Alberta (for an I. W. Killam Postdoctoral Fellowship), Sigma Xi, the University of Michigan Rackham Graduate School (for four grants), the University of Michigan Alumnae Society, and UCLA (for two Faculty Career Development grants). MB thanks the University of California-Riverside Graduate Division (for three grants), Earthwatch, UREP, and NIH-MIRT (for a grant to E. Rodriguez). LF's research is funded by an ongoing grant (A7723) from the Natural Sciences and Engineering Research Council of Canada (NSERCC). JG thanks the University of Pennsylvania and NSF for a graduate fellowship and a dissertation improvement grant. KJ's research was supported by the National Geographic Society, the NSERCC (postgraduate scholarship), the Alberta Heritage Scholarship Fund (Ralph Steinhauer Award), the Ruggles-Gates Fund for Biological Anthropology (Royal Anthropological Institute), Sigma Xi, the Faculty of Graduate Studies and Research/Department of Anthropology at the University of Alberta, and the above-mentioned NSERCC grant to LF. KM's fieldwork was supported by an NSF dissertation improvement grant (#SBR-9732926) and a University of California Berkeley Social Sciences and Humanities Research Grant. JM was supported by a University of California Los Angeles Faculty Career Development Award. MP thanks the Costa Rican National Park System (park fee exemption grant), the Organization for Tropical Studies (especially M. Quesada and K. Stoner), and the University of California Berkeley's Anthropology Department (three grants) for helping to make her research possible. LR was supported by an NSERCC postgraduate scholarship, NSF, the National Geographic Society, the L. S. B. Leakey Foundation, Sigma Xi, and Ammonite Ltd. [Supplementary materials appear on the journal's web page (<http://www.journals.uchicago.edu/CA/home.html>).]

behavioral domain. Is it the case that most nonhumans lack interpopulation variability in social conventions? Or has there merely been a dearth of research effort in this domain?

Most researchers who have attempted to document social traditions or social learning in mammals have focused on foraging techniques (e.g., Itani 1958; Kawai 1965; Scheurer and Thierry 1985; Watanabe 1989, 1994; McGrew 1992; Matsuzawa 1994; Boesch 1996a; Matsuzawa and Yamakoshi 1996; Fragaszy and Visalberghi 1996; Galef 1996; Terkel 1996; Boran and Heimlich 1999; Byrne 1999; Hudson, Schaal, and Bilks 1999; Kitchener 1999; Laland 1999; Nel 1999; van Schaik, Deaner, and Merrill 1999; Wilkinson and Boughman 1999; chapters in Fragaszy and Perry n.d.a; see also, for a review of the role of social learning in foraging in vertebrates generally, Galef and Giraldeau 2001), and therefore most of the theory that has been developed concerning the emergence and maintenance of traditions has focused on this behavioral domain. However, there are also some intersite or intergroup differences reported for some species that can best be described as social conventions. Some examples are the various styles of grooming in Japanese macaques (e.g., alternative forms of louse-egg-handling techniques) and chimpanzees (e.g., social scratching, leaf grooming, and hand-clasp grooming) that are unique to particular matriline or sites (Nakamura et al. 2000; McGrew and Tutin 1978; Tanaka 1995, 1998; Boesch 1996a, b; Whiten et al. 1999; McGrew et al. 2001). Some social signals (e.g., leaf-clipping) are found at multiple sites in almost identical forms but are used for different purposes at different sites (Boesch 1996a, b). Other signals are different in their form but can serve the same function at different sites (e.g., knuckle-knocking and leaf-clipping are both used as courtship gestures by chimpanzees at different sites [Boesch 1996b]).

In this paper, we will focus exclusively on traditions in the behavioral domain of social conventions. Using data collected at four study sites over 13 years, we will describe several social conventions that seem to qualify as traditions in wild white-faced capuchin monkeys (*Cebus capucinus*), and we will attempt to determine the functions of these behaviors. Three classes of behaviors will be discussed: hand-sniffing, sucking on body parts, and “games.” We will go on to consider the putative functions of such signals, the design features that are optimal for such signals, and the transmission dynamics of social conventions. Most models of social transmission are about behaviors performed by single individuals that have a clear adaptive function (e.g., food choice, tool use, food processing). Given that (a) social conventions are necessarily performed dyadically rather than by single individuals and (b) the role that social conventions play in the behavioral biology of the animals is quite different from the role of foraging-related behaviors, it is to be expected that the transmission dynamics of social conventions will be different from those of behaviors that are more frequently modeled.

Identifying a Tradition

We define a “behavioral tradition” as a practice that is relatively long-lasting and shared among members of a group, each new practitioner relying to some extent upon social influence to learn to perform it. We imposed the following three criteria on the data to determine whether a behavior pattern qualified as a “tradition”: (a) *Intergroup variation*: The behavior in question must be present in at least one social group and absent in at least one group. To qualify as “present” or common in a particular group, the behavior must be seen at a rate of at least once per 100 hours of observation and must be performed by at least three individuals; to qualify as “absent,” the behavior must never have been seen, and the group must have been observed for at least 250 hours. (b) *Expansion*: The behavior must exhibit an expansion in the number of performers over time (unless all group members perform it). Ideally, we tried to document more than two links in a social transmission chain, but because methodological difficulties such as gaps in observation time precluded the use of such a stringent criterion in many cases we also allowed behaviors to qualify if there was simply an increase in the number of performers over time. (c) *Durability*: The behavior must be durable. We arbitrarily coded behaviors as durable if they were observed spanning at least a six-month period.

These criteria are ways of operationalizing traditions, rules of thumb that are designed to detect traditions with a minimum of error in a messy collection of datasets. It is possible to think of ways in which they could be violated even while the behavior qualified as a tradition according to our definition. For example, animals at all sites could conceivably learn to identify a particular species as a predator through some combination of trial-and-error learning and social transmission; this would be a true tradition, though it would violate the intergroup-variation criterion. However, in the behavioral domain of social conventions, use of the variation criterion is less likely to rule out true traditions (see discussion). It is also possible to think of ways in which some of the above criteria might be met even if social learning were not the mechanism for acquiring the trait (i.e., the behavior was not a true tradition). For example, regarding the expansion criterion, it is possible to conceive of some ecological condition that would cause an expansion in number of performers regardless of whether social learning was the mechanism for expansion; again, while this is quite possible for foraging-related behaviors, it is improbable in the domain of social conventions. The durability criterion is entirely arbitrary, as even a very short-lived “fad” can be purely the consequence of social learning. This criterion was imposed primarily to make the datasets more comparable across sites and to give some indication of whether the behavior had become a regular part of the group’s behavioral repertoire.

Previous research programs designed to detect traditions in wild populations (e.g., Whiten et al. 1999) emphasize the importance of excluding the possibility that

interpopulation genetic and/or ecological differences underlie behavioral differences between populations. We believe the genetic and ecological differences between our four study sites to be fairly trivial (see below). Furthermore, we are not convinced that this “process of elimination” approach is a necessary or sufficient means of detecting traditions in wild populations, although it is quite useful as a first step in isolating phenomena for future research. In our view (Fragaszy and Perry n.d.b) the most critical feature of a tradition is a substantial role of social influence in the acquisition of the trait by new practitioners. There may well be genetic differences between individuals (e.g., in their perceptual abilities or temperaments) that make some individuals more likely than others to exhibit particular behaviors, but as long as social influence is demonstrated to be important in the acquisition of the trait it may still qualify as a tradition.

The Study Species

Capuchin monkeys are long-lived animals, living 40+ years in captivity and having a prolonged juvenile period (Harvey, Martin, and Clutton-Brock 1987, Fragaszy, Visalberghi, and Robinson 1990, Ross 1988). Among white-faced capuchins (*Cebus capucinus*), females first give birth at about six to eight years of age (Fedigan and Perry, unpublished data), whereas males are considered sexu-

ally mature at about eight years (Freese and Oppenheimer 1981). These monkeys live in multimale, multifemale groups. Females are philopatric, whereas males migrate multiple times in their lifetime and often form “migration alliances” of two to four males that have affiliative relationships and migrate together, invading new groups and evicting some or all of the resident males (Fedigan, Rose, and Avila 1996, Fedigan 1993, Fedigan and Jack 2001). Group sizes tend to average around 17–19 individuals at Santa Rosa (SR) and Palo Verde (PV), though the study groups at Lomas Barbudal (LB) are larger (ranging from 20–37) (Fedigan, Rose, and Avila 1996, Fedigan and Jack 2001, Panger 1997, Perry, Manson, and Gros-Louis, unpublished data). Sex ratios range from 1 male to 1.2 females at PV and SR (Panger 1997, Fedigan and Jack 2001) to 1 male to 2 females at LB (Perry, Manson and Gros-Louis, unpublished data). Female-female dyads typically have the closest bonds, as measured by proximity, grooming frequencies, and reliable coalitionary aid (Perry 1996, Manson et al. 1999). The alpha male plays a central role in group politics as the preferred partner of both males and females in coalitionary aggression and the primary male recipient of females’ grooming (Perry 1997, 1998a, b). However, subordinate adult males are also active in the social life of the group and are particularly active in alloparenting and play sessions with juveniles (Perry and MacKinnon, unpublished data). Coalitionary aggression both within and between social

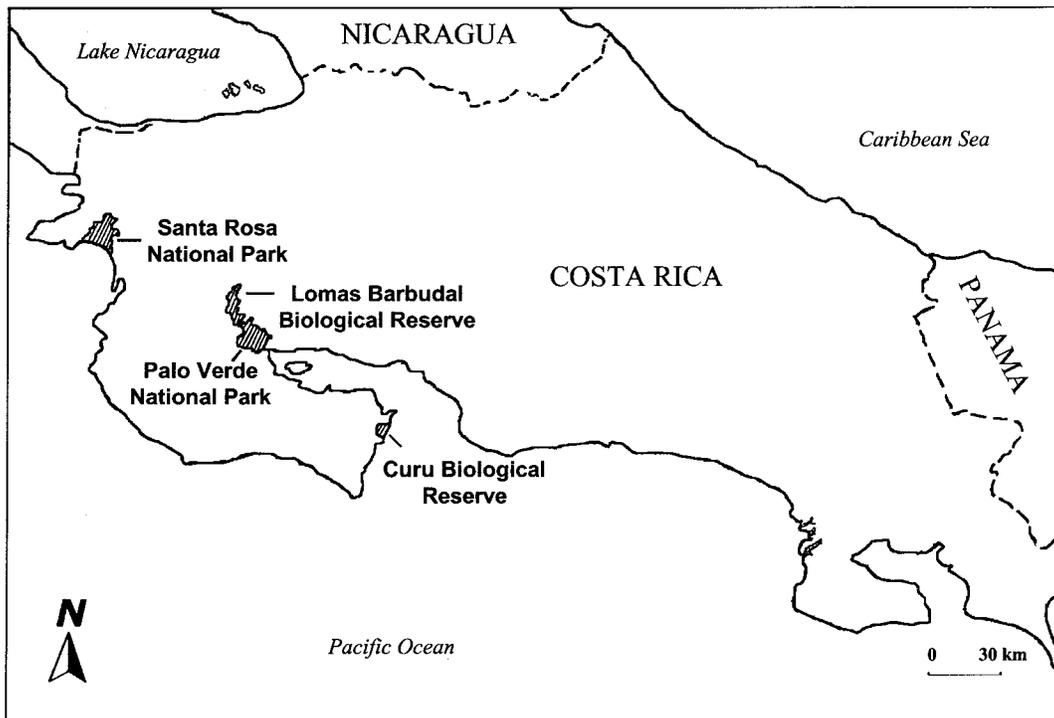


FIG. 1. Costa Rica, showing the capuchin study sites.

groups is an integral aspect of capuchin social life (Perry 1996, 1997, 1998a, b, n.d.).

The Study Sites and Databases

Data were contributed from four study sites in northwestern Costa Rica: Lomas Barbudal (LB), Santa Rosa (SR), Palo Verde (PV), and Curú (CU) (see figs. 1 and 2). All of these sites consist largely of tropical dry forest. The first three of these sites have been the subjects of many ecological studies over the past few decades, and we can say with some degree of confidence that they are ecologically very similar (Panger et al. 2002). Because deforestation has only quite recently (i.e., in the past three decades) become a problem in Costa Rica, we consider it very unlikely that there are any major genetic differences between the study populations, because there

were forest corridors connecting these sites in the recent past. In fact, forest corridors still connect LB to PV. Table 1 details the observation periods for each researcher at each study site. The number of observation hours in the table represents the number of contact hours (i.e., the number of hours that at least one observer was collecting ad lib and/or focal-animal samples [Altmann 1974]). Jack and Fedigan did not record ad lib data, so the number reported for them is the number of hours of focal samples. The total number of contact hours from which the data in this paper are drawn is 19,145 (or well over 25,000 hours of behavioral records, because there were often multiple observers collecting data simultaneously). In this paper, the study groups will be referred to by a code consisting of the site name followed by the first two letters of the group name at that site (see table 1 for the full names of each study group and site, which can be

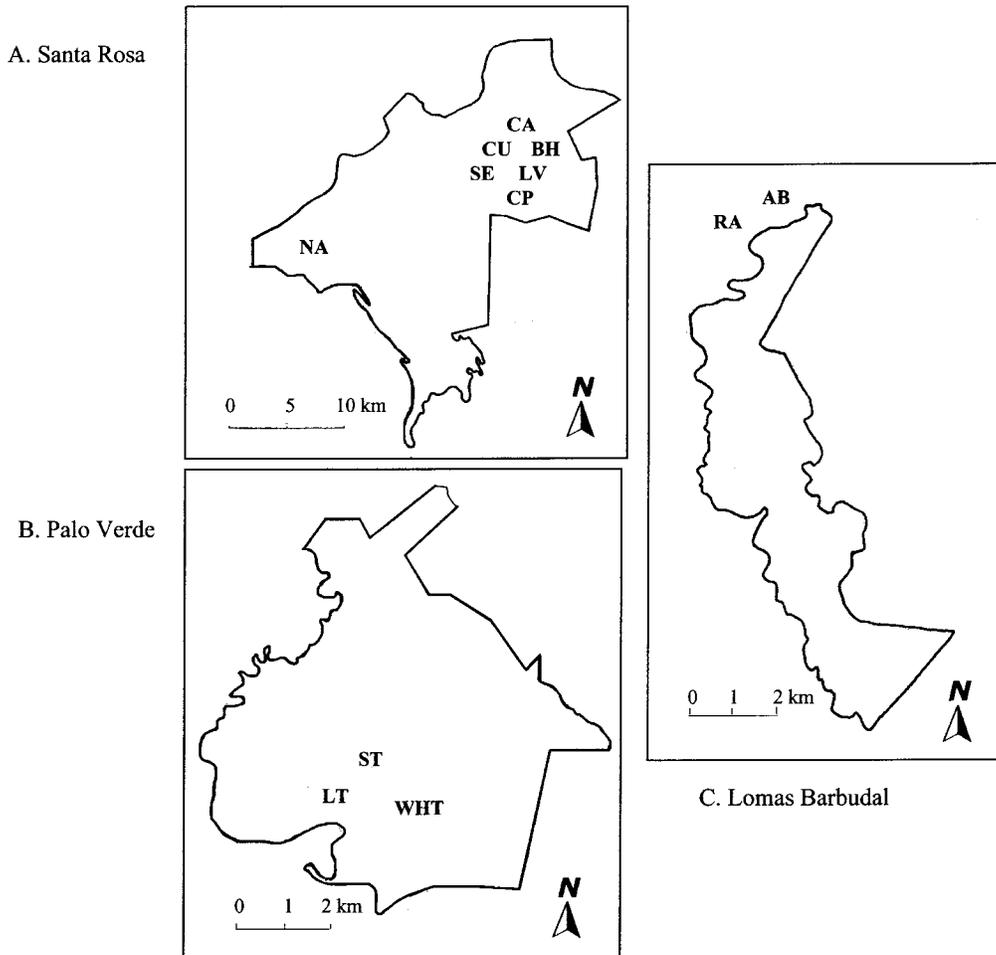


FIG. 2. Core areas of study troops. A, Santa Rosa: NA, Nancite; CA, Cafetal; BH, Bosque Humido; CU, Cuanjiquil; SE, Sendero; LV, Los Valles; B, Palo Verde: LT, Lagoon Troop; ST, Station Troop; WHT, Water Hole Troop; C, Lomas Barbudal: RA, Rambo's group; AB, Abby's group. (The latter two groups' broadly overlapping ranges extend into the northern tip of the reserve.)

