

TRADITIONS IN WILD WHITE-FACED CAPUCHIN MONKEYS.

Susan Perry, Melissa Panger, Lisa Rose, Mary Baker, Julie Gros-Louis, Katherine Jack,

Katherine C. MacKinnon, Joseph Manson, Linda Fedigan, and Kendra Pyle

Address of corresponding author:

Until July 1, 2002:

Susan Perry

Dept. of Anthropology, UCLA

405 Hilgard Ave.

Los Angeles, CA 90095-1553

sperry@anthro.ucla.edu

phone 310/267-4338

FAX 310/206-7833

email: [sperry@anthro.ucla.edu](mailto:sperry@anthro.ucla.edu)

July 1, 2002-Dec. 2002:

Susan Perry

Max Planck Institute for Evolutionary Anthropology

Inselstrasse 22

D-04103 Leipzig

Germany

email: perry@eva.mpg.de

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Primatologists have long recognized that social learning could play an important role in food choice and food processing in primates, since the discovery (by Itani in 1958) of innovative food processing techniques disseminated among Japanese macaques (see Huffman and Hirata, this volume for a review of subsequent findings). It is somewhat surprising that after the initial discovery of the importance of social learning in Japanese macaques, practically all subsequent research on social learning in wild nonhuman primates has been on apes (e.g. Boesch, 1996a,b; Boesch and Boesch-Achermann, 2000; Boesch and Tomasello, 1998; Huffman and Hirata, this volume; McGrew, 1992, 1998; van Schaik, Deaner, and Merrill, 1999; van Schaik, this volume; Whiten, Goodall, McGrew, Nishida, Reynolds, Sugiyama, Tutin, Wrangham, and Boesch, 1999). To remedy the gap in what we know about social learning in natural settings in other primates, and because a truly comparative framework is necessary to understand the biological underpinnings of social learning (see chapter one), we began a comprehensive study of social learning in wild capuchin monkeys. Our study investigates the probable role of social learning in a number of behavioral domains.

Capuchins seem particularly likely to exhibit extensive reliance on learning, and social learning in particular, for the following reasons (Fragaszy, Fedigan, and Visalberghi, in prep). First, several aspects of capuchin ecology promote behavioral flexibility. (1) The genus *Cebus* occupies a wider geographic area than any other New World genus aside from *Alouatta* (Emmons, 1997), and uses many different habitat types. Thus, capuchins face a wide variety of environmental challenges. (2) Capuchins include a wide range of plants and animals in their diets

(Freese, 1976; Terborgh, 1983), and diets vary even between adjacent groups at the same site (Chapman and Fedigan, 1990). (3) Capuchins are capable of producing a great variety of motor movements, enabling them to have more "building blocks" in their behavioral repertoire that can be used in the production of new behaviors (see Huffman and Hirata, this volume). For example, capuchins, like chimpanzees, spontaneously exhibit many types of tool use in laboratory settings (e.g., using objects as hammers, probes, levers, containers, etc.: Fragaszy et al., in press; Westergaard, 1994, 1995). Occasionally they use objects as tools in the wild as well (see Boinski, this volume, for a review). Capuchins' propensity for tool use in captivity would seem to make them likely candidates for "material culture" (sensu McGrew, 1992; van Schaik et al., 1999) in the wild.

In addition to the above-mentioned factors that are expected to favor innovation and advanced generalized learning capacities in capuchins, there are several factors that would seem to favor social learning in particular, in a variety of behavioral domains:

- (1) Because capuchins are extraordinarily tolerant of the close proximity of others (particularly immatures) while they are foraging (Perry and Rose, 1994), there is ample opportunity for group members to observe food choice and processing. Documentation of learning opportunity does not, of course, necessarily demonstrate that social learning is actually occurring (see Chapter 1).
- (2) Interactions with members of other species are typically also social activities; i.e. they involve multiple capuchins mobbing a predator, chasing a prey item, or harassing an ecologically

neutral species (Rose et al., in prep). Therefore, there is ample opportunity for young animals to observe adults' mode of interaction with other species.

(3) Capuchins rely on one another's cooperation in a number of important behavioral domains: e.g. for protection from predators, for cooperation in within-group aggression, for expulsion of would-be (and potentially infanticidal) immigrants (Perry, 1996a,b, 1997, 1998a,b, in press; Rose, 1994). Thus, they have devised many means of negotiating aspects of their social relationships. Some of these communication signals are fairly stereotypical, but others appear to be more flexible, and hence prime candidates for traditions (Perry, unpubl. data).

In addition to these reasons why we expect capuchins to show an unusual degree of social learning (beyond most primates), we also expect them to show typical degrees of social learning propensities in the domain of vocal communication (in which social learning has been documented for vocal usage and comprehension – e.g. Cheney and Seyfarth, 1990; see also Janik and Slater, this volume).

In this chapter, we review how capuchin monkeys at four sites in Costa Rica vary in social connections, in behavior toward other species, and in feeding techniques. This work adopts some of the logic of the “Group Contrast” approach to identify candidate traditions (see Chapter 1). We also seek evidence of traditions within groups in a joint analysis of patterns of acquisition by individuals and their patterns of social affiliation, adopting the process model of traditions laid out in Chapter 1. We are clearly at the beginning of this project. This chapter constitutes a preliminary report, not a definitive statement. More important, this chapter serves

as an example of how researchers can move from using a Group Contrast approach (which prompted our initial inquiries) to using the process model to guide the study of potential traditions in nonhuman animals living in natural conditions.

## **1. Methods**

### 1.1 The study sites

There have been multiple long-term studies of groups of *Cebus capucinus* (the white-faced capuchin monkey). The sites of these studies are closely spaced geographically, thus increasing the N for these analyses and thereby minimizing the likelihood of substantive ecological or genetic differences between study populations (addressing the concerns of those adopting a Group Contrast approach). Figure 14.1 shows the locations of the study sites. Two of the study sites, Palo Verde (hereafter PV) and Lomas Barbudal (hereafter LB), are connected by a thin forest corridor, and wider corridors were available until quite recently. Hence, it is safe to assume that there has been genetic intermingling of these two populations at least until the past generation, and probably continuing into the present. Santa Rosa (hereafter SR) is about 50 km from Lomas Barbudal. It is not known exactly when deforestation would have separated these two populations, but it probably occurred sometime within the past 30-50 years. All three of these sites consist largely of tropical dry forests and have broadly overlapping plant species lists. The fourth site, Curú, is least similar to the others; it is a coastal forest, including most of the dry forest plants but also some species not present at the other three sites. It is not known when Curú

became geographically isolated from the other sites, but it probably happened within the past 50 years.

- Insert Figure 14.1 here -

Detailed descriptions of the sites are available in other publications (Lomas Barbudal: Frankie, Winston, Newstrom, and Barthell, 1988; Santa Rosa: Fedigan, Rose, and Avila, 1996; Hartshorn, 1983; Palo Verde: Panger, 1997, 1998). Detailed descriptions of habitat are unavailable for Curú. Secondary dry forest is the most common habitat type at all sites. The monkeys' ranges at LB include far more riparian forest than is typical at the other sites. Curú and Nancite group at Santa Rosa both have some coastal forest, including mangroves, which is lacking for other study groups. PV monkeys have access to a large seasonal marsh, though they rarely utilize it while foraging. There are many domestic fruit trees at Curú, which the monkeys frequent. <sup>1</sup>

## 1.2 The data sets

The data discussed in this chapter come from 10 different researchers studying 13 social groups of monkeys at 4 sites. In most cases, the data sets were collected to answer quite different questions than those addressed in this paper, so the methods used vary from study to study, and not all data sets can be used to address all topics in this chapter. The full data set of 20,786 contact hours is shown in Table 14.1. Approximately 19,000 hours were used for

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<sup>1</sup>

analysis of social conventions; smaller subsets of the data were used for analysis of food processing and interspecific interactions, as described below.

- Insert Table 14.1 here -

The Lomas Barbudal researchers (Perry, Manson, Gros-Louis, and Pyle) all studied social behavior. Their methods consisted of focal animal follows (hereafter, follows), during which all-occurrence sampling of social behavior involving a single focal animal was noted along with 2.5-minute scan samples of activity (including foraging behaviors) and proximity of other group members to the focal animal. The length of focal samples was typically 10 minutes, though the standard sampling protocol was supplemented by 4-hour dyad follows in 1997 (Perry) and all-day focal animal follows in 2001 (Perry and Manson). Extensive ad lib data were collected in all years of the study. Adults as well as juveniles were focal subjects at LB during most years. All of the data from PV were collected by Panger, who focused on object manipulation and handedness in all age-sex classes and collected her data primarily in the form of 10-minute follows and ad lib data. Baker studied fur rubbing in members of all age-sexes and provided all of the observations for Curú. Most of the data included from her study come from ad libitum observations. The following researchers all collected data on some aspect of social behavior at SR, though they varied as to the age-sex classes studied: Fedigan (adults), Rose (adults and subadults), Jack (adult and juvenile males), and MacKinnon (primarily infants and juveniles, but also some data on adults). Most data were in the form of 10- or 15-minute follows