TABLE 1
Periods of Data Collection on Social Behavior at Each Study Site

Site and Study Group	Time Period (months/year)	Observation Hours	Principal Investigators	
Lomas Barbudal Abby's (AB)	5-8/90	337	SP	
	5-12/91	619	SP	
	1-12/92	1,850	SP	
	1-5/93	1,234	SP	
	2/94	72	SP, JM	
	7-8/95	282	SP, JM	
	12/96	48	SP, JM	
	1-8/97	914	SP, JM, JGL	
	2-5/98	381	JGL	
	1-7/99	356	SP, JM, JGL	
	1-6/00	372	JGL	
	1-6/01	784	SP, JM	
	Rambo's (RA)	1-8/97	964	SP, JGL
		1-5/98	315	JGL
		1-7/99	759	SP, JGL, JM
		1-5/00	542	JGL
1-6/01		655	SP, JM	
Santa Rosa Sendero (SE)	1-6/86	69	LMF	
	5-9/92	10	KM	
	1-4/93	35	KM	
Cerro de Piedra (CP)	1-6/86	123	LMF	
	1-7/91	285	LR	
	5-9/92	150	KM	
	1-4/93	120	KM	
	1-9,12/95	405	LR	
	1-7/96	327	LR	
	1-12/98	471	KM, KJ	
	1-4/99	86	KJ	
Los Valles (LV)	1-7/91	260	LR	
	5-9/92	170	KM	
	1-4/93	200	KM	
	1-9,12/95	656	LR	
	1-7/96	341	LR	
	1-12/98	673	KM, KJ	
	1-4/99	133	KJ	
Nancite (NA)	12/95-6/96	408	LR	
	Cuajiniquil (CU)	2-12/98	126	KJ
		1-2/99	1	KJ
Cafetal (CA)	3-4/99	56	KJ	
	Bosque Humido (BH)	2-12/98	305	KJ
		1-4/99	131	KJ
Palo Verde Station Troop (ST)	4-12/95	852	MP	
	1/96	36	MP	
	Water Hole Troop (WHT)	3/95	84	MP
		3-7/95	228	MP
	Lagoon Troop (LT)	8-9/91	189	MB
1-6/93		692.5	MB	
7-8/94		147.5	MB	
1-4,6-9/95		665	MB	
7-9/96		226	MB	

used to link these results with information on these groups in other publications).

The study of social traditions was never the primary focus at any site. The methods of data collection varied from site to site and from year to year because the research topics varied. Panger (PV) studied handedness and object manipulation and observed members of all age-sex classes, collecting ten-minute focal-animal samples (including proximity scans at the end of each sample)

and ad lib data on rare behaviors. Baker (CU) focused on fur-rubbing in members of all age-sex classes. All of the LB researchers have studied some aspect of social behavior. Data collection consisted primarily of ten-minute focal samples of individuals of all age-sex classes during 1992-93 (Perry), 1996-2000 (Gros-Louis), and 1999 (Perry). Adult and juvenile males were the focus of study in 1996-97 (Perry), and adult females were the focus of study in 1995-97 and 1999 (Manson), whereas

adults of both sexes were followed in 1990–91 (Perry) and 2001 (Perry and Manson). Ad lib data were recorded on all odd social behaviors observed in any age-sex class throughout the course of the study, particularly when the behavior observed was not on existing ethograms. Fedigan (SR) studied social behavior in adults of both sexes. Rose (SR) collected data on social and foraging behaviors in adults and subadults. Although she spent more time in the field than is indicated in table 1, the table includes only those observation periods for which she is certain handsniffing and other odd ad lib social behaviors were reliably recorded. Jack (SR) studied social behavior in males (both adult and juvenile). MacKinnon (SR) studied social development, and most of her data consisted of ten-minute samples of immatures, though she also collected some ten-minute samples and group scans of adults. Although each researcher had a different research agenda, all of the researchers at LB, SR, and PV were in regular contact with one another from the beginnings of their studies. We made a point of collecting data on these odd behaviors (handsniffing, games, and sucking) and comparing notes on them throughout our studies, even before we had formal research plans for analyzing the data. Because of our mutual interest in these striking behaviors, we are confident that we recorded all instances of these behaviors in focal data, and we probably failed to record very few observations even in ad lib data, though our different sampling schedules may have biased observations toward some age-sex classes rather than others.

Handsniffing

Handsniffing (fig. 3) was first reported by Fedigan (1993: 861) and described as follows: "One monkey places another's hand or foot over its own face and, with eyes closed, inhales deeply and repeatedly over ≥ 1 min." This behavior has been seen at other sites as well, with some minor alterations. At LB-AB, where the behavior has been most common, one monkey takes the hand of another monkey and either covers its own nose and mouth with it, as if putting on a gas mask, or else inserts the other monkey's fingers up its own nostrils. This is often a mutual behavior, with each monkey simultaneously having the other's hand on or in its own nose. Participants will sit in this pose for up to several minutes with trancelike expressions on their faces, sometimes swaying. Grooming typically precedes and/or follows handsniffing. Sometimes the sniffers sneeze, blowing the fingers out of their noses, but they always rapidly reinsert the partner's fingers when this happens. At LB, it is always the hands, rather than the feet, that are used. One female at LB typically sniffed her own hand while inserting the fingers of her other hand up her partner's nose. In SR-CU and also in PV-ST, handsniffing was often combined with finger-sucking rather than inserting fingers up the nose. Visual images of handsniffing behavior, as well as some of the other social conventions described in this paper, can be viewed at the following

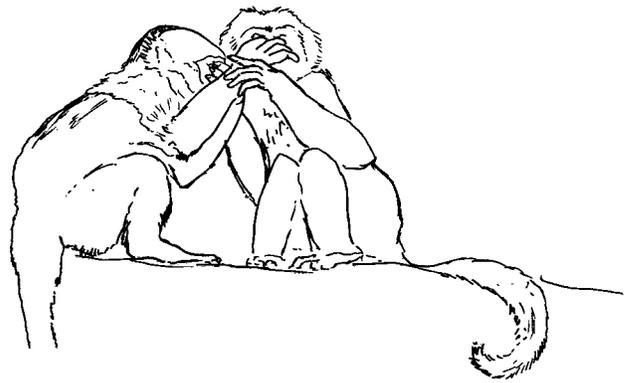


FIG. 3. *Two females handsniffing.*

web site: <http://www.sscnet.ucla.edu/o2S/anthro128a-1/cebustraditions.htm>.

The researchers who made the initial reports of handsniffing assumed that handsniffing was a species-typical behavior and speculated that some sort of olfactory communication was occurring, perhaps involving communication about reproductive states via pheromones in urine, bonding via transmission of semiochemicals (see Nicholson 1984), or information exchange about recent foraging or social activities (Fedigan 1993, Perry 1995). However, subsequent research has revealed that handsniffing is by no means a universal feature of capuchin communication. If olfactory communication is occurring along with handsniffing, then the chemical messages being conveyed are likely to be different in different groups, because the distribution of handsniffing across age-sex classes is strikingly different in different groups and at different times. For example, the pheromones transmitted by female urine would not necessarily be the same ones transmitted via male urine; also, the types of pheromonally transmitted information about conspecifics that would be useful to females are not necessarily the same pieces of information that would be interesting to males.

Table 2 details the distribution of handsniffing observations across study sites and years. Handsniffing was observed on a fairly regular basis in 5 out of 14 study groups and three out of four sites. It appears that it is not universal across study groups at any site (though data are scant for some groups at some study sites). Thus, handsniffing appears to have been invented or imported (i.e., transmitted socially by a migrant) multiple times. Once it is established, it does not remain in the repertoire permanently. The behavior disappeared for a period of several years at SR-CP before being reinvented. It may have disappeared at SR-SE as well, though there were insufficient hours of observation to confirm this. After being a frequent behavior at LB-AB for at least seven years, handsniffing vanished from the repertoire in 1998, at the time the most avid handsniffer disappeared. Although the form of handsniffing was roughly consistent

TABLE 2
Temporal Distribution of Handsniffing across Social Groups

	1986	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
SR-SE	CD ₃	—	—	xxx	xxx	—	—	—	—	—	—
SR-CP	CD ₃	—	o	xxx	xxx	—	o	RN ₁	—	CD ₃	xxx
SR-LV	—	—	o	xxx	xxx	—	o	RN ₁	—	RD ₃	o
SR-NA	—	—	—	—	—	—	—	o	—	—	—
SR-CA	—	—	—	—	—	—	—	—	—	—	xxx
SR-CU	—	—	—	—	—	—	—	—	—	CD	Cx ₁
SR-BH	—	—	—	—	—	—	—	—	—	2,4	o
LB-AB	—	o	CN ₂	CD ₄	CD ₄	Cx ₁	Cx ₃	Cx ₁	CD ₃	o	o
LB-RA ^a	—	—	—	—	—	—	—	xxx	o	o	o
PV-LT	—	—	—	—	—	—	xxx	—	—	—	—
PV-WHT	—	—	—	—	—	—	xxx	—	—	—	—
PV-ST	—	—	—	—	—	—	CD ₄	xxx	—	—	—
CU-BE	—	—	xxx	—	o	xxx	o	xxx	—	—	—

NOTE: First letter indicates frequency, second durability, number spread across social network; —, no data; xxx, some observation time but insufficient data to confirm absence (i.e., < 250 contact hours or < 100 focal hours: < 6 months); C, common (> 1 observation per 100 hours); R, rare (< 1 observation/100 hours); o, absent (no observations); D, durable (behavior observed over a 6+-month period); N, not durable; 1, only one dyad performs the behavior; 2, multiple dyads perform the behavior but all of them have one individual in common; 3, multiple dyads perform the behavior; 4, all members of at least one age-sex class perform the behavior.
^aThere were anecdotal observations of handsniffing in LB-RA in 2000.

across sites, the distribution of handsniffing across age-sex classes is strikingly different across study groups. Thus, it is worthwhile to describe the direction and distribution of handsniffing among males and females for each site (table 3), particularly in light of previously proposed hypotheses regarding the possible olfactory functions of handsniffing. Handsniffing was exhibited almost exclusively by female-female dyads at LB-AB, the site where it was most common, whereas it was seen exclusively in male-male and male-female dyads at SR-SE, SR-CU, and PV-ST.

Further information on the form, rate, and distribution of handsniffing across social networks can be summarized as follows: (a) the precise form of handsniffing varied somewhat from site to site; (b) the successful propagation of handsniffing seemed to depend very much on the social characteristics of its practitioners (e.g., age, sex, rank, position in a social network), and handsniffing vanished from the repertoire when key handsniffers vanished; and (c) in those groups for which datasets permitted analysis, handsniffing was associated with fre-

quent proximity and grooming (for details, see the electronic edition of this issue on the journal's web page).

Handsniffing met all of the criteria for a tradition. It was common in five groups, rare in two, and completely absent in six groups (three of which were observed for a sufficient amount of time to be confident that the behavioral repertoire was adequately sampled). For two of these groups, it was possible to document an expansion of the number of performers over time. The behavior was durable in six groups.

Sucking of Body Parts

In some groups, pairs of monkeys were observed to spend long periods of time sucking on one another's fingers, toes, ears, or tails. This behavior was similar to handsniffing with regard to its social context in that it occurred in relaxed social contexts, such as resting in contact or grooming, while pairs of monkeys were fairly isolated from the rest of the group. Sucking was partic-

TABLE 3
Distribution of Handsniffing (percentage) across Sex Classes

Group	Male Sniffs Male	Male Sniffs Female	Female Sniffs Male	Female Sniffs Female	N ^a
LB-AB	< 1	< 1	2	96	168
SR-SE	71	14	14	0	7
SR-CP 1986	86	10	0	5	21
SR-CP 1996-99	0	0	75	25	16
SR-CU	64	27	9	0	10
PV-ST ^b	33	50	33	0	12

^aTotal number of handsniffing observations in the sample.

^bTotal exceeds 100% because some of these male-female bouts are mutual.

ularly prevalent at LB-RA, where it was often a mutual activity that could last for over an hour at a time. Of 34 observations of this behavior spanning a six-month field season, over half involved mutual sucking. This activity was equally common in male-male and male-female dyads but was not seen in female-female dyads. The vast majority of the observations involved a particular young adult male. Sucking virtually vanished from the group's behavioral repertoire when this male disappeared in July 1997.

On rare occasions, tail-sucking was observed at LB-AB as well. Virtually all of it involved a single adult male, Guapo. In 1990–96, Guapo's tail-sucking behavior was unreciprocated and seemed to function as a way for him to invite grooming. In 1997 he began to engage in mutual tail-sucking with a new immigrant male, Hongo. As far as we know, *mutual* sucking of body parts has not been observed at sites other than LB.

Finger-sucking has been observed in some of the SR groups and generally conforms to the same patterns seen for handsniffing in these groups. In SR-CU, a pair of males that migrated together between SR-LV, SR-CU, and SR-CA often engaged in both finger-sucking and handsniffing, sometimes combining them in the same interaction. Finger-sucking was observed once at SR-CP. Occasionally it was observed at CU-BE in the context of playing the "toy" game (see below).

Sucking, therefore, met only two of the criteria for a tradition. It was common only in two groups and seen occasionally in three more in slightly different contexts. It was durable at all sites where it was observed. However, documentation of the expansion in the number of performers for sucking was difficult, because we are not sure exactly when the behavior entered the repertoire and how individuals' acquisitions of the behavior coincided with the timing of field seasons. There was no marked expansion of number of performers during observation periods.

Games

What we will refer to as "games," because they are often initiated in a play context, differ from rough-and-tumble play in being more relaxed and quiet. They are dyadic, and the pair performing the behavior tends to be on the periphery of the group, often during a group siesta. Games are typically preceded by either slow-motion wrestling or grooming, particularly of the mouth and face. With one exception (the "toy" game, which is played at CU-BE as well), games are found exclusively at LB-AB. Circumstantial evidence suggests that all of the games at LB-AB may have been transmitted initially by a single individual, Guapo. When the study began in 1990, Guapo was a young adult male, probably about 8–10 years of age judging from his size. He was a subordinate male for most of 1990–99; he was alpha male for a few days in 1998 and became alpha male on a more permanent basis in 1999, until he disappeared from the group toward the end of the year 2000. Guapo was the

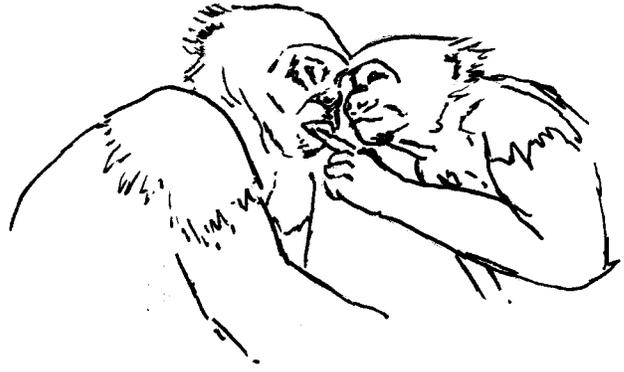


FIG. 4. *Guapo and a juvenile playing the finger-in-mouth game.*

first individual observed to play each of these games and also the most frequent game player, especially in the early years of observation. Aside from Guapo, the most frequent participants in games were juvenile males, but some games were also played by adult females. The group size for most of the study of LB-AB was approximately 21 individuals (ranging in size from 17 to 31), and each game was played by 10–13 individuals.