supplemented by ad lib data and scans. Further details about the data set are provided in Perry, Baker, Fedigan, Gros-Louis, Jack, MacKinnon, Manson, Panger, Pyle and Rose, in press.

## **2. The study animal**

White-faced capuchin monkeys live in relatively stable, female philopatric social groups. The closest bonds (measured by proximity and grooming frequencies) are typically among female-female dyads (Perry 1996, Rose 1998). The alpha male is highly central and has much closer relationships with females than do subordinate males (Perry 1997), but subordinate males do regularly associate with other group members, particularly with juveniles (Perry 1998b). Capuchins are exceedingly tolerant of close-range observation and begging during foraging (Perry & Rose 1994). When resting or foraging on fruit, it is fairly common for the group to be compact enough that most group members can be seen from a single vantage point, at least during the dry season. However, during foraging for insects or travelling, the group is often widely dispersed such that only a few monkeys can be seen at any one time.

Group size at SR is about 18 animals and 19 at PV, though group size for the 2 study groups at LB has ranged from 20-37 (Fedigan et al., 1996; Panger, 1997; Perry, unpubl. data). Sex ratio at SR and PV is 1 male to 1.3 females and 1.2 females, respectively (Fedigan et al., 1996; Panger, 1997). At LB, sex ratio is closer to 1 male to 2 females, and immatures constitute about 55% of the population (Perry, unpubl. data). Thus, although group sizes were a bit larger and groups contained more females in LB than at SR and PV, the slight differences in

demography between the three main sites seem insufficient to explain the inter-site behavioral differences noted below.

### **3. Social conventions**

#### 3.1 Operational definitions

Social conventions are dyadic social behaviors of a communicative nature that are shared among members of particular social networks. Although much work has been done on vocal traditions in birds and marine mammals (see the review by Janik and Slater, this volume), and many of the geographically distinct communication patterns in birds might well be termed “social conventions,” there is surprisingly little in the primate literature about social conventions. Some noteworthy exceptions include unique grooming styles in Japanese macaques (Tanaka, 1995, 1998) and chimpanzees (Boesch, 1996a,b; de Waal and Seres, 1997; McGrew and Tutin, 1978; Nakamura, McGrew, Marchant, and Nishida, 2000; Whiten et al., 1999), such as social scratching, hand-clasp grooming, and leaf grooming, which are found only in particular social networks or sites. Some social conventions, such as leaf-clipping (Boesch, 1996a,b) are exhibited at multiple sites in identical form, but are used to convey different meanings at different sites. Other social conventions are different in their form, yet are apparently used to convey the same meaning (e.g. leaf-clipping and knuckle-knocking are both used by chimpanzees at different sites in the context of courtship: Boesch, 1996b).

Most communicative signals in primates are standard elements of the species-typical behavioral repertoire. Although a certain amount of social influence may be necessary to

facilitate a juvenile primate's proper contextual usage of, and response to, particular signals, the production of these signals is relatively inflexible developmentally (Seyfarth and Cheney, 1997; see also Janik and Slater, this volume). We were interested not so much in documenting the ontogeny of species-typical signals, but in documenting the innovation and subsequent acquisition by new practitioners of signals that are not part of the species-typical repertoire. As explained in chapter one of this volume, we defined a behavioral tradition as a behavioral practice that is (1) relatively long-lasting, (2) shared among members of a group, and (3) the generation of the practice in new individuals is aided to a measurable degree by social context. We imposed some additional criteria so as to be conservative in our assessments of the likelihood that these behaviors are traditions (see Perry et al., in press, for discussion of the rationale for these criteria):

(1) The trait in question must exhibit some intergroup variation – i.e. be present in some groups and absent in others. To qualify as unequivocally present in a particular group, the behavior had to have been seen at a rate of at least once per hundred hours of observation, and must have been performed by at least 3 different individuals. To qualify as absent in a particular group, the behavior must never have been seen, and the observer must have logged at least 250 hours of observation.

(2) The trait in question must exhibit some within-group variation, and there must be an increase over time in the number of performers of the behavior. Whenever possible, we tried to document more than 2 links in a social transmission chain (i.e. when B acquires a behavior “from” A, that

is one link; when C acquires the same behavior “from” B, that is a second link), but gaps in observation did not permit the reliable construction of social transmission chains at all sites.

(3) The behavior must endure, spanning at least 6 months within a particular group.

Using an electronic network, we invited capuchin researchers to submit behaviors that they considered to be likely candidates for a behavioral tradition. Many behaviors were quickly dismissed from our analysis because they were observed in a single individual, or because they were exhibited universally (thus making it difficult to determine social contribution to their acquisition). The following behaviors remained as likely candidates for behavioral traditions: hand-sniffing, sucking of body parts, and “games” (see below for definitions, and Perry et al., in press for further details). Each potential tradition is discussed in turn, and further details for all of these behavioral patterns are provided in Perry et al. (in press).

## 3.2 The behaviors

### *3.2.1 Hand-sniffing*

In “hand-sniffing,” one monkey inserts his/her fingers up the other’s nose or cups his/her hand over the nose and mouth of the other monkey. This behavior is often performed mutually, with each monkey inserting his/her fingers in or over the mouth of the other. The behavior can be initiated either by placing one’s own hand on the partner’s face, or by seizing the partner’s hand and placing it on one’s own nose. Hand-sniffing can last for several minutes at a time, and the participants have a trance-like expression on their faces while performing it. Hand-sniffing qualified as a likely behavioral tradition according to our criteria: (a) social context apparently

contributed to the generation of the practice in new individuals. It was common in 5 groups and clearly absent in 3 groups (and one site), and appeared not to be universal at any site (see Figure 14.2), (b) it was possible to document an increase in the number of performers for 2 groups, and (c) the behavior was durable for 6 groups. Even at sites where it reached high frequencies, it did not remain a permanent part of the behavioral repertoire. For example, hand-sniffing was common among female-female dyads at LB for a period of 7 years, and disappeared from the repertoire when the most avid hand-sniffer vanished from the group. In SR's CP group, hand-sniffing was common among male-male dyads in 1986 and vanished from the repertoire for a period of several years (approximately a decade) before reappearing primarily among male-female dyads. Hand-sniffing was statistically associated with grooming in female-female dyads at LB (Perry, 1996). At PV, dyads that hand-sniffed spent more time in close proximity than did dyads that never hand-sniffed (Perry et al., in press). Although hand-sniffing tended to be associated with particular age-sex classes within each social group, there was no consistency across social groups regarding which age-sex exhibited the behavior most predominantly. For example, hand-sniffing was almost exclusively a female-female behavior in one group at LB, whereas it was seen primarily among male-male dyads at SR (with the exception of CP group post-1996) and primarily among male-female dyads at PV and in SR's CP group (post-1996). Further details about hand-sniffing (intersite variation in form, temporal distribution, and distribution across social networks) are provided in Perry et al. (in press).

- Insert Figure 14.2 here -

### *3.2.2 Sucking of body parts*

In some groups, particular dyads sucked on one another's fingers, toes, ears or tails for prolonged periods of time. Sucking, like hand-sniffing, occurred during periods of relaxed socializing, such as grooming or resting in contact, when the pair was fairly isolated from other group members. Sucking was particularly common in one group (Rambo's group) at LB, in which monkeys often mutually sucked one another's body parts, sometimes for over an hour at a time. Over half of all observations at LB involved mutual sucking, and the behavior occurred in male-male and male-female dyads. Although 13 different individuals were seen to engage in sucking (11 of them taking an active sucking role), 88% of observations included a single young adult male. The behavior has virtually vanished since his disappearance. Some tail sucking was observed involving a male-male dyad in the neighboring group, but they performed this behavior infrequently. The only other site at which sucking of body parts was common was SR, where one male routinely sucked the fingers of his closest male associate; these two males migrated together from group to group. Sucking met our third criterion for being a social tradition (i.e. it was found in some sites and groups, but not others, and it was durable). However, it was difficult to document social contribution to acquisition except on the basis of its distribution, and it was difficult to document expansion in the number of performers (criterion 2) because we were not sure when the behavior entered the repertoire or how individuals' acquisitions of the behavior coincided with the timing of field seasons. Most of the data on sucking at LB were collected during the first 7 months for which behavioral data had been collected on Rambo's

group, and we could not know whether we were seeing the first occurrences of sucking for any particular dyad.