The most commonly observed game was the finger-in-mouth game (fig. 4), which was first observed in November 1991. In this game, monkey A puts its finger in monkey B's mouth—this can start in the context of grooming the inside of the mouth. Monkey B clamps down on A's fingers, apparently not enough to hurt but hard enough that A cannot readily remove its fingers. Monkey A goes through various contortions to extract its finger—this may involve using both hands and feet to pry open B's mouth or putting the feet on B's face for leverage while pulling hard on the captured hand. Once A's finger has been successfully extracted, either A reinserts its hand in B's mouth for another bout of the game or B inserts its fingers in A's mouth so that the game continues with the roles reversed.

Most dyads observed to play this game included Guapo. Prior to 1993 all 30 finger-in-mouth games observed involved Guapo. In 1993 others began to play without Guapo, and in the last three field seasons approximately half of the dyads observed to play this game did not involve him. Figure 5 shows the social transmission pathways (i.e., social transmission chains) for the finger-in-mouth game. In this figure, arrows designate the probable transfer of the convention from one individual to another. Most of the females acquired the game as adults, whereas the males were all juveniles when they acquired it from Guapo. Aside from one possible instance involving two juvenile males, we never observed this game in neighboring LB-RA. This game was still being played in 1999, and a less elaborate form of the game was seen in two dyads in 2000. The dyads that played together after Guapo's withdrawal from game

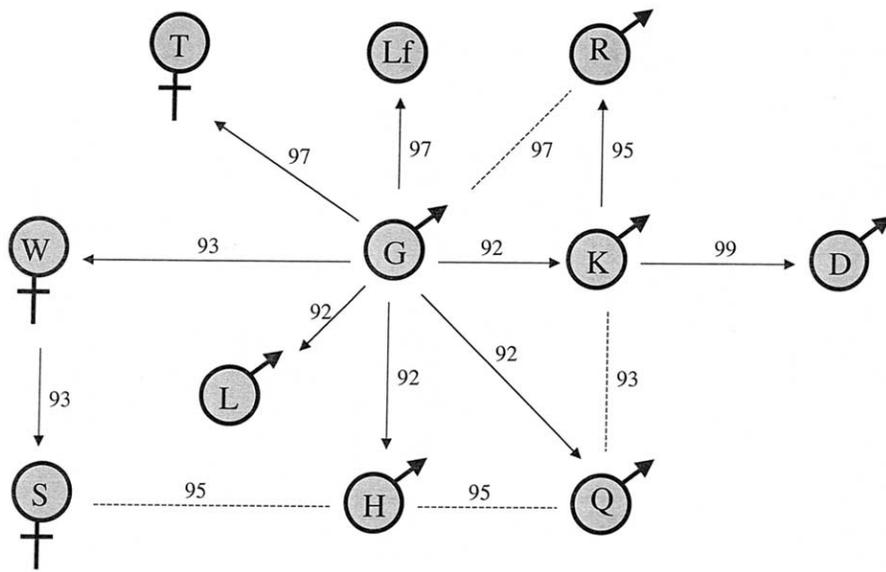


FIG. 5. Social transmission chain for the finger-in-mouth game. Arrows indicate the presumed direction of social transmission. The letters inside the male/female symbols indicate the names of the individuals. Solid arrows indicate dyads in which one member has never previously been seen to play with other partners; dotted lines indicate dyads in which both members have previously played with other partners. Numbers indicate the year in which the game was first played by that dyad.

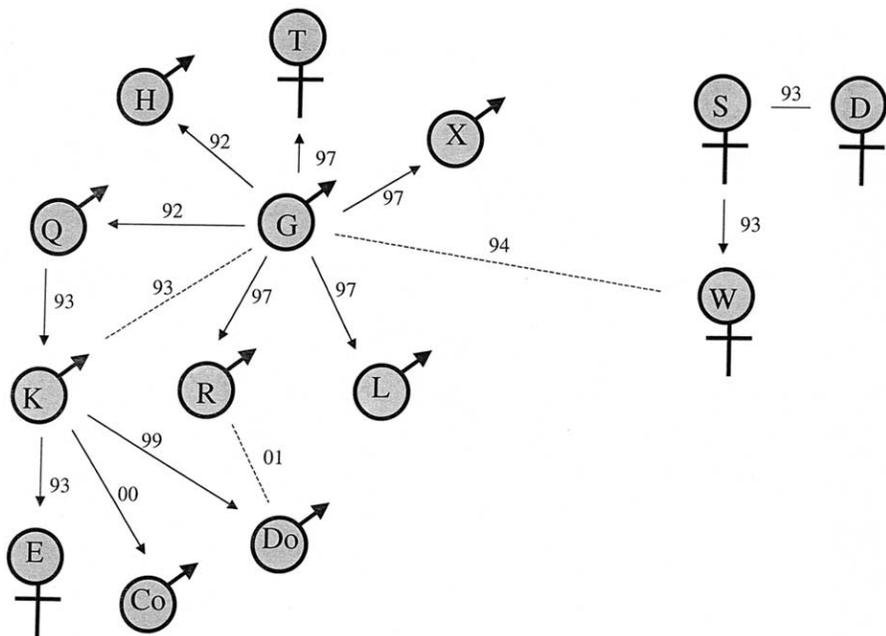


FIG. 6. Social transmission chain for the hair-passing game. X, a juvenile that was unnamed at the time of the observation.

TABLE 4
Number of Individuals Observed to Play Each Role in the Games

	Seen Playing Mouth Role	Seen Playing Retriever Role	Overlap between Mouth and Retriever Role	Mouth Role Remaining When Game Last Played	Retriever Role Remaining When Game Last Played	Overlap between Mouth and Retriever Categories in 1999–2000
Finger-in-mouth game	8	8	7	4	4	4
Hair-passing game	7	9	5	3	5	2
Toy game	8	13	8	3	3	3

alpha male in 1999; nor were any previous alpha males of LB-AB observed playing games.

Baker has observed a slightly modified version of the toy game at CU-BE. She describes the game as follows: Monkey A sits by monkey B, picks up some object (a piece of bark, leaf, or fruit), and places it in its own mouth, leaving the lips slightly parted. Monkey B then uses its fingers and/or mouth to attempt to remove the object from A's mouth. They may hold hands, or B may leave its fingers in A's mouth. Monkey A sometimes holds B's hand to prevent transfer of the object. If B successfully removes the object, A may try to regain it and reinsert it in its mouth. During this game, the monkeys do not make eye contact but stare off into the distance as if in a daze. Following this game, the monkeys often groom or remain in contact for several minutes with B's fingers in A's mouth. This behavior was first observed in 1993, and it was still part of the group's behavioral repertoire in 1996. Thirty-eight observations of the behavior were made over a period of four years (1,920 contact hours). Seventeen of these involved juveniles of unknown sexes, but of the remaining 21 observations 3 occurred in female-female dyads and 18 involved male-male dyads; all of these observations involved at least one adult. Thus, the game was never observed to be played in opposite-sexed dyads. At least 16 different dyads and 14 identifiable individuals (plus some unidentified juveniles) were observed to play the game. The group included 20 adults and 14 juveniles, so approximately half of all group members exhibited the behavior. The temporal patterning of the behavior across dyads suggested that the behavior had been a part of the repertoire well before the 1993 field season began; diverse dyads exhibited the behavior in 1993, and the number of dyads did not increase dramatically over the course of the study.

One of the most intriguing aspects of the games was the fact that there were two distinct roles in these conventions. Because the fact that there are two roles could be relevant to the transmission dynamics of the behavior, we decided to investigate the connection between role playing and group demography at the time the games vanished from the repertoire. Guapo was the most frequent player of all three games, and the rate at which they were played dropped precipitously when he became alpha male and stopped playing. Perhaps the failure of games to thrive after Guapo's withdrawal was due to the fact that the remaining players did not know how to

perform both roles. Povinelli, Parks, and Novak (1992) have demonstrated experimentally that role reversal is a challenging cognitive feat for rhesus monkeys, so it seems reasonable to think that capuchins might also have difficulty learning both roles. Role reversals were common within bouts for some games (27% in the finger-in-mouth game, 48% in the toy game) but relatively uncommon in the hair-passing game (3%). We will refer to the "mouth" role as the role (common to all games) in which the monkey holds the object (finger, hair, or toy) in its mouth and the "retriever" role as the role in which the monkey is trying to remove the object from the mouth. The finger-in-mouth game can be initiated by a monkey playing either the mouth role (by biting the partner's fingers) or the retriever role (by inserting the fingers in the partner's mouth), whereas for the other games the monkey playing the mouth role is the initiator. Table 4 shows the number of monkeys observed to play each role in the three games. The lefthand columns show the number of monkeys observed in each role over the entire study period; the righthand columns show the number of game-playing monkeys who were still residing in the group in 1999, when games were last observed (excluding Guapo, who ceased to play games when he assumed alpha rank), or in 2000 in the case of the hair-passing game. Therefore, although only a few individuals definitely knew both roles by the time the game-playing traditions were extinguished, there were at least two per role for each game, and therefore the disappearance of the games from the repertoire cannot be attributed entirely to a lack of practitioners of a particular role.

At LB-AB, the most frequent game-playing pairs were adult male–juvenile male dyads. Dyads that played one game tended to play other games as well (for details see the electronic edition of this issue on the journal's web page). During the 1991–93 field seasons (for which the richest behavioral data are available), there was a slight tendency for game-playing individuals to spend more time in close proximity to their game-playing partners than to individuals who did not play games with them (Wilcoxon: $n = 12$, 1.3% time with partners vs. 0.8% time with nonpartners, $T = 18$, $p < 0.10$).

The games meet all of the criteria for a tradition. Two of the games were observed only in a single group, and one was found in two groups at different sites. All games were common (at least during some field seasons) and durable, remaining in the repertoire for several years, and for LB-AB it was possible to document a clear expansion

in the number of performers and to infer that there were two or three links in the transmission chain over the years.

Discussion

As McGrew (2001:235) notes, most interdisciplinary discussions of the evolution of culture center around three approaches: (1) Anthropologists most often ask “*What is culture?*” (which I interpret as meaning “Can we demonstrate the presence of social traditions in a given population?”) (2) Evolutionary biologists ask “*Why is culture?*”—in other words, What is the biological significance of culture? What are the fitness consequences to individuals exhibiting cultural traits? And why is it more effective to have such practices transmitted socially rather than genetically? And (3) Psychologists tend to ask “*How are cultural elements acquired and transmitted?*” This latter question is too difficult to address with any great sophistication using the methods available in field studies of primates, but we will address the other two.

Several behaviors met our criteria for a tradition in capuchins. Whether these collections of traditions qualify as “culture” depends on one’s definition of culture. The most commonly used definition of culture in cultural primatology is McGrew’s (1992:304) adaptation of Kroeber’s (1928:331) definition. The capuchin data qualify according to the first three criteria of this definition (i.e., innovation, transmission, and consistency of form), but the latter three criteria (durability, vertical transmission, and spread across social units) are somewhat more questionable. Thus, the temporal and geographic distribution of social conventions merits further discussion here.

How durable are capuchin social conventions? Some of these traditions (the games) have lasted for as long as ten years and have spanned at least one genetic generation and three links in a social transmission chain. Nonetheless, one of the most remarkable things about this dataset is the number of apparent extinctions of traditions that have been observed in a relatively short time. Handsniffing died out after seven years at LB-AB. It died out at SR-CP (reappearing several years later) and also appears to have vanished from SR-SE. Sucking vanished from both LB-RA and LB-AB. It appears likely that the three games have basically vanished from LB-AB after nine or ten years, since they were observed very rarely in 1999–2001.

Why do such traditions become extinct so quickly in capuchins? The LB data suggest two possibilities: demographic instability in small groups and, to a far lesser extent, the difficulty of preserving traditions that require an understanding of two roles. The extinction of handsniffing at LB-AB is particularly mysterious because it was a high-frequency behavior, practiced by all adult females in the group. The decline and disappearance of handsniffing may be in part due to the presumed deaths of two avid handsniffers. Sucking was most common at

LB-RA, but a single individual was a participant in 88% of all sucking bouts, despite the fact that 12 other monkeys participated in sucking and 10 of those took active roles. Sucking has been seen only three times in the three years since the primary sucker’s disappearance. Game playing declined precipitously when the presumed inventor became alpha male and stopped playing. Additionally, there was a drop in the number of players who knew both roles (though there were still two to five individuals remaining in the group who definitely knew each role for each game at the time the games became extinct). Thus, for all of the social conventions, it appears that the disappearance of particularly enthusiastic practitioners of a behavior can cause it to vanish from a group’s repertoire even when several other members of the group know how to perform it. Traditions such as these are particularly fragile in small groups. Demographic changes such as migrations, deaths, and rank reversals pose a major challenge to the stability of traditions in small groups. If traditions are so readily disrupted by demographic changes even in capuchins, which have quite low mortality rates (Fedigan, Rose, and Avila 1996) and fairly stable group compositions and dominance hierarchies, it seems likely that they would be even less durable in more demographically fragile species.

Why is it that some of these behaviors have appeared at multiple sites when there appears to be no migration between sites today? The geographic patterning of handsniffing is difficult to account for. Handsniffing may be common in one group and completely absent in another group with a broadly overlapping home range. This fact makes social transmission seem fairly likely and allows ecological differences to be readily ruled out. Yet handsniffing is observed in some groups at three different sites for which social transmission via migration is implausible, which suggests the possibility of independent invention at each site.

Comparison of the social contexts (i.e., distribution across age-sex classes) in which handsniffing occurs reveals extreme differences between groups and also differences over time (at SR-CP, for example, handsniffing was observed primarily in male-male dyads in 1986 but primarily in male-female and female-female dyads in 1998). It is possible that the suites of behaviors we are calling handsniffing and sucking conveyed different social messages in different groups and at different periods of each group’s history. It seems likely that handsniffing was independently invented at a number of sites. The behavioral elements that make up handsniffing (e.g., putting a hand over the nose and mouth, inhaling, sticking a finger up the nose or in the mouth) are already in the behavioral repertoire in slightly different forms and therefore readily occur to monkeys (see Huffman and Hirata n.d. for similar reasoning regarding the appearance of similar traditions at multiple Japanese macaque sites). For example, capuchins routinely stick their fingers into small holes in the context of extractive foraging for insects, and so sticking a finger into another monkey’s nostril or mouth probably does not involve a big mental

leap. Likewise, the task of removing a finger, toy, or hair from someone else's mouth involves basically the same motor skills (prying, digging, pulling, probing) that are routinely performed in the course of extractive foraging. The restrained biting seen in the games is similar to that seen in play bouts except that it is of much longer duration. Thus, any particular element of these odd behavioral patterns is something that would readily occur to a capuchin; all that the monkeys need to do is to assemble these elements into chains and induce other individuals to cooperate in the details of performance (e.g., agree on which parts of the bodies should be involved, decide which roles to play when). With our current dataset, we cannot rigorously address the question of which social learning processes lead to the construction of these social conventions, but the most likely scenario is that they come about via a process akin to "ontogenetic ritualization" (*sensu* Tomasello and Call 1997:301; Tomasello et al. 1997; Boesch and Tomasello 1998), in which the two participants shape one another's behavior during the course of repeated interaction rather than one animal's being the model and the other the learner. Because there are rarely if ever third parties in the immediate vicinity when these social conventions are performed, it seems unlikely that social learning mechanisms requiring imitation after observation (as opposed to direct interaction) would be very effective. In chimpanzees gestural signals have been found to be not readily learned via imitation; ontogenetic ritualization is far more effective (Tomasello et al. 1997).