### *3.2.3 Games*

Three of the behaviors observed that were candidates for traditions were quite similar in their form and social context, and we termed them “games” because they were often initiated in a play context. Unlike rough-and-tumble play, they were of a quiet, relaxed nature, and tended to occur when the two game partners were relatively isolated from the rest of the group. Grooming of the face or slow motion wrestling often preceded these games, and the two partners maintained a quiet focus on one another that is fairly unusual for capuchins. All three games involve two partners trying to extract something from one another’s mouths. Another element they have in common is that there is frequently turn-taking, with the partners switching roles repeatedly during a bout of game-playing. Partner A will hold the prized object (partner B’s finger or hair, or an inanimate object) tightly in his/her mouth, while the partner B uses hands, feet and mouth to try to pry open A’s mouth and retrieve the object. Once B has succeeded in prying the object from A’s mouth, he either reinserts it to begin the game anew, or the monkeys switch roles. There were three basic variants of the game. In the “Finger-in-Mouth” (FIM) game, one partner bites down hard enough on the other’s finger that it is quite difficult to remove, but is not damaged. In the “hair” game, one monkey bites a large tuft of hair out of the face or shoulder of the other, and they forcibly pass the hair from mouth to mouth until it has all fallen out, at which time one of them bites another tuft of hair from the partner’s shoulder.

Although both the finger-biting and hair-biting look extremely uncomfortable, the animals apparently enjoy the activity enough to volunteer for another round of the game. In the “toy” game, the monkeys play with some object – a twig, green or otherwise inedible fruit, a piece of bark, or a leaf, for example – passing it back and forth until it is too mangled to use. No one eats the toy.

These games were observed exclusively in Abby’s group at LB, with the exception of the toy game, which was also played in virtually identical form at Curú. Circumstantial evidence suggests that all three games at LB were invented by a single individual, Guapo, who was a subordinate young adult male at the time. Guapo was always the first player observed to play these games, and also the most frequent player, at least in the early years of observation. After becoming alpha male in 1999, he ceased to play games, but the games continued to be played by other monkeys (albeit at a lower rate) after Guapo ceased to play. It was possible to create social transmission chains for all three games at LB (see Figures 14.3-14.5). At Curú, however, the toy game was already widespread when Baker’s observations began (i.e. approximately half of all group members played it), and so it was impossible to document the social transmission process. At Curú, only same-sexed adults played the game, though both sexes played with juveniles, who may have been responsible for transmitting the behavior from one sex to the other. In figures 3-5, arrows show the probable transmission of the behavior from one individual to another at LB. Dotted lines connect those individuals who played the game with one another, but who had previously played it with someone else. The males who acquired games from Guapo did so as

juveniles, while most of the females learned the behavior as adults. The most avid players were dyads including one adult male (usually Guapo) and one juvenile male; to our knowledge, most game players were not matrilineal kin. All three games qualified as traditions according to our criteria: (a) social context contributed to their acquisition, (b) we were able to document social transmission in detail at LB: there were 2 documented links in the FIM game transmission chain, and 3 in the hair and toy games, and (c) these games were highly durable, lasting for 10 years for the FIM game, 10 years for the hair game (which was still being played in 2001 by two male emigrants from Abby's group who are currently residing in an all-male group), and 9 years for the toy game.

- Insert Figures 14.3,4,5 here -

### 3.3 Explaining the geographic and temporal patterning of social conventions

The geographic and temporal patterning of the observed traditions (Figure 14.2) is puzzling in many ways. First, bizarre behaviors such as hand-sniffing and the toy game spring up at multiple sites that are too far apart to permit migration between sites. The most likely explanation is that these behaviors were independently invented at multiple sites. As Huffman & Hirata point out (this vol.), each species has particular perceptual biases and a finite set of movement patterns that make them more likely to create certain types of innovations than others. They have a limited set of "building blocks" in their behavioral repertoire that they can recombine to produce innovations. Many of the behavioral elements that are present in hand-sniffing and in these games are elements that are borrowed from the foraging repertoire and are

common motor actions in the monkeys. For example, capuchins frequently poke their fingers into small holes and crevices during foraging; therefore, it does not require much stretching of the imagination for them to insert fingers up their companions' nostrils or in their mouths. The task of removing fingers, toys or hair from a partner's mouth also involves many of the skills that are typically practiced in the course of extractive foraging: prying, digging, probing, and pulling. Thus, it is no surprise that the traditional social conventions found at different sites share many elements. The tricky part of creating new social conventions is not so much stringing together some "building blocks" from other parts of the behavioral repertoire in a novel combination, but rather persuading other group members to cooperate in the performance of these new "rituals." For example, whereas it may be perfectly comfortable for the innovator to stick his/her fingers up some one else's nostril, it may seem surprising and uncomfortable to the recipient of these actions initially to feel someone's long fingernails in his/her delicate nasal passages. And it may also be difficult to induce the partner to learn both roles in the interaction for those behaviors (such as the games) that involve role reversals.

### 3.4 What is the function of social conventions?

It is possible that although the social conventions described above show convergences with regard to their form, they do not share common function (as in the chimpanzee example in which leaf-clipping is used for different purposes at different sites – Boesch, 1996b). However, all of the traditional social conventions described do share some noteworthy elements in common, which are suggestive of a common function: (a) these behaviors are performed in

relaxed social contexts (grooming or slow play) by dyads that are fairly isolated from the rest of the group, (b) the monkeys slow down and concentrate on the activity, with trance-like expressions on their faces, for long periods of time; this is a striking deviation from the rest of the capuchin's daily routine; (c) all of these behaviors involve a certain amount of risk or discomfort. Hand-sniffers risk laceration of their nostrils from fingernails, and also have their movement severely restricted. The hair game involves the presumably painful removal of large tufts of hair. The FIM game and the sucking conventions involve the insertion of body parts between the sharp teeth of another monkey. Since capuchins routinely lose digits and tail tips in bite injuries, it is safe to assume that a monkey would not voluntarily insert a finger or tail in someone else's mouth unless s/he trusted that individual. The high level of risk involved in these conventions suggests that they may be ways of testing the bonds between individuals (Zahavi, 1977; see also Smuts and Watanabe, 1990).

Zahavi (1977) proposed that stressful stimuli are ideally suited for the testing of bonds. Such a signal would have a strong sensual component, such that it would be perceived as pleasurable if the relationship is on solid ground, but aversive if the relationship was not good. A French kiss is a good example of such a signal in humans. Unlike most signals, the important information is not contained in the signal itself, but in the recipient's response to the signal. For example, if A sticks her finger up B's nose and B responds positively, this could indicate to A that B is positively disposed to A and likely to be supportive in the near future. If B responds

apathetically or negatively to having A's fingers up her nose, this could tell B that A is not positively disposed to her and is unlikely to be a reliable source of aid in the near future.

Another body of theory relevant to explaining the function of traditional social conventions is Collins' theories regarding "interaction rituals," which comes from microsociology and was originally designed primarily to explain the role of human conversations in building up social structures (Collins, 1981, 1993). Collins assumes that, because humans cannot assess their exact positions in the power structure of the group, they use the emotional tones generated from conversations as cues to the way conversational partners value them relative to other people. The exact content of these conversations is virtually irrelevant compared to the affective displays of the participants. It is the enthusiasm, coordination or agreement, and engagement of the partners during the interaction that informs partners about their willingness to support one another in the future. In capuchins, therefore, it may not matter whether the task at hand is extracting a stick from someone else's mouth, or inserting fingers in one another's noses. What is important is that both monkeys agree on what is to be done and who is to play which role, and that they focus deeply on this task for a long period of time, coordinating their movements.

### 3.5 Design features of social conventions

What design features in a signal would be optimal for providing information regarding emotional engagement and ability to cooperate? If the adaptive problem is the design an interaction ritual that challenges the animals' abilities to coordinate their actions and understand

one another's behavioral goals, thus forcing them to devote their full attention to the social partner, then the following features seem desirable for a bond-testing behavior: (a) complex behavioral sequences, rather than simple ones, (b) turn taking and/or role reversals, and (c) flexibility and individually idiosyncratic forms, such that partners will need to familiarize themselves with one another's quirks and adjust their own behavior to produce a mutually satisfying interaction. It is important to note that, whereas such flexible bond-testing signals may be highly appropriate for eliciting information about the quality of relationships in dyads that already have a fairly comfortable relationship, due to the richness of the information they afford, they are not always superior to more stereotyped, species-universal signals. The use of such idiosyncratic signals would be too risky in the very earliest stages of relationship formation, when the two individuals have not yet sorted out their dominance ranks and do not know what to expect from one another or whether they can trust one another; in such cases, more stereotyped signals would be more appropriate for communicating about their relationship.