What is the function of these behaviors? To an evolutionary biologist attempting to assess the biological significance of social traditions, the first order of business is to determine the function of the traits. What are their probable fitness consequences, and why is it more effective for the trait to be transmitted socially rather than genetically? As noted above, it is possible that each tradition described has a different function—that the behaviors involved convey different meanings to the monkeys performing and witnessing them. However, all of the behaviors described here have certain features in common, which may suggest that they are "designed" to communicate similar messages. All of these behaviors occur in relaxed social contexts, in which the participants are typically somewhat isolated from the rest of the group (perhaps not visually isolated but at least a few meters from neighboring monkeys). The participants move slowly (which is highly unusual for a capuchin) and have trancelike expressions on their faces, staring out into space or else looking at their fingers (as in the retriever role of the games). Perhaps the most noteworthy feature that they have in common is that all of them involve a certain amount of risk or discomfort to one or both participants. Handsniffers have one another's fingernails delicately lodged in their nostrils, which restricts their movement; tail-sucking and the finger-in-mouth game involve placing a body part between the sharp teeth of the partner (since many capuchins are missing digits and tail tips, it is reasonable to assume that this is risky); the hair-passing game involves yank-

ing significant amounts of hair out of the face and shoulders, which cannot be very comfortable. Perhaps these conventions are ways of testing the bonds between individuals, in the same sense in which male savanna baboon "diddling" has been proposed to test bonds between coalition partners (Smuts and Watanabe 1990).

Zahavi (1977) proposed that stressful stimuli are often imposed by one individual (A) on another (B) in order to test the strength of A and B's social bond. The stressful signal is typically something that has a strong sensual component that is perceived by B to be pleasant if the bond is strong or unpleasant if the relationship is not good. Examples of such a signal would be a French kiss, a child's using an adult as a climbing toy, or a capuchin's sticking its fingers up a conspecific's nose. B's response to A's signal conveys useful information to A about the quality of the relationship: If B tolerates the stressor or responds positively to it, then this indicates to A that B is positively disposed to A and presumably likely to be supportive (e.g., when asked for aid in the near future, though this is only one type of possible benefit). If B responds negatively, for example, by ignoring A, terminating the interaction, or responding aggressively, then this indicates to A that B is not currently positively disposed toward A and is unlikely to be a reliable source of benefits in the near future. The forms of the handsniffing, sucking, and game-playing behaviors make them ideally suited to be Zahavian bond-testing signals. In order to test whether this model is applicable to the behavioral phenomena we are trying to explain, it would be necessary to have more precise data on the initiations and terminations of each interaction, baseline data on the quality of each dyad's relationship, and data on the dyad's interactions for a few hours following the interaction. Regrettably, our datasets do not allow us to test this hypothesis, because they were designed to answer quite different questions.

Do the culturally variable social signals described for chimpanzees and Japanese macaques exhibit any parallels to capuchin social conventions that conform to this Zahavian bond-testing hypothesis? One possibility comes to mind: hand-clasp grooming in chimpanzees (McGrew et al. 2001, de Waal and Seres 1997). This is a dyadic behavior in which both participants are focused on grooming one another with one hand while their other hands are clasped or propping one another up with their arms extended above their heads. One of the most intriguing aspects of the patterning of hand-clasp grooming at Mahale is that it is always the subordinate individual who is supporting the weight of the dominant's arm (McGrew et al. 2001). It is not clear from the published literature who initiates these interactions, but it is possible that the dominant is using hand-clasps as a test of the bond—by imposing the weight of his arm upon the subordinate he is testing the subordinate's acknowledgment of his higher rank and his willingness to provide continued political support. Such rank asymmetries are not apparent in capuchin social conventions, perhaps because capuchins are less obsessed with rank than chimpanzees (and particularly male chimpanzees) are.

Whereas chimpanzees regularly remind one another of their ranks via formalized dominance signals (e.g., the pant grunt, which acknowledges higher rank in the receiver of the signal [de Waal 1982:87]), capuchins do not so clearly advertise rank.

Another body of theory that has potential relevance to explaining social conventions comes from microsociology. Collins (1981, 1993) has proposed that "interaction rituals" (e.g., human conversations, though virtually any type of social interaction would qualify) inform the participants about the status of their relationship with other participants in the interaction. He assumes that because group-living individuals lack the computational capacity to assess their relative competitive ability or their place in the constantly fluctuating power structure of the group directly, they rely on the emotions generated in interaction rituals in order to estimate these variables. The form or content of the interaction ritual is generally not as important as the emotions and corresponding affective displays that are generated from them. For example, in terms of the interaction's effect on the quality of that dyad's future interactions, it does not matter whether the content of a conversation was the relative merits of particular football teams or the weather; nor does it matter whether the information conveyed is true. What matters is the amount of enthusiasm, engagement, and coordination/agreement between the human conversational partners; this is what informs them about their willingness to cooperate reliably with one another in the near future. Likewise, it may not be terribly important whether a capuchin sticks its fingers up its partner's nose or in its mouth as long as they agree that this is the right thing to do. The real information in the signal comes from the affective responses of the two partners. On the basis of Collins's theory, we would predict that the following variables will be positively associated with a dyad's willingness to cooperate in future interactions: duration of the current signaling interaction, degree of focus or concentration on the interaction, and extent of coordination between the participants (i.e., agreement about what elements should be included in the task and who should play which role at any given time). Again, our data collection protocols did not allow such tests of this model, but future research can perhaps be designed with these questions in mind. Collins's and Zahavi's models make some similar predictions about the relevant qualities of bond-testing interactions. In both types of signals, the affect of the signal recipient, which tells the signaler about the current state of the social relationship, is the most critical information. In Zahavi's model, the costliness of the signal (i.e., degree of risk or discomfort to the recipient) is its most salient feature, whereas in Collins's model the degree of coordination and focus in the interaction is the most critical feature.

What is the phylogenetic distribution of bond-testing social conventions, and why? Another angle to consider when discussing the function of the social conventions that are the subject of this paper is why similar behaviors have not often been observed in other primates. What is

remarkable about the invention of these behaviors is not the motor patterns they exhibit (which, as we note above, are present in other domains of the capuchin behavioral repertoire) but the extent to which they are coordinated between individuals. Turn taking is quite rare in non-human primates (aside from the contexts of grooming and rough-and-tumble play in some species), and the role switching, particularly in the games (which involve the assumption of some fairly novel roles, unlike the more stereotyped behaviors exhibited in grooming and most rough-and-tumble play), may require cognitive skills that are lacking or poorly developed in many other primates (e.g., Povinelli, Parks, and Novak 1992). To our knowledge, interactions involving role switching are rare in primates, and thus it is worthwhile to ask why such interactions should appear in capuchins but not others. One possibility is that such coordinated interactions provide practice for dyads that need to engage in cooperative activities involving complex motor coordination. One such domain of cooperation might be aggressive coalitions, which are extremely common in capuchins relative to most other primate species. For example, 23% of conflicts were polyadic during the LB 1997 field season, though at some points in a particular group's history the rate of polyadic conflicts has been as high as 65% (Perry, unpublished data). To put this in comparative perspective, 24% of macaque conflicts are polyadic, 40% of chimpanzee conflicts are polyadic (de Waal and Harcourt 1992), and intragroup coalitionary conflict is essentially absent in the published literature for New World primates outside the genus *Cebus*. Intragroup coalitionary conflicts are common both within and between groups, and capuchins also cooperate in defense against predators and feeding competitors (Perry n.d.). Cooperation has also been documented in tasks requiring motor coordination in captive *C. apella* (de Waal and Berger 2000). If it is the case that turn-taking games in wild capuchins provide practice for future cooperative behaviors, then we might expect to find social interactions incorporating role switching in other species that routinely engage in coalitionary aggression, such as baboons, chimpanzees, macaques, and bottle-nosed dolphins (Harcourt and de Waal 1992). Another domain in which coordination and role reversal might be important is cooperative hunting, as seen in chimpanzees (Boesch 1994a, b; cf. Stanford 1995, 1998; Stanford et al. 1994), social carnivores (e.g., Packer and Ruttan 1988, Scheel and Packer 1991, Stander 1992, Kruuk and Turner 1967, Nel 1999), cetaceans (Boran and Heimlich 1999), and perhaps capuchins under very limited circumstances (Rose 1997). This sort of information is difficult to pull out of the published literature, but some papers suggest that there is an element of turn taking and role reversal in baboon greetings, which have been suggested to function as communication about future cooperation in coalitionary aggression for the purpose of consort takeovers (Smuts and Watanabe 1990).

Yet another domain in which cooperation and coordination of actions is important is parental care, for monogamous species. Many monogamous species, includ-

ing many birds and also monogamous primates, engage in some form of duetting or joint ritualized display, which occurs not just during courtship but also at many other times once the pair bond has been formed (see review by Wachtmeister 2001). At least in some of these species there is considerable complexity, as well as interpair variation, in the details of the duetting behavior (Wickler 1980). It has often been proposed (see Wachtmeister 2001 for a history of the debate) that duets and other forms of display in monogamous pairs aid in pair bonding, though the evolutionary logic of why the behavior should strengthen bonds is typically unclear in these models. Perhaps such displays, rather than strengthening the bond, merely provide current information about commitment within the pair, which may then aid the individuals in deciding whether to invest more or less in the relationship. If so, then the degree of synchrony and intensity of display should predict the loyalty of the pair when subsequently provided with opportunities for one partner to desert a mate in favor of another. It might also be expected that the frequencies of such displays would be higher when the pair is in need of information, for example, after separations when one pair member has had opportunities to interact with other individuals out of view of the other.

What design features would be optimal for signals used to test social bonds and practice coordination? If there are indeed signals that function to provide social partners with (a) practice in coordinating their actions or (b) information about emotional engagement/commitment as indicated by the attention they pay to coordination in a conventional social interaction, the following design features may be optimal for such signals: (1) More complex behavioral sequences will be preferable to simple ones because they will require more concentration and coordination between partners, thus providing them with more practice and more information about emotional engagement. (2) Interactions that involve turn taking and/or role reversal will require more coordination than interactions in which both members have the same role and perform it simultaneously. (3) Signals that are flexible and individually idiosyncratic in their form, rather than rigidly stereotyped, will require more concentration and coordination; partners will have to familiarize themselves with one another's quirks and adjust their own behavior slightly to produce an interaction that is mutually satisfying. Taking the time to do this will provide the partners with coordination practice and simultaneously provide them with the information that there is mutual interest in interacting. It is easy to see how mutual adjustments of idiosyncratic behaviors might eventually produce social traditions in social conventions among networks of individuals that regularly engage in cooperative activities.

It is important to emphasize that flexible, idiosyncratic signals are expected to emerge only in dyads that are already somewhat familiar with one another and have some degree of trust and predictability. Such flexible signals will not be optimal for negotiation of relationships in dyads that are in the initial stages of rela-

tionship formation, when the participants are uncertain of one another's fighting ability, tendency toward aggression, etc. Most species that have cooperative long-term relationships already have some more stereotyped signals (e.g., grooming, various vocal signals, nonconceptive sex) for communicating about the status of their social relationships and about their intentions in the near future. Stereotyped signals are easier to interpret than more flexible ones and therefore more valuable/reliable for interpreting the intentions of social partners among dyads that are just becoming acquainted. Flexible signals like the ones described in this paper may provide richer information about the cooperative potential of a dyad, but they will be too costly to use in the early stages of relationship formation because of the potential for misinterpretation.

How might functional hypotheses for capuchin social conventions be tested? Current data-sets are inadequate to test these hypotheses about the functions of traditional social conventions in capuchins in any sophisticated way. However, there is some weak evidence that such behaviors are performed among dyads that have fairly solid social bonds: game players spent slightly more time with their game-playing partners than with other animals, and handsniffing rates were correlated with grooming rates at LB (Perry 1996). If game playing is associated with the development or testing of cooperative relationships, we might expect an increase in game playing during periods of social instability or just prior to rank reversals, when monkeys need allies the most. The rates of game playing at LB-AB (as crudely measured by number of ad libitum observations per hour of contact with the group) varied from year to year. In the first phase of the project (1991-92), group membership was completely stable, and there were no rank reversals. During this phase, games were played at a rate of 1.8 bouts per 100 hours. During the six months following a rank reversal and male immigration, there was tremendous social upheaval accompanied by heightened rates of both aggression and affiliation (Perry 1998b); during this phase, the game-playing rate was 2.7 bouts/100 hours. In the 1997 field season, there was no social upheaval (though the alpha male was unpopular and was killed by his groupmates—including some of Guapo's game-playing partners—the following year [Gros-Louis, unpublished data]); during this season, games were played at a rate of 3.3 bouts/100 hours. Group membership and ranks were stable in the 1999 field season, when Guapo was alpha male, and then game playing occurred at a rate of 1.0 bout/100 hours. These data are quite difficult to interpret because of the challenges involved in operationalizing social instability and accurately estimating rates of rarely performed behaviors and because of the numerous confounding factors, but it is possible that games are played more frequently in periods of social upheaval (or just preceding major social upheaval). It is also worth noting that the only four game players to continue game playing after Guapo's withdrawal subsequently emigrated together and continued to play games in an all-male group. Also, finger-sucking (another

putative bond-testing signal) was exceedingly common in the pair of males at SR that migrated from group to group together. Given the high risks associated with migration and takeovers of new groups, it is likely that males who choose to migrate together have fairly solid bonds. No doubt even those members of male-male dyads that feel comfortable with one another will need to test their bonds frequently as the males stage takeovers of new groups because of the potential for shifting alliances in the new social context.

To summarize our working hypothesis about the probable function of the interactions described in this paper: We suspect that such interactions share the function of negotiating the status of social relationships. This may take the form of practicing coordination and/or using the interactions to obtain information about partners' current disposition toward one another. The precise motor details of the interactions are expected to be arbitrary and variable between groups or social networks; the utility of these interactions is in the coordination of behavioral elements between partners. Because such interactions have their origins in individually idiosyncratic behaviors, which are presumably modified over the course of time by coordination with other individuals who are members of a social network, traditions are expected to emerge. Because the motor details are fairly arbitrary, the precise form of these traditions is not expected to be particularly stable, and traditions of this sort are expected to dissolve (or be replaced by similar traditions) when key individuals vanish, causing disruption of social networks. If our hypothesis is correct, then we might expect to find similar traditions in other species that have well-developed cooperative relationships and signals that are apparently designed to communicate about these relationships.

Is the durability of a tradition necessarily a good indicator of its biological significance? When thinking about the biological importance of traditions, it is important to maintain a conceptual distinction between the behavior itself and the psychological machinery that is responsible for producing it. Not all behaviors that are culturally transmitted are necessarily fitness-enhancing (Richerson and Boyd 1989, Boyd and Richerson 1992); nonetheless, the psychological machinery enabling social learning (possibly including particular perceptual skills, emotional proclivities facilitating close associations with others and attentiveness to conspecifics' actions, and perhaps imitative abilities) will be adaptive even if it sometimes causes animals to acquire maladaptive behaviors as long as its net effect is to enable acquisition of fitness-enhancing behaviors. One issue that has long persisted in the study of culture in non-humans (see, e.g., McGrew 1992) is whether the longevity of a social tradition is correlated with its biological importance. Some scholars would insist that vertical transmission (i.e., transmission across generations) is an essential feature of culture and that behaviors remaining in a population's behavioral repertoire for shorter time periods are of lesser biological significance and should be denied the label of "culture" or "tradition" and re-

labeled "fad." I will leave aside the question of labels for the moment and address the question of biological importance. For most evolutionary biologists, the biological importance of a trait is measured in terms of fitness consequences for the individual bearing the trait. According to this framework, would capuchin social conventions be biologically important? Regrettably, we lack data on the fitness consequences of handsniffing, game playing, etc., and it will be difficult to obtain accurate estimates of the fitness consequences of practicing any particular social convention for any species. Therefore, for the time being we will resort to the far less satisfying option of doing thought experiments such as the following:

A human couple may have many "couples rituals" that are signals to them of their mutual devotion (e.g., being ready with a towel when the other is ready to get out of the shower or reciting lines from their mutual favorite movie on every possible socially appropriate occasion). Such behaviors would not seem to have any great fitness-enhancing value on the surface, but the social context and ontogenetic ritualization process in which they were created are what gives them their importance (i.e., they are used to signal commitment to a particular social relationship). Consequently, failure to perform one of these rituals when it is expected can initiate the breakdown of a valuable social relationship by signaling inattentiveness to the partner. The particular behaviors are important only in the context of this particular social relationship, and the particular behaviors used to signal commitment may be fairly arbitrary—the members of this particular couple may not use these same signals in their subsequent romantic relationships, though they will produce other "couples rituals." Thus, the precise details of the particular behaviors involved are fairly arbitrary, and the behaviors may be short-lived, but the propensity to invent and adopt these interaction rituals may have great adaptive value and should be the target of natural selection.