### 3.6 Stability of social conventions

Because the motor details of these traditional social conventions vary and are expected to “mutate” slightly as new practitioners are added, these social conventions are not expected to be highly stable in their form over long periods of time. Ontogenetic ritualization, the social learning process most likely to produce the social conventions described in this chapter, is a transmission process that affords low fidelity, and therefore is unlikely to result in stable traditions spanning multiple generations (Boesch and Tomasello, 1998; Tomasello and Call,

1997, p. 309). Although the basic structure of the convention may stay the same for several links in a transmission chain, some of the fine details are expected to change, since part of the presumed adaptive value of this sort of signal is its malleability, which requires more focus on the part of the practitioners and hence provides more information about emotional engagement. Indeed, there is evidence in our data sets for inter-dyadic variation in the precise details of these rituals. Traditional social conventions are expected to dissolve when key members of social networks die or emigrate. If our hypothesis about the function of these social conventions is correct, then we might expect to find similar sorts of traditions in other species that have complex social relationships and signals that are apparently designed for communicating about their cooperative relationships.

#### **4. Food processing**

##### 4.1 Methods and data

Because capuchins are so well known for their manipulative behavior and their skill at extractive foraging, we thought that we might find evidence for traditions among the wide range of techniques used for the processing of particularly hard-to-open fruits (see Boinski, this volume). Our first step in investigating food processing techniques (begun in 1999) was to look for differences in the ways foods were prepared. We began by comparing the food lists for SR, LB, and PV, to identify foods (both plant and animal) that were common to more than one site. Then we asked researchers to describe the techniques used by their monkeys to process each food on the list. Only one researcher (Panger) had collected detailed systematic data on food

processing techniques during focal follows. Perry and Rose did, however, collect ad lib data on the typical patterns of food processing for each food type, even though they did not have data on each individual's processing style for each food. Gros-Louis, MacKinnon and Baker also supplemented these data sets with additional observations. Once we had made a "short list" of foods for which we suspected extensive variation in processing technique, Perry (in 2001) and Gros-Louis (in 2000) went back to the field and collected more systematic observations on the range of techniques used by each individual for those foods we had identified as potentially interesting.

#### 4.2 Intersite differences in processing

The results of this investigation of food processing are described in detail in Panger, Perry, Rose, Gros-Louis, Vogel, MacKinnon, and Baker (in press), and will be summarized briefly here. Forty-nine plant and 12 animal foods overlapped between at least two of the three main study sites. Of these, intersite variation in processing was noted for 20 foods, though in some cases only one individual at one site was observed to use the unusual technique. For 17 of the 20 foods that were processed differently at one or more sites, the difference consisted of the animals at one site pounding and/or rubbing the food, whereas animals at other sites declined to pound or rub those particular food species. Pounding (beating the food against a substrate with one or two hands), rubbing (sliding the food against a substrate while holding it in one or two hands) and tapping (rapid, rhythmic percussive contact of a finger tip against an object) are quite common elements in the standard behavioral repertoire of capuchins, and therefore pounding,

rubbing or tapping a food does not represent a particularly striking variant. However, six other processing variations involved less common, and hence potentially more innovative, behavior patterns. The differences associated with two of the food species involved a behavior called “leaf wrap”, two others involved tapping with the fingertips, one involved fulcrum-use, and one involved following army ant swarms. The LB and SR capuchins sometimes wrap noxious *Automeris* caterpillars in leaves and then scrub them against a branch, removing urticating hairs before eating the caterpillar (i.e., ‘leaf wrap’). One SR monkey wrapped *Sloanea* fruits in leaves to scrub the irritating hairs off. The other striking intersite difference was army ant following. At Curú and SR, but not at PV or LB, monkeys actively followed columns of army ants as they foraged, capturing the insects flushed out by the ants. Army ants are quite common at LB and PV, and yet the ants are ignored by these monkeys.