This example deals with two-person "cultures," and some anthropologists will object that the term "culture" is more often applied at the population level or at the very least to social networks larger than two individuals. However, the logic above applies to larger groups as well as to couples. Whenever there is a situation in which there is a need for large coalitions, there should be selection also for interaction rituals that help define group membership and locate individuals in the coalitional structure. The more complex and multilayered the coalitional structure in the society, the more need there should be for such signaling and hence the greater selective pressure to invent and acquire from others the signals used in these interaction rituals. We would predict that dolphins and hamadryas baboons, with their supercoalitions and multitiered societies (Connor, Smolker, and Richards 1992, Kummer 1995), might exhibit such behaviors. And humans, of course, have the most complex layering of coalitional networks known in the animal kingdom, even participating in coalitions with people they do not know personally.

Conclusion. Despite the fact that so many traits

deemed to be “cultural” in humans fall in the domain of social conventions rather than subsistence technology, most theorizing about the evolution of culture has focused on the technological domain. This is perhaps in part because technological culture leaves material remains that can be traced over long periods of time. It may also be because it is far easier to compare the efficiencies of alternative technologies than it is to estimate fitness costs and benefits of particular social conventions. Nonetheless, the evolution of social conventions is a fascinating topic that is crying out for a better comparative database. It is our hope that researchers of other social, cooperative animals will begin to collect data on this issue so that we can better assess the phylogenetic distribution of such behaviors and the circumstances under which they arise. We also hope to stimulate researchers of human populations to attend to the form (i.e., “signal design”), transmission dynamics, social contexts, and ontogeny of social conventions so that there can be more cross-disciplinary exchange on this topic.

Comments

R. L. DAY, I. COOLEN, Y. VAN BERGEN,
AND K. N. LALAND

Sub-Department of Animal Behaviour, University of Cambridge, Cambridge CB3 8AA, U.K. (Day, Coolen, van Bergen)/ Centre for Social Learning and Cognitive Evolution, School of Biology, St. Andrews University, St. Andrews, Fife KY16 9JU, U.K. (Laland) (knl1@st-andrews.ac.uk). 18 x 02

Perry and colleagues are to be congratulated for this valuable collaborative exercise, which we regard as not only a milestone in the study of animal traditions but also a contribution to a deeper understanding of the roots of human culture. As they suggest, the study of animal culture has mostly focused on the technological domain, yet much human culture is based on social conventions. Animal conventions are important not just because they have been neglected but because, unlike behaviour in the technological domain, they are not easily explained away by differences in ecology (e.g., Tomasello 1994). We share the authors' hope that others will be encouraged to design studies specifically with social conventions in mind in order to create a comparative dataset that goes beyond apes. It is important that anthropologists be aware of the extent to which the behaviour of a multitude of animals, including fish, birds, and mammals, is shaped by socially transmitted traditions. “Culture” can be regarded as the exclusive domain of humans only if it is defined according to arbitrary and anthropocentric criteria.

Yet readers of CA will be well aware of the problems associated with defining culture, and to date the animal literature has been no more successful than its human counterpart in establishing consensual criteria by which

culture can be classified and analysed. Purported defining criteria (or necessary conditions) for animal culture include interpopulation variation in behaviour, differences between groups that cannot be attributed to genetic or ecological variation, socially transmitted information, transgenerational traditions, universality, uniformity, behavioural innovation, cumulative traditions, teaching, imitation, and others (Tomasello 1994, McGrew 1998, Whiten et al. 1999). Because this is not the place to enter into a detailed discussion of the merits of such criteria, we will concentrate on two points on which we feel we can make constructive suggestions.

The first concerns the “durability” criterion emphasized by Perry et al., which implies that investigations of animal culture require long-term studies. While we appreciate the value of long-term field observation, we are concerned that this emphasis on durability may be counterproductive. A vast amount of human culture is transient, fickle, and spreads horizontally, but it is no less cultural for that. The same is likely to be true for animals (Laland, Richerson, and Boyd 1993), and interesting cultural phenomena in capuchins and other species might be neglected if the durability criterion were strictly applied. Indeed, it is debatable to what extent the capuchin data genuinely meet the arbitrary six-month criterion. Furthermore, short-term studies can contribute to the study of culture too, particularly through controlled experimentation. For instance, features of social transmission can be investigated using transmission-chain procedures in which the passage of learned behaviour is tracked as the composition of experimental groups changes. This design has been successfully applied to fish (Laland and Williams 1997), birds (Curio, Ernst, and Vieth 1995, Zeltner, Klein, and Huber-Eicher 2000), and rats (Galef and Allen 1995). While such procedures may be more difficult with primates, they are surely not impossible. Ultimately, experimentation provides the only truly adequate means of satisfying critics that a particular animal “has culture.”

Second, the data presented by Perry et al. resonate with current thinking on animal innovation. Reader and Laland (2001) invoke the adage “Necessity is the mother of invention” to highlight the fact that poor competitors, such as subordinates, frequently appear to be driven to innovate while good competitors can satisfice using tried-and-tested strategies. We note that the innovators amongst the capuchins were typically subordinates and that the innovator, Guapo, ceased performing the novel behaviour once he achieved alpha status. In species such as capuchins the alpha male may dominate reproductive and foraging success, forcing subordinate males to innovate in order to gain necessary resources. The capuchin conventions tend to occur on the periphery of the group, where presumably low-status individuals will be found. Moreover, it appears that all of the capuchin social conventions were initiated by males, an observation that also corresponds to the findings of a recent survey of the primate literature (Reader and Laland 2001). Given the greater variability in male than in female mating success, it may pay low-status males to innovate to gain re-

sources. Because capuchin females are philopatric, migrant males may be expected to be innovative in the social domain, as they must establish their social position in order to achieve alpha status and form coalitions to avoid fatal conflicts.

We also note that Guapo was the inventor of several social conventions, which brings to mind the multiple innovations of Imo, the celebrated Japanese macaque. No doubt similar plaudits will be landed on Guapo, but we propose a note of caution. It has never been established that Imo's achievements are a result of her "innovative personality" (as opposed to more mundane motivational factors), and even if it were, it is not clear that the relevant personality trait is "intelligence" or "creativity" as opposed to, say, "boldness," "perseverance," or "non-conformity." Imo's fame has led to the widespread but probably false impression that primate innovators are likely to be juvenile and female (Reader and Laland 2001). The strength of the kind of comparative analysis carried out by Perry et al. is that researchers can go beyond the misleading impressions that can emerge from a single population.

WILLIAM C. MC GREW
Departments of Anthropology and Zoology, Miami University, Oxford, Ohio 45056, U.S.A. (mcgrewwc@muohio.edu). 24 IX 02

Researchers on white-faced capuchin monkeys in Costa Rica have produced an impressive comparative analysis of a set of behavioral patterns that seem to qualify as social conventions. They have done so rigorously and systematically, by collaboration, collating data-sets from four sites. In doing so, they have advanced the emerging field of cultural primatology beyond any previous cross-population study, including those on great apes (Whiten et al. 1999). Their results are all the more notable because these New World primates are phylogenetically distant from *Homo sapiens*, showing that argument by analogy can be as fruitful as argument by homology. This is not always appreciated by anthropologists, who when being comparative tend to focus on great apes.

Perry et al. stress that they deal only with social patterns, not with subsistence ones such as the elementary technology of foraging. Although the former have been less commonly analyzed, they were the subject of the very first cross-population study in primates, that of the chimpanzees' social custom of the grooming hand-clasp (McGrew and Tutin 1978). Obviously, there is much more to be done in the social domain (e.g., on courtship, display, etc.).

The authors rightly emphasize explicit operational criteria for what qualifies in their analysis, but all three are debatable. Variation across groups is likely a sufficient condition but not a necessary one. One can imagine a study of a single population's revealing fascinating customs. Expansion is more problematic, as this is surely a matter of timing, that is, when the observations begin

vis-à-vis the origins of the behavioral pattern. Early observations may yield rapid expansion in the number of performers, while later ones may show no expansion if the pattern is established. Durability seems to be a matter of "horses for courses." Students of fads in popular culture would not like to be constrained chronologically, any more than students of traditional culture would be happy with a time-scale that is less than transgenerational.

The ethnography is fascinating in its richness, but one looks for common elements underlying the patterns. In addition to those proposed by the authors, a common strand seems to be that of one individual's constraining the activities of another. This suggests dominance-subordination relations and the possibility that the conventional performances not only *test or reinforce* relationships but also *signal them to others*. (The same may apply to the grooming hand-clasp of chimpanzees. When the subordinate supports the weight of the joint effort, this is obvious for all to see [McGrew et al. 2001].) This idea can be tested by looking more closely at who is or is not the "audience" for behavioral performance.

The distinction between complementarity, turn taking, and role reversal in such conventional interactions is heuristically useful, especially in going beyond dyadic to polyadic exchanges. This is the stuff of social complexity. Perry et al.'s study sets new standards for future analyses in cultural primatology.

ELISABETTA VISALBERGHI AND ELSA ADDESSI
Istituto di Psicologia, Consiglio Nazionale delle Ricerche, via U. Aldrovandi 16 b, 00197 Rome, Italy (elisa@pml.it). 3 X 02

Do capuchins' "social conventions" function to test the quality of the relationship between group members, as suggested by Perry and coworkers? Do social conventions provide useful information for deciding how to behave towards group members? We argue that if this kind of information were necessary, then social conventions would be present most of the time and performed/received by most individuals, but this is not the case for capuchins. Social conventions are rarely observed and confined to a few individuals even though there is no reason to think that the pairs in which they occur are the only ones in need of testing their bonds, and their high rate of extinction makes them short-lived. Furthermore, why do Perry et al. consider grooming and nonconceptive sex to be "stereotyped signals" not flexible enough to perform the function of testing bonds? This position is puzzling to those of us who observe capuchins' behavior in the laboratory, where we have found a high rate of innovation and marked interindividual behavioral differences in a closely related species (*Cebus apella*) (e.g., sexual behavior [Carosi and Visalberghi 2002] and tool use [Visalberghi and Trinca 1989]). Other less demanding explanations may account for the occurrence of social conventions. For example, it is possible that the smell of someone else's hands, being in

very intimate contact, or being involved in a social object-play situation provides pleasurable feedback that rewards both partners. In short, to attribute a bond-testing function to social conventions seems unwarranted to us, and to persevere in this direction might turn out to be a Sisyphean effort.

Field (and laboratory [see below]) experiments provide insights for interpreting culture and social traditions. On the one hand, ecological differences between field sites should be carefully scrutinized when examining a candidate case of cultural behavior; on the other hand, it is almost impossible not to underestimate the ecological differences among sites. An enlightening example of how ecological differences may affect cultural behavior comes from recent field experiments on chimpanzees' ant-dipping at Bossou. Humle and Matsuzawa (2002) found that prey behavior (i.e., gregariousness and/or aggressiveness) and the ant-dipping context (e.g., whether the ants are at the nest or migrating) influence the length of the tool and the technique used to dip. Therefore, differences between sites in prey-species behavior and the context in which dipping takes place may result in different tool lengths and ant-dipping techniques.

Perry et al. limit their analyses to social conventions, disregarding the food-related behaviors that are also fundamental to human cultures (Rozin 1996). Laboratory research may provide insights in this domain. We examined the widespread assumption that observational learning from experienced group members is quicker and safer than individual learning as a way of overcoming neophobia (i.e., caution about eating something never tasted before) (see Visalberghi and Addessi n.d.). If this were the case, influences provided by the social context could lead to safe feeding only if the target food encountered by naïve individuals and the food eaten by knowledgeable group members were the same. Tufted capuchin monkeys (*Cebus apella*), a species closely related to *C. capucinus*, were tested to assess the extent to which social influences on feeding behavior foster a safe diet. Using an observer-demonstrator(s) paradigm in which a naïve observer and experienced group member(s) could see each other through a Plexiglas window, we found that the observers ate significantly more of a novel food when demonstrators were eating by the window than when alone. Surprisingly, however, this occurred regardless of what food the demonstrators were eating (Visalberghi and Addessi 2000, 2001). Moreover, when the observer could choose between two colored novel foods only one of which matched the food being eaten by the demonstrators, it did not eat the matching food more than the other (Visalberghi and Addessi 2001). In short, in tufted capuchins social influences were not directed to a specific food target, and the behavior of group members was not used to assess, without risk, whether a novel food was safe. In another experiment we assessed the effect of social (encountering novel foods with group members) or non-social (encountering the same novel foods when alone) treatment on individuals' preferences for the novel foods presented in a binary-choice test and found that whereas feedback from nutrients and expo-

sure affected food preferences, the treatment did not (Sabbatini, Stammati, and Visalberghi n.d.). These findings should caution field observers against assuming that sophisticated social learning processes underlie feeding habits. Instead, we should consider how very simple mechanisms bias individual learning (Fragaszy and Visalberghi 2001).

ANDREW WHITEN

Centre for Social Learning and Cognitive Evolution and Scottish Primate Research Group, School of Psychology, University of St. Andrews, St. Andrews KY16 9JU, Scotland (aw2@st-andrews.ac.uk). 7 x 02

Perry et al. have here assembled a very special and important contribution to our knowledge of traditions within the animal kingdom. In particular, their impressively detailed documentation supports their main hypothesis that the behaviour patterns they describe are indeed traditions defined by their social content and also their supplementary hypothesis that the function of these particular behaviours lies in social bond-testing. Neither phenomenon has been so well supported before for non-human species, and accordingly this new database should have a significant impact on our conceptual map of the subject. The successful collaborative effort of these researchers provides a model of what can be achieved by this route as decades of research offer increasing opportunities to construct the large-scale perspective required for a "cultural primatology" (de Waal 1999, Whiten 2003). It is also encouraging to see such an excellent example of true discovery—data that, whatever the issues of interpretation that remain to be debated, can fairly straightforwardly be described as a cluster of exciting new facts about behaviour, contrasting with the disappointingly sterile theoretical and methodological hand-wringing of so much contemporary effort in mainstream "cultural anthropology."

In the context of these celebratory comments, I have just two main critical comments to make. The first concerns inconsistencies in the analysis of criteria for identifying traditions under natural conditions. Perry et al. say that the exclusion of genetic and ecological differences is not "necessary or sufficient," but this is also true of their own three operational criteria—intergroup variation, expansion, and durability. A stable tradition certainly need not meet the first two requirements; equally, none of the three is sufficient to guarantee that a tradition exists. Isn't it rather the case that the three criteria of Perry et al. *plus* the other two provide a set of criteria that offer stronger circumstantial evidence for traditions the more of them are met? For the five behaviour patterns they highlight, is there in fact evidence that appeals to all five criteria?

Second, can "ontogenetic ritualization" really explain the social transmission implied? Ontogenetic ritualization, as described by Tomasello and Call (1997), is meant to explain how an action of animal A towards animal B (e.g., arm raise) that initially has no communicative in-

tent comes to have such intent through anticipatory learning (e.g., animal A eventually raises its arm intentionally to elicit play after both B and A have come to anticipate that this often *leads* to play). To my knowledge, evidence that could prove that such a process operated in a particular instance of behavioural development has not yet been forthcoming. But in any case, ontogenetic ritualization cannot explain how the critical aspect of *reciprocation* is acquired. For example, where monkey A begins the finger-in-mouth game by clamping its teeth onto B's fingers, how does B acquire the reciprocal "idea" of clamping its own teeth onto A's fingers? Or how does A get to the reciprocal idea of getting B's fingers in its nose, given that A has its fingers in B's nose? Using the principles of ontogenetic ritualization alone, it is not clear that this leap can be made. To the contrary, the reciprocation leap appears an inherently imitative one, sophisticated insofar as, in the case of teeth-clamping, monkey B has to translate from having its fingers clamped in A's mouth, which it can feel but perhaps not see (?), to clamping A's fingers in its own mouth, which it certainly cannot see.

Two sets of recent findings may be worth bearing in mind in tackling the mystery that I am arguing still exists here. First, there is now evidence that Neotropical primates, including capuchins, are capable of more imitative social learning than the reviews of Visalberghi and Frigaszy (1990, 2002) would suggest (Voelkl and Huber 1999, Fredman and Whiten 2002). Second, the characteristics of "mirror neurons" in monkeys suggest that perceptions of others' actions are coded motorically or at some supramodal level (e.g., Rizzolatti et al. 2002), a phenomenon that might help to explain how the kind of "reciprocation leap" discussed above could be achieved by a monkey. To be sure, the mirror neurons described to date are all concerned with linkage of actions with matching visual input (e.g., the neuron fires when one performs a precision grip or when one sees another monkey doing this). Is it possible that others exist for touch, such that the brain of a monkey that feels its fingers clamped in another's mouth registers this in a neural representation of clamping the other's fingers in its own mouth? Whatever the answer to such speculations, we would be wise not to underestimate the difficulty of explaining the social learning and diffusion of reciprocal conventions.

AMOTZ ZAHAVI

Institute of Nature Conservation Research, Tel-Aviv University, 69978 Tel-Aviv, Israel (zahavi@post.tau.ac.il). 14 XI 02

Perry et al. present Collins's theory and mine (Zahavi 1977) as different, but they are not. My theory suggested that the strength of the bond may be assessed by imposing a test on a social partner. The information acquired by the test reflects the strength of the bond and helps one to decide whether to maintain the bond or break it. Collins's suggestion that interaction rituals

function to inform participants about the social relationship between them is not essentially different. We agree that what strengthens the bond is not the social interaction itself but the information acquired through that interaction—that is, that although many bonds are strengthened as a consequence of the interaction, some are disrupted. Collins further suggested that it is change in emotions that affects the bond, while I only discussed the logic of the patterns of the interaction by which the information is acquired. The decision to break a bond or improve it may be a consequence of one's emotional state, a cognitive decision, or some other mechanism.

I do not think that there is a functional difference between a genetically acquired ritual and one which is developed as a culture. Many birds, fishes, and reptiles learn to assess the danger presented by predators or conspecific rivals in a particular place and vary in their reaction to them by fright or mobbing according to the circumstances. Learning to understand the readiness of others to bond, which is learning to assess a positive response, need not be different from learning to avoid a particular species or an individual predator. I therefore expect that detailed studies of social interactions of other animals besides primates may reveal learned and possibly cultural differences in the patterning of their social rituals.

The cooperative birds that I am studying, Arabian babblers (*Turdoides squamiceps*), are faced with social problems similar to those of cebus monkeys. They have developed analogous social interactions; they allopreen, they play games (Posis 1984), they clump, and they have social communal dancing (Ostreihner 1995, Zahavi and Zahavi 1997). There are quantitative and sometimes qualitative differences in the way in which they interact socially. Some groups mob certain predators while others do not, and some groups allopreen or dance more than others (Zahavi, unpublished observations). Posis observed social plays that were invented in a particular group and were absent in others. I would not be surprised if part of that variation were found to be cultural rather than innate.

Reply

SUSAN PERRY

Leipzig, Germany. 25 XI 02

Because my many collaborators are currently scattered around the world, busy with fieldwork or end-of-term teaching commitments, I am unable to coordinate a joint reply in time to meet the deadline. I will therefore take the liberty of responding myself.¹ I thank Zahavi for explaining his perspective on the ways in which his and

1. I thank Joe Manson and Clark Barrett for comments on this manuscript and the Max Planck Institute for Evolutionary Anthropology for support of my research.

Collins's theories articulate and for confirming the value of using this theoretical approach for cultural as well as "genetically acquired" rituals. His comment that such social conventions are likely to be present also in the cooperative Arabian babblers he studies is encouraging, and we hope that researchers will investigate this possibility further. I also thank McGrew, Whiten, and Day et al. for their cogent critiques of the various methodological issues involved in identifying traditions and in pinpointing the mechanisms by which social transmission can occur. The commentators' criticisms fall into four categories.

Operational criteria for identifying traditions. Day et al., McGrew, and Whiten comment on our operational criteria for identifying traditions. As we state in the article, these were intended primarily as "rules of thumb that are designed to detect traditions with a minimum of error in a messy collection of datasets," and this set of criteria is neither necessary nor sufficient to pinpoint social learning as the mechanism for the spread of the trait in question. To the extent that this set of criteria produces errors in the identification of traditions, it is likely to be overly conservative (i.e., to overlook true traditions). As Whiten points out, despite the fact that neither my three criteria nor his "non-genetic" and "non-ecological" criteria are necessary or sufficient conditions for attribution of social learning, the more of these criteria that a behavior meets, the greater the likelihood that it is a true tradition.

McGrew objects that intergroup variation is not necessary to conclude that a behavior is "traditional." In a sense, I agree: for example, if a behavior is highly adaptive, multiple groups are likely to converge on the same behavior even if social learning is pivotal in its acquisition (as in the case of response to particular predators). But for the class of behaviors which we term social conventions (as defined in this article), I see no reason to expect such a precise convergence of form across groups; in fact, a certain degree of arbitrariness of form is to be expected. Hence, if all groups exhibit the same behavior, then there are serious grounds for suspicion that the behavior is part of the species-typical repertoire and social learning is unlikely to be required for its acquisition. But perhaps what McGrew is envisioning is a long-term study of a single population in which, after many years of study, a new social convention appears, is propagated, and perhaps eventually vanishes. Under such circumstances, I would agree with him that there may be sufficient grounds to term this a tradition in the absence of data on interpopulation variation.

I agree with McGrew that the "expansion of performers" criterion is a difficult one, since the detection of it depends very much on the timing of the study relative to the timing of the introduction of the trait. Certainly insistence on this criterion will produce some "false negatives" in the identification of traditions (as was almost certainly the case for sucking of body parts). However, I do think that attention to the *process* of social transmission is extremely important and is something that is

sorely lacking in much of the published literature on animal traditions to date.

Durability is, as I said in the article, the most arbitrary of our criteria. I agree with Day et al. that even a brief fad can be termed "culture" if it is spread via social learning. My main reason for including durability, in combination with frequency and intragroup distribution of the trait, was to prevent the false attribution of a tradition to a group in which a particular behavior was a one-time experiment by a single individual or dyad. As it happens, there were no candidates for traditions that were both frequent across multiple individuals and very short-term, so I do not think that we mislabeled any true traditions as nontraditions by employing the six-month criterion.

I sympathize also with Day et al.'s concern that I am overemphasizing the necessity of long-term field observations. Certainly I agree that field experiments (which can be accomplished in relatively short time frames) have much to contribute to the study of social learning. Field experiments are, of course, more tractable in some species than in others (e.g., they work extremely well in fish and rodents and less well in species such as primates that have highly differentiated social relationships, strong social bonds, and sometimes extreme xenophobia that makes translocation experiments ethically questionable). For some behavioral domains, such as food choice, reactions to predators, or possibly even food processing, it should be possible to introduce an experimental apparatus (e.g., a feeding platform with novel foods, a model predator, or a novel food-processing challenge such as Whiten's artificial fruits) and then document the transmission pattern of the relevant behaviors from the beginning. It is difficult to imagine, however, how such an experiment could be implemented for social conventions. How could wild animals be prompted by human experimenters to produce a novel social signal? Time-consuming as it is, the best way to see whether capuchins transmit their favorite social conventions to other groups is to wait until males migrate, follow them to their new groups, and pray that the migrants do not get killed in the process of migrating as has happened to two practitioners of the games described in this paper. The two remaining practitioners of the games have finally succeeded in migrating, and we are now waiting to see whether they will transmit the games to their new groupmates once their relationships with them have stabilized.

Are they testing bonds? Visalberghi and Addessi discourage the attribution of any function to social conventions because they suspect that the reason capuchins are performing the behavior is to get pleasurable feedback. Here they are confusing proximate and ultimate explanations for behavior, making the all too common mistake of claiming that if a proximate explanation is likely to be true, then ultimate explanations have been falsified. We do not dispute that the monkeys might get pleasurable feedback from the performance of these behaviors (at least, when the quality of their relationships is good), but acknowledging that the experience is pleas-

urable begs the question why it is pleasurable for some but not all capuchins, bringing us back to the necessity of asking about the behavior's evolved function. Niko Tinbergen (1963), one of the founders of ethology, cogently described the four complementary levels at which behavior can be explained: function, cause, development, and evolution (or, to use the terms favored by more recent writers, ultimate, proximate, developmental, and phylogenetic). Explaining a behavior at one level does *not* eliminate the need to explain it at other levels. A full understanding of the evolutionary biology of a behavior must take all four levels of explanation into account, and this is true for behaviors deemed to be traditional as well as for others (Fragaszy and Perry n.d.). Of course, some traits have no function and are merely by-products of other traits, and traits may acquire secondary functions, but the refusal even to test hypotheses about adaptive functions will set the field back rather than advancing understanding (Alcock 2001).

I am just as puzzled by Visalberghi and Addessi's claim that a functional explanation is consistent only with behavioral uniformity as I am by their claim that a proximate explanation such as "It feels good" would adequately explain a pattern that exhibits considerable interindividual variation. First let us consider their general claim that if social conventions were useful they would be present in most or all individuals most of the time. Surely they would not dispute the fact that there are numerous human conventions (e.g., marriage ceremonies, swearing-in ceremonies of parliamentarians, and authority-related rituals) that, although they clearly provide information about how to behave toward group members, are performed as infrequently as once in a lifetime and perhaps only by a small subset of the population. Regarding capuchin social conventions specifically, their proposed proximate explanation gives us no way of generating hypotheses about the observed variation. Why are these behaviors seen in only some primate species, in only some dyads, and only at some times? Why aren't they equally pleasurable to all dyads of all species at all times? To explain a behavior by saying that it is pleasurable is tautological: "They do it because it's pleasurable, and we know it's pleasurable because we see them do it." Operationalizing an independent measure of pleasure sounds even more Sisyphean than testing the functional explanation that we have proposed.

Integration of multiple levels of analysis is clearly the route to a productive research program for the study of signaling about social relationships, and Joseph Manson and I have already launched a research program designed to test many of the theoretical issues raised in this paper. Our more recent datasets involve all-day follows of individual monkeys in which we meticulously record initiations and terminations of interactions as well as subtleties of posture and arousal levels. Such data, in combination with our baseline data on the quality of each dyad's relationship as relationship quality shifts over time, allow us to examine each dyad's interactions for several hours preceding and following putative bond-testing signals so that we can more accurately test hy-

potheses generated by Zahavi's and Collins's theories and hypotheses about the assessment of competitive ability (e.g., Silk 1994) and low-cost signals of benign intent (Silk, Kaldor, and Boyd 2000). The capuchin vocal and gestural repertoire is rich in signals that appear to function to negotiate aspects of social relationships. These range from signals such as grooming, which have a long phylogenetic history, are highly stereotyped, and thus appear to be readily interpreted by the recipients of the action, to the social conventions described in this paper, which are idiosyncratic, more complex, and less readily interpreted because they are not part of the species-typical repertoire and most likely involve sensations of both pleasure and pain. As we have said, even if both grooming and these more novel and flexible social conventions serve approximately the same function—providing information about the quality of a bond—they still differ in important ways such as interpretability and signal reliability and therefore are not interchangeable signals. Easily misinterpreted signals such as handsniffing or hair-biting games should not be used in early stages of relationship formation, because they may trigger severe aggression if the recipient does not understand the signaler's intent. However, these idiosyncratic social conventions may provide more reliable (i.e., more difficult to fake) signals of commitment to a relationship than grooming does because they require more trust, more focus in each interaction, and willingness to spend a lot of time working out the details of who does what to whom such that the interaction is mutually satisfying. In the past few months we have been documenting the initial stages of some new social conventions in LB-AB, and it is apparent that much time and effort go into constructing a convention for which both members of the dyad are content to perform their roles.

As is the case with *C. apella*, the *C. capucinus* sexual repertoire is rich, involving numerous vocalizations and gestures which can be combined in various ways, although each behavioral element is stereotyped and part of the species-typical repertoire. Visalberghi and Addessi make the claim that there is a high rate of innovation in female sexual behavior in *C. apella*, but I do not see this variation (which consists essentially of interindividual differences in the frequencies of performing the same stereotyped species-typical behavioral elements [Carosi and Visalberghi 2002]) as being highly innovative. At any rate, if we are to understand the role that these behaviors play in negotiating relationships (either in coordinating a mating or in bond testing, as in nonconceptive sexual interactions), we must understand the role of each element separately. At Lomas Barbudal, our preliminary analyses of the frequencies of signal types across dyads with different demographic characteristics have revealed consistent patterns across dyads as to which behaviors emerge in which social contexts. The dance (pacing, spinning, piloerection, and direct gaze) is common to courtship and relationship negotiation in dyads of all stages of relationship formation. However, the vocalizations used differ according to the stage of relationship formation, reproductive state, and the current

amount of stress on the social relationship. Likewise, the outcome of the dance (i.e., the likelihood that it will end in mounting and thrusting and other physical-contact sexual gestures) depends on the stage of relationship formation, recent events in the dyad's interaction history, and the amount of pressure the dyad is receiving from audience members trying to break up the dance. Analysis of the new datasets (the all-day follows, which provide more microcontextual information) is currently under way to pinpoint the types of information that each signal is likely to provide the animals and the consequences for the dyad of performing these behaviors. At any rate, it is clear that different types of social signals, by virtue of their differing design features and phylogenetic histories, serve different purposes. No single relationship negotiation signal, whether it is stereotyped or traditional, will be appropriate for all dyads in all contexts, and hence it is not reasonable to assume that social conventions do not provide useful information for guiding future interactions simply because of a lack of uniformity in the expression of the behavior across dyads and across time, as Visalberghi and Addessi suggest. Social relationships are dynamic. This is why they need to be tested.

McGrew suggests that, rather than (or in addition to) signaling *to each other* about their relationship quality, the members of the dyad are using the convention as a display by which they signal their relationship quality (not only rank relations but also perhaps commitment to an alliance) *to other members of the group*. I had considered this line of reasoning myself in trying to make sense of the patterns I was seeing but ended up rejecting it. If the purpose of the signal is to advertise something to other group members, it should be conspicuous and performed in front of an audience. Neither of these conditions is true: the behaviors are performed on the periphery of the group and are very quiet (in contrast with the more stereotyped wheeze dance, which may very well serve to announce relationship status and invite attempts to break up alliances [Perry 1995]). Even when other monkeys are near the performers of the social convention, they show no interest at all in the behavior, which suggests that it is not providing them with useful information.

Are capuchin conventions transmitted via imitation? Although I initially doubted that imitation was involved in the acquisition of capuchin conventions because of the difficulty Tomasello et al. (1997) had in getting chimpanzees to imitate gestures, I find Whiten's arguments quite persuasive. It really is difficult to see how the reciprocal element of these gestures could arise via ontogenetic ritualization alone, and the recent data on the imitative capacities of brown capuchins and callitrichids make Whiten's imitation interpretation all the more plausible. Unfortunately, I cannot conceive of a way to address this issue rigorously using observational field data.

Who innovates? I agree with Day et al., as well as Reader and Laland (2001), that "necessity is the mother of invention." Nonetheless, this tendency is better sup-

ported in some behavioral domains (e.g., food choice and food-processing techniques) than in others (e.g., social conventions). First of all, it is somewhat less clear that subordinates need allies more than dominants do. Subordinates need allies to increase their rank, but dominants need them to maintain their rank; it is hard to say which is more important. Also, I would like to correct the impression that it is just low-rankers and males who engaged in social conventions in the capuchin dataset. Guapo, though he was not the alpha male at the time of his innovations, was nonetheless tied for the second rank in the group. Also, handsniffing was invented and practiced by females, many of them high-ranking, in LB-AB group and in SR-CP group. I am intrigued by the hypothesis that capuchin males will be more innovative in the social domain than females because of their greater need to form coalitions. Certainly males' social relationships are more dynamic than those of females, such that frequent testing of the bonds would be desirable, and the consequences of having no allies are more dire (i.e., eviction from groups, severe wounding and killing by male conspecifics). At the same time, males, relative to females, more rarely reach a stage of relationship formation that is secure enough to risk employing these more flexible and intimate bond-testing signals.

References Cited

- ALCOCK, JOHN. 2001. *The triumph of sociobiology*. Oxford: Oxford University Press.
- ALTMANN, J. 1974. Observational study of behavior: Sampling methods. *Behaviour* 49:227-67.
- BOESCH, CHRISTOPHE. 1994a. Chimpanzees-red colobus monkeys: A predator-prey system. *Animal Behaviour* 47: 1135-48.
- . 1994b. Cooperative hunting in wild chimpanzees. *Animal Behaviour* 48:653-67.
- . 1996a. "The emergence of cultures among wild chimpanzees," in *Evolution of social behaviour patterns in primates and man*. Edited by W. G. Runciman, John Maynard Smith, and R. I. M. Dunbar, pp. 251-68. Proceedings of the British Academy 88.
- . 1996b. "Three approaches for assessing chimpanzee culture," in *Reaching into thought: The minds of the great apes*. Edited by A. E. Russon, K. Bard, and S. T. Parker, pp. 404-29. Cambridge: Cambridge University Press.
- BOESCH, CHRISTOPHE, AND MICHAEL TOMASELLO. 1998. Chimpanzee and human cultures. *CURRENT ANTHROPOLOGY* 39:591-614.
- BOJNSKI, S. 1988. Use of a club by a wild white-faced capuchin (*Cebus capucinus*) to attack a venomous snake (*Bothrops asper*). *American Journal of Primatology* 14:177-79.
- BORAN, J. R., AND S. L. HEIMLICH. 1999. "Social learning in cetaceans: Hunting, hearing, and hierarchies," in *Mammalian social learning: Comparative and ecological perspectives*. Edited by H. O. Box and K. R. Gibson, pp. 282-307. Cambridge: Cambridge University Press.
- BOYD, ROBERT, AND PETER J. RICHESON. 1985. *Culture and the evolutionary process*. Chicago: University of Chicago Press.
- . 1992. Punishment allows the evolution of cooperation (or anything else) in sizeable groups. *Ethology and Sociobiology* 13:171-95.

- . 1996. "Why culture is common, but cultural evolution is rare," in *Evolution of social behaviour patterns in primates and man*. Edited by W. G. Runciman, John Maynard Smith, and R. I. M. Dunbar, pp. 77–93. Proceedings of the British Academy 88.
- BYRNE, RICHARD. 1995. *The thinking ape: Evolutionary origins of intelligence*. Oxford: Oxford University Press.
- . 1999. "Cognition in great ape ecology: Skill-learning ability opens up foraging opportunities," in *Mammalian social learning: Comparative and ecological perspectives*. Edited by H. O. Box and K. R. Gibson, pp. 333–50. Cambridge: Cambridge University Press.
- CAROSI, MONICA, AND ELISABETTA VISALBERGHI. 2002. Analysis of tufted capuchin (*Cebus apella*) courtship and sexual behavior repertoire: Changes throughout the female cycle and female inter-individual differences. *American Journal of Physical Anthropology* 118:11–24. [EV, EA]
- CHAPMAN, C., AND L. FEDIGAN. 1990. Dietary differences between neighboring *Cebus capucinus* groups: Local traditions, food availability, or responses to food profitability? *Folia Primatologica* 54:177–86.
- COLLINS, R. 1981. On the microfoundations of macrosociology. *American Journal of Sociology* 86:984–1014.
- . 1993. Emotional energy as the common denominator of rational action. *Rationality and Society* 5:203–30.
- CONNOR, RICHARD C., RACHEL A. SMOLKER, AND ANDREW F. RICHARDS. 1992. "Dolphin alliances and coalitions," in *Coalitions and alliances in humans and other animals*. Edited by Alexander H. Harcourt and Frans B. M. de Waal, pp. 415–43. Oxford: Oxford Science Publications.
- COUSI-KORBEL, S., AND D. FRAGASZY. 1995. On the relation between social dynamics and social learning. *Animal Behaviour* 50:1441–53.
- CURIO, E., U. ERNST, AND W. VIETH. 1995. The adaptive significance of avian mobbing. 2. Cultural transmission of enemy recognition in blackbirds: Effectiveness and some constraints. *Zeitschrift für Tierpsychologie* 48:184–202. [RLD, IC, YV, KNL]
- CUSTANCE, DEBORAH, ANDREW WHITEN, AND TAMAR FREDMAN. 1999. Social learning of an artificial fruit task in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology* 113:13–23.
- DE WAAL, F. B. M. 1982. *Chimpanzee politics*. New York: Harper and Row.
- . 1997. Food transfers through mesh in brown capuchins. *Journal of Comparative Psychology* 111:370–78.
- . 1999. Cultural primatology comes of age. *Nature* 399: 635–36.
- . 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour* 60:253–61.
- DE WAAL, FRANS B. M., AND MICHELLE L. BERGER. 2000. Payment for labour in monkeys. *Nature* 404:563.
- DE WAAL, FRANS B. M., AND ALEXANDER H. HARCOURT. 1992. "Coalitions and alliances: A history of ethological research," in *Coalitions and alliances in humans and other animals*. Edited by Alexander H. Harcourt and Frans B. M. de Waal, pp. 1–19. Oxford: Oxford Science Publications.
- DE WAAL, FRANS B. M., AND MICHAEL SERES. 1997. Propagation of handclasp grooming among captive chimpanzees. *American Journal of Primatology* 43:339–46.
- DEWAR, GWEN. n.d. "The cost-benefit approach to social transmission: Designing tests for adaptive traditions," in *The biology of traditions: Models and evidence*. Edited by Dorothy Fragaszy and Susan Perry. Cambridge: Cambridge University Press. In press.
- DUGATKIN, L. 1996. "Copying and mate choice," in *Social learning in animals: The roots of culture*. Edited by Cecilia M. Heyes and Bennett G. Galef, pp. 85–106. San Diego: Academic Press.
- FEDIGAN, L. M. 1990. Vertebrate predation in *Cebus capucinus*: Meat eating in a neotropical monkey. *Folia Primatologica* 54:196–205.
- . 1993. Sex differences and intersexual relations in adult white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology* 14:853–77.
- FEDIGAN, L. M., AND K. M. JACK. 2001. Neotropical primates in a regenerating Costa Rican dry forest: A comparison of howler and capuchin populations. *International Journal of Primatology* 22:689–713.
- FEDIGAN, LINDA M., L. M. ROSE, AND R. M. AVILA. 1996. "See how they grow: Tracking capuchin monkey populations in a regenerating Costa Rican dry forest," in *Adaptive radiations of Neotropical primates*. Edited by M. Norconck, A. Rosenberger, and P. Garber, pp. 289–307. New York: Plenum Press.
- FRAGASZY, DOROTHY, AND SUSAN PERRY. Editors n.d.a. *The biology of traditions: Models and evidence*. Cambridge: Cambridge University Press. In press.
- . n.d.b. "Towards a biology of traditions," in *The biology of traditions: Models and evidence*. Edited by Dorothy Fragaszy and Susan Perry. Cambridge: Cambridge University Press. In press.
- FRAGASZY, D., AND E. VISALBERGHI. 1996. "Social learning in monkeys: Primate 'primacy' reconsidered." in *Social learning in animals: The roots of culture*. Edited by Cecilia M. Heyes and Bennett G. Galef Jr., pp. 65–84. San Diego: Academic Press.
- . 2001. Recognizing a swan: Socially-biased learning. *Psychologia* 44:82–98. [EV, EA]
- FRAGASZY, DOROTHY M., E. VISALBERGHI, AND J. G. ROBINSON. 1990. Variability and adaptability in the genus *Cebus*. *Folia Primatologica* 54:114–18.
- FREDMAN, TAMAR, AND ANDREW WHITEN. 2002. The nature and function of observational learning of tool use by capuchin monkeys (*Cebus apella*) in relation to human and conspecific models. Poster prepared for the conference "Perspectives on Imitation," Royaumont Abbey, France, April. [AW]
- FREESE, C. H. 1976. Food habits of white-faced capuchins *Cebus capucinus* L. (Primates: Cebidae) in Santa Rosa National Park, Costa Rica. *Brenesia* 10/11:43–56.
- FREESE, C. H., AND J. R. OPPENHEIMER. 1981. "The capuchin monkey, genus *Cebus*," in *Ecology and behaviour of Neotropical primates*, vol. 1. Edited by A. F. Coimbra-Filho and R. H. Mittermeier, pp. 331–90. Rio de Janeiro: Academia Brasilia.
- GALEF, BENNETT G., JR. 1996. "Social enhancement of food preferences in Norway rats: A brief review," in *Social learning in animals: The roots of culture*. Edited by Cecilia M. Heyes and Bennett G. Galef Jr., pp. 49–64. San Diego: Academic Press.
- . n.d. " 'Traditional' foraging behaviors of brown and black rats (*Rattus rattus* and *Rattus norvegicus*)," in *The biology of traditions: Models and evidence*. Edited by Dorothy Fragaszy and Susan Perry. Cambridge: Cambridge University Press. In press.
- GALEF, B. G., JR., AND C. ALLEN. 1995. A model system for studying animal traditions. *Animal Behaviour* 50:705–17. [RLD, IC, YV, KNL]
- GALEF, BENNETT G., JR., AND LUC-ALAIN GIRALDEAU. 2001. Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Animal Behaviour* 61:3–15.
- GIRALDEAU, LUC-ALAIN, AND THOMAS CARACO. 2000. *Social foraging theory*. Princeton: Princeton University Press.
- HARCOURT, A. H. 1995. Sexual selection and sperm competition in primates: What are male genitalia good for? *Evolutionary Anthropology* 4:121–29.
- HARCOURT, A. H., AND F. B. M. DE WAAL. Editors. 1992. *Coalitions and alliances in humans and other animals*. Oxford: Oxford University Press.
- HARVEY, P., R. D. MARTIN, AND T. H. CLUTTON-BROCK. 1987. "Life histories in comparative perspective," in *Primate societies*. Edited by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, pp. 181–96. Chicago: University of Chicago Press.
- HEYES, CECILIA M., AND BENNETT G. GALEF JR. Edi-

- tors. 1996. *Social learning in animals: The roots of culture*. San Diego: Academic Press.
- HEYES, CECILIA, AND LUDWIG HUBER. Editors. 2000. *The evolution of cognition*. Cambridge: MIT Press.
- HUDSON, R., B. SCHAAL, AND A. BILKÓ. 1999. "Transmission of olfactory information from mother to young in the European rabbit," in *Mammalian social learning: Comparative and ecological perspectives*. Edited by H. O. Box and K. R. Gibson, pp. 1441-57. Cambridge: Cambridge University Press.
- HUFFMAN, MICHAEL, AND Y. HIRATA. n.d. "Biological and ecological foundations of primate behavioral traditions," in *The biology of traditions: Models and evidence*. Edited by Dorothy Fragaszy and Susan Perry. Cambridge: Cambridge University Press. In press.
- HUMLE, TATYANA, AND MATSUZAWA TETSURO. 2002. Chimpanzees, safari ants, tools, and technique: A new perspective. Paper presented at the 19th Congress of the International Primatological Society, Beijing, China, August 4-9. [EV, EA]
- ITANI, J. 1958. "On the acquisition and propagation of a new food habit in the troop of Japanese monkeys at Takasakiyama," in *Japanese monkeys: A collection of translations*. Edited by K. Imanishi and S. Altmann, pp. 52-65. Edmonton: University of Alberta Press.
- ITANI, J., AND A. NISHIMURA. 1973. "The study of infra-human culture in Japan," in *Symposia of the Fourth International Congress of Primatology*, vol. 1. Edited by E. W. Menzel Jr., pp. 26-60. Basel: Karger.
- JANIK, VINCENT M., AND PETER J. SLATER. n.d. "Traditions in mammalian and avian vocal communication," in *The biology of traditions: Models and evidence*. Edited by Dorothy Fragaszy and Susan Perry. Cambridge: Cambridge University Press. In press.
- KAWAI, M. 1965. Newly acquired pre-cultural behavior of a natural troop of Japanese monkeys on Koshima Island. *Primates* 6:1-30.
- KAWAMURA, S. 1959. The process of sub-human culture propagation among Japanese macaques. *Primates* 2:43-60.
- KING, BARBARA J. 1991. Social information transfer in monkeys, apes, and hominids. *Yearbook of Physical Anthropology* 34:97-115.
- . 1994. *The information continuum: Evolution of social information transfer in monkeys, apes, and hominids*. Santa Fe: SAR Press.
- KITCHENER, A. C. 1999. "Watch with mother: A review of social learning in the Felidae," in *Mammalian social learning: Comparative and ecological perspectives*. Edited by H. O. Box and K. R. Gibson, pp. 236-58. Cambridge: Cambridge University Press.
- KROEBER, A. L. 1928. Sub-human culture beginnings. *Quarterly Review of Biology* 3:325-42.
- KRUUK, H., AND M. TURNER. 1967. Comparative notes on predation by lion, leopard, cheetah, and wild dog in the Serengeti area, East Africa. *Mammalia* 31:1-27.
- KUMMER, HANS. 1995. *In quest of the sacred baboon: A scientist's journey*. Princeton: Princeton University Press.
- LALAND, K. 1996. "Developing a theory of animal social learning," in *Social learning in animals: The roots of culture*. Edited by Cecilia M. Heyes and Bennett G. Galef Jr., pp. 129-54. New York: Academic Press.
- . 1999. "Exploring the dynamics of social transmission with rats," in *Mammalian social learning: Comparative and ecological perspectives*. Edited by H. O. Box and K. R. Gibson, pp. 174-87. Cambridge: Cambridge University Press.
- LALAND, K. N., P. J. RICHERSON, AND R. BOYD. 1993. Animal social learning: Towards a new theoretical approach. *Perspectives in Ethology* 10:249-77. [RLD, IC, YV, KNL]
- LALAND, K. N., AND K. WILLIAMS. 1997. Shoaling generates social learning of foraging information in guppies. *Animal Behaviour* 53:1161-69. [RLD, IC, YV, KNL]
- LEFEBVRE, LOUIS, AND LUC-ALAIN GIRALDEAU. 1996. "Is social learning an adaptive specialization?" in *Social learning in animals: The roots of culture*. Edited by Cecilia M. Heyes and Bennett G. Galef Jr., pp. 107-28. New York: Academic Press.
- MC GREW, W. C. 1992. *Chimpanzee material culture: Implications for human evolution*. Cambridge: Cambridge University Press.
- . 1998. Culture in non-human primates? *Annual Review of Anthropology* 27:301-28.
- . 2001. "The nature of culture: Prospects and pitfalls of cultural primatology," in *Tree of origin: What primate behavior can tell us about human social evolution*. Edited by Frans de Waal, pp. 231-54. Cambridge: Harvard University Press.
- MC GREW, W. C., L. F. MARCHANT, S. E. SCOTT, AND C. E. G. TUTIN. 2001. Intergroup differences in a social custom of wild chimpanzees: The grooming hand-clasp of the Mahale Mountains. *CURRENT ANTHROPOLOGY* 42:148-53.
- MC GREW, W. C., AND C. TUTIN. 1978. Evidence for a social custom in wild chimpanzees? *Man* 13:234-51.
- MANSON, J. H. 1999. Infant handling in wild *Cebus capucinus*: Testing bonds between females? *Animal Behaviour* 57: 911-21.
- MANSON, J. H., S. E. PERRY, AND A. R. PARISH. 1997. Nonconceptive sexual behavior in bonobos and capuchins. *International Journal of Primatology* 18:767-86.
- MANSON, J. H., L. ROSE, S. PERRY, AND J. GROS-LOUIS. 1999. Dynamics of female-female social relationships in wild *Cebus capucinus*: Data from two Costa Rican sites. *International Journal of Primatology* 20:679-706.
- MATSUZAWA, T. 1994. "Field experiments on use of stone tools by chimpanzees in the wild," in *Chimpanzee cultures*. Edited by R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, and P. G. Heltne, pp. 351-70. Cambridge: Harvard University Press.
- MATSUZAWA, T., AND G. YAMAKOSHI. 1996. "Comparison of chimpanzee material culture between Bossou and Nimba, West Africa," in *Reaching into thought: The minds of the great apes*. Edited by A. E. Russon, K. Bard, and S. T. Parker, pp. 211-34. Cambridge: Cambridge University Press.
- NAKAMURA, MICHIO, WILLIAM C. MC GREW, LINDA F. MARCHANT, AND TOSHISADA NISHIDA. 2000. Social scratch: Another custom in wild chimpanzees? *Primates* 41: 237-48.
- NEL, JAN A. J. 1999. "Social learning in canids: An ecological approach," in *Mammalian social learning: Comparative and ecological perspectives*. Edited by H. O. Box and K. R. Gibson, pp. 259-78. Cambridge: Cambridge University Press.
- NICHOLSON, B. 1984. Does kissing aid human bonding by semiochemical addiction? *British Journal of Dermatology* 111: 623-27.
- O'BRIEN, T. G., AND J. G. ROBINSON. 1991. Allomaternality care by female wedge-capped capuchin monkeys: Effects of age, rank, and relatedness. *Behaviour* 119:30-50.
- OSTREIHER, R. 1995. Influence of the observer on the frequency of the "morning dance" in the Arabian babbler. *Ethology* 100:320-30. [AZ]
- OTTONI, EDUARDO B., AND MASSIMO MANNU. 2001. Semi-free-ranging tufted capuchin monkeys (*Cebus apella*) spontaneously use tools to crack open nuts. *International Journal of Primatology* 22:347-58.
- PACKER, C., AND L. RUTTAN. 1988. The evolution of cooperative hunting. *American Naturalist* 132:159-98.
- PANGER, MELISSA. 1997. *Hand preference and object-use in free-ranging white-faced capuchins (Cebus capucinus) in Costa Rica*. Ann Arbor: University Microfilms International.
- PANGER, MELISSA A., SUSAN PERRY, LISA ROSE, JULIE GROS-LOUIS, ERIN VOGEL, KATHERINE C. MACKINNON, AND MARY BAKER. 2002. Cross-site differences in the foraging behavior of white-faced capuchins (*Cebus capucinus*). *American Journal of Physical Anthropology* 119:52-66
- PERRY, SUSAN. 1995. *Social relationships in wild white-faced capuchin monkeys, Cebus capucinus*. Ann Arbor: University Microfilms International.
- . 1996. Female-female social relationships in wild white-

- faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology* 40:167–82.
- . 1997. Male-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *Behaviour* 134: 477–510.
- . 1998a. Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behaviour* 135:1–34.
- . 1998b. A case report of a male rank reversal in a group of wild white-faced capuchins (*Cebus capucinus*). *Primates* 39: 51–69.
- . n.d. "Coalitional aggression in white-faced capuchins," in *Animal social complexity: Intelligence, culture, and individualized societies*. Edited by F. B. M. de Waal and P. Tyack. Cambridge: Harvard University Press. In press.
- PERRY, S., AND L. ROSE. 1994. Begging and transfer of coat meat by white-faced capuchin monkeys, *Cebus capucinus*. *Primates* 35:409–15.
- POSIS, O. 1984. Social play in babblers (in Hebrew with English summary). M.Sc. thesis, Tel-Aviv University, Tel-Aviv, Israel.
- POVINELLI, DANIEL J., KATHLEEN A. PARKS, AND MELINDA A. NOVAK. 1992. Role reversal by rhesus monkeys, but no evidence of empathy. *Animal Behaviour* 44: 269–81.
- READER, SIMON. n.d. "Relative brain size and the distribution of innovation and social learning across the nonhuman primates," in *The biology of traditions: Models and evidence*. Edited by Dorothy Fragaszy and Susan Perry. Cambridge: Cambridge University Press. In press.
- READER, S. M., AND K. N. LALAND. 2001. Primate innovation: Sex, age and social rank differences. *International Journal of Primatology* 22:787–806. [RLD, IC, YV, KNL]
- RICHERSON, PETER J., AND ROBERT BOYD. 1989. The role of evolved predispositions in cultural evolution, or, Human sociobiology meets Pascal's Wager. *Ethology and Sociobiology* 10:195–219.
- RIZZOLATTI, GIACOMO, LUCIANO FADIGA, LEONARDO FOGASSI, AND VITTORIO GALLESE. 2002. "From mirror neurons to imitation: Facts and speculations," in *The imitative mind*. Edited by Andrew Meltzoff and Wolfgang Prinz, pp. 247–66. Cambridge: Cambridge University Press. [AW]
- ROSE, L. 1992. Benefits and costs of resident males to females in white-faced capuchins, *Cebus capucinus*. *American Journal of Primatology* 32:235–48.
- . 1997. Vertebrate predation and food sharing in *Cebus* and *Pan*. *International Journal of Primatology* 18:727–65.
- ROSS, C. 1988. The intrinsic rate of natural increase and reproductive effort in primates. *Journal of Zoology* 241:199–219.
- ROZIN, P. 1996. "Sociocultural influences on human food selection," in *Why we eat what we eat: The psychology of eating*. Edited by E. D. Capaldi, pp. 233–63. Washington, D.C.: American Psychological Association. [EV, EA]
- RUSSON, A. 1996. "Imitation in everyday use: Matching and rehearsal in the spontaneous imitation of rehabilitant orangutans (*Pongo pygmaeus*)," in *Reaching into thought: The minds of the great apes*. Edited by A. E. Russon, K. Bard, and S. T. Parker, pp. 152–76. Cambridge: Cambridge University Press.
- RUSSON, ANNE E., KIM A. BARD, AND SUE TAYLOR PARKER. 1996. *Reaching into thought: The minds of the great apes*. Cambridge: Cambridge University Press.
- SABBATINI, GLORIA, MARGHERITA STAMMATI, AND ELISABETTA VISALBERGHI. n.d. Social influences on preferences towards novel foods in tufted capuchin monkeys. *Folia Primatologica*. In press. [EV, EA]
- SHEEL, D., AND C. PACKER. 1991. Group hunting behavior of lions: A search for cooperation. *Animal Behaviour* 41: 697–709.
- SCHEURER, J., AND B. THIERRY. 1985. A further food-washing tradition in Japanese macaques (*Macaca fuscata*). *Primates* 26:491–94.
- SILK, JOAN B. 1994. Social relationships of male bonnet macaques: Male bonding in a matrilineal society. *Behaviour* 130: 271–91.
- SILK, JOAN B., E. KALDOR, AND R. BOYD. 2000. Cheap talk when interests conflict. *Animal Behaviour* 59:423–32.
- SMUTS, BARBARA B., AND JOHN M. WATANABE. 1990. Social relationships and ritualized greetings in adult male baboons (*Papio cynocephalus anubis*). *International Journal of Primatology* 11:147–72.
- STANDER, P. E. 1992. Co-operative hunting in lions: The role of the individual. *Behavioral Ecology and Sociobiology* 29: 445–54.
- STANFORD, CRAIG B. 1995. The influence of chimpanzee predation on group size and anti-predator behaviour in red colobus monkeys. *Animal Behaviour* 49:577–87.
- . 1998. *Chimpanzee and red colobus: The ecology of predator and prey*. Cambridge: Harvard University Press.
- STANFORD, CRAIG B., JANETTE WALLIS, ESLOM MPONGO, AND JANE GOODALL. 1994. Hunting decisions in wild chimpanzees. *Behaviour* 131:1–18.
- STEPHAN, H., G. BARON, AND H. D. FRAHM. 1988. "Comparative size of brains and brain components," in *Comparative primate biology*, vol. 4. Edited by H. D. Steklis and J. Erwin, pp. 1–39. New York: Liss.
- TANAKA, I. 1995. Matrilineal distribution of louse egg-handling techniques during grooming in free-ranging Japanese macaques. *American Journal of Physical Anthropology* 98:197–201.
- . 1998. Social diffusion of modified louse egg-handling techniques during grooming in free-ranging Japanese macaques. *Animal Behaviour* 56:1229–1236.
- TERBORGH, J. 1983. *Five New World primates: A study in comparative ecology*. Princeton: Princeton University Press.
- TERKEL, J. 1996. "Cultural transmission of feeding behaviour in the black rat (*Rattus rattus*)," in *Social learning in animals: The roots of culture*. Edited by Cecilia M. Heyes and Bennett G. Galef Jr., pp. 17–48. San Diego: Academic Press.
- TINBERGEN, N. 1963. On aims and methods of ethology. *Zeitschrift für Tierpsychologie* 20:410–33.
- TOMASELLO, M. 1994. "The question of chimpanzee culture," in *Chimpanzee cultures*. Edited by R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, and P. G. Heltne, pp. 301–17. Cambridge: Harvard University Press. [RLD, IC, YV, KNL]
- TOMASELLO, MICHAEL, AND JOSEF CALL. 1997. *Primate cognition*. Oxford: Oxford University Press.
- TOMASELLO, MICHAEL, JOSEF CALL, JENNIFER WARREN, G. THOMAS FROST, MALINDA CARPENTER, AND KATHERINE NAGELL. 1997. The ontogeny of chimpanzee gestural signals: A comparison across groups and generations. *Evolution of Communication* 1:223–59.
- URBANI, BERNARDO. 1999. Spontaneous use of tools by wedge-capped capuchin monkeys (*Cebus olivaceus*). *Folia Primatologica* 70:172–74.
- VAN SCHAİK, C. P., R. O. DEANER, AND M. Y. MERRILL. 1999. The conditions for tool use in primates: Implications for the evolution of material culture. *Journal of Human Evolution* 36:719–41.
- VAN SCHAİK, C. P., E. A. FOX, AND A. F. SITOMPUL. 1996. Manufacture and use of tools in wild Sumatran orangutans. *Naturwissenschaften* 83:186–88.
- VISALBERGHI, E. 1990. Tool use in *Cebus*. *Folia Primatologica* 54:146–54.
- VISALBERGHI, ELISABETTA, AND ELSA ADDESSI. 2000. Seeing group members eating a familiar food enhances the acceptance of novel foods in capuchin monkeys. *Animal Behaviour* 60:69–76.
- . 2001. Acceptance of novel foods in *Cebus apella*: Do specific social facilitation and visual stimulus enhancement play a role? *Animal Behaviour* 62:567–76.
- . n.d. "Food for thoughts: Social learning and the feeding behavior in capuchin monkeys, insights from the laboratory," in *Traditions in non-human animals: Models and evidence*. Edited by D. Fragaszy and S. Perry. Cambridge: Cambridge University Press. In press.
- VISALBERGHI, ELISABETTA, AND DOROTHY FRAGASZY. 1990. "Do monkeys ape?" in *"Language" and intelligence in monkeys and apes*. Edited by Sue Taylor Parker and Kathleen

- R. Gibson, pp. 247–73. Cambridge: Cambridge University Press. [AW]
- . 2002. “Do monkeys ape? Ten years after,” in *Imitation in animals and artifacts*. Edited by Kerstin Dautenhahn and Christopher L. Nehaniv, pp. 471–99. Cambridge: MIT Press. [AW]
- VISALBERGHI, ELISABETTA, AND WILLIAM C. MC GREW. Editors. 1997. *Cebus meets Pan*. *International Journal of Primatology* 18.
- VISALBERGHI, ELISABETTA, AND LOREDANA TRINCA. 1989. Tool use in capuchin monkeys: Distinguishing between performing and understanding. *Primates* 30:511–21. [EV, EA]
- VOELKL, BERNHARD, AND LUDWIG HUBER. 2000. True imitation in marmosets. *Animal Behaviour* 60:195–202. [AW]
- WACHTMEISTER, C.-A. 2001. Display in monogamous pairs: A review of empirical data and evolutionary explanations. *Animal Behaviour* 61:861–68.
- WATANABE, K. 1989. Fish: A new addition to the diet of Japanese macaques on Koshima Island. *Folia Primatologica* 52: 124–31.
- . 1994. “Precultural behavior of Japanese macaques: Longitudinal studies of the Koshima troops,” in *The ethological roots of culture*. Edited by R. A. Gardner, A. B. Chiarelli, B. T. Gardner, and F. X. Plooi, pp. 182–92. Dordrecht: Kluwer Academic Publishers.
- WEST, M., AND A. KING. 1996. “Social learning: Synergy and songbirds,” in *Social learning in animals: The roots of culture*. Edited by Cecilia M. Heyes and Bennett G. Galef Jr., pp. 155–78. San Diego: Academic Press.
- WESTERGAARD, GREGORY C. 1994. The subsistence technology of capuchins. *International Journal of Primatology* 15: 899–906.
- WESTERGAARD, GREGORY C., AND STEPHEN J. SUOMI. 1995. The stone tools of capuchins (*Cebus apella*). *International Journal of Primatology* 16:1017–24.
- WHITE, D. J., AND B. G. GALEF. 1999. Mate choice copying and conspecific cueing in Japanese quail, *Coturnix coturnix japonica*. *Animal Behaviour* 57:465–73.
- WHITEN, ANDREW. 2000. Primate culture and social learning. *Cognitive Science* 24:477–508.
- . 2003. Cultural panthropology. *Evolutionary Anthropology*. In press. [AW]
- WHITEN, A., J. GOODALL, W. C. MC GREW, T. NISHIDA, V. REYNOLDS, T. SUGIYAMA, C. E. G. TUTIN, R. W. W. WRANGHAM, AND C. BOESCH. 1999. Cultures in chimpanzees. *Nature* 399:682–85.
- WHITEN, A., AND R. HAM. 1992. “On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research,” in *Advances in the study of behaviour*, vol. 21. Edited by P. J. B. Slater, J. S. Rosenblatt, C. Beer, and M. Milinski, pp. 239–83. San Diego: Academic Press.
- WICKLER, WOLFGANG. 1980. Vocal dueting and the pair bond. *Zeitschrift für Tierpsychologie* 52:201–9.
- WILKINSON, G., AND J. BOUGHMAN. 1999. “Social influences on foraging in bats,” in *Mammalian social learning: Comparative and ecological perspectives*. Edited by H. O. Box and K. R. Gibson, pp. 188–204. Cambridge: Cambridge University Press.
- ZAHAVI, A. 1977. The testing of a bond. *Animal Behaviour* 25: 246–47.
- ZAHAVI, A., AND A. ZAHAVI. 1997. *The handicap principle*. New York: Oxford University Press. [AZ]
- ZELTNER, E., T. KLEIN, AND B. HUBER-EICHER. 2000. Is there social transmission of feather pecking in groups of laying hen chicks? *Animal Behaviour* 60:211–16. [RLD, IC, YV, KNL]