Table 14.2 details the processing techniques that differed across sites, and the frequency of use of these patterns within groups in general terms, following Whiten et al. (1999) approximately. In Table 14.2, the category "Eat" means that the food was ingested, but no sophisticated processing technique was employed: the food was simply placed in the mouth, chewed, and swallowed. In all, there were a total of 40 different processing techniques reported for the three main study sites (since several of the 20 food species that showed food preparation differences across the sites were processed differently in more than one way). Of these 40 differences, 5 were exhibited by a single individual, 26 were exhibited by multiple individuals in

one or more groups, and 9 were exhibited by all members of at least one age/sex class in one or more groups.

- Insert Table 14.2 here -

#### 4.3. The role of social learning in establishing individual differences in processing

It is premature to label particular food processing behaviors as traditions in the absence of data indicating that social influence plays a role in the acquisition of particular foraging techniques. As argued in Chapter 1, although it is impossible to *directly* establish a causal role for social learning in creating intersite variation, and because it is impossible in principle to eliminate other potential factors the contribution of geographic variation in techniques, it should be possible to examine the role of social learning in establishing *within*-group differences in foraging techniques. This is the process model of traditions, as laid out in Chapter 1. Moreover, if social influence proves important for explaining within-group patterns of variation, then these behaviors can be identified as traditions. The inference is then stronger that social learning can be responsible at least in part for between-group variation in processing techniques, if one wants to explain variation at that level as well.

In Panger's data set, for which there were detailed data on intragroup variation in processing techniques, we can examine the correspondence between proximity patterns and the distribution of processing techniques across group members. In many cases, dyads that shared in common a relatively rare foraging technique (i.e. the less common of two or more techniques used for the same food) also shared relatively high proximity scores (i.e. they spent a lot of time

together). Statistical comparison was only possible for those foods in which more than one dyad shared a quirky processing technique. Four foods (*Annona reticulata*, *Mangifera indica*, *Randia* spp., and *Stemmadenia donnell-smithii*) met these criteria. In all four cases, the matched dyads (i.e. those sharing the odd technique) had higher proximity scores than the remaining dyads, and the difference was statistically significant in three cases.

The most difficult question to address in field studies is what role social learning plays in the production of shared practices. Clearly, many of the interindividual and intersite differences observed in this study could be attributable to individual experience independent of social influences. This is particularly true for variants such as "pound" or "rub," in which the animal is merely utilizing a standard element of the behavioral repertoire in a slightly novel context. Slight differences in the physical properties of these fruits (e.g. differences in soil quality, which enable the plants at some sites to grow harder rinds than those at other sites; or differences in the monkeys' tendency to choose mature fruits rather than green ones, which could stem from the availability of alternative food sources) could lead to intersite differences in the tendency to pound a particular species of fruit. However, Panger's data clearly show that, even for relatively common processing techniques such as "pound" or "rub," the distinctive technique is shared by those monkeys that spend more time together, which implicates social context as promoting shared usage.

## **5. Interspecific interactions**

### 5.1 The data sets

Few studies have attempted to discern the role of social learning in interactions with allospecifics (members of other species), although it is certainly plausible that traditions could form in this behavioral domain. We examined datasets from three sites to assess the response of capuchins to vertebrates that could be classified as potential predators, potential prey, feeding competitors, or ecologically neutral. The data were drawn primarily from the following sources: Perry, Manson and Gros-Louis systematically recorded responses to all allospecifics during 3703 hours of observation of one group at LB during 1991-1993; these observations were supplemented with anecdotes regarding rarely encountered animals from subsequent years and an additional monkey group from Perry's, Manson's and Gros-Louis's datasets. The majority of the SR observations came from Rose's observations (2682 hours of data from 1991 and 1995-96) and Jack's observations (>1500 hours from 1997-99) of 5 groups; K.MacKinnon contributed additional anecdotes. All of the PV data (>1200 observation hours of 3 groups) were contributed by M. Panger.

## 5.2 Prey

Capuchins were highly predatory at all three sites, though a wider range of prey was taken at SR and at LB than at PV (Rose, Perry, Panger, Jack, Manson, Gros-Louis, MacKinnon, and Vogel, in prep). There were some interesting differences between LB and SR in the ways the monkeys interacted with adult squirrels, all of which are discussed in more detail in Rose et al. (in prep): Adult squirrels were hunted at both sites, but hunting rates were higher at SR than at LB. LB capuchins encountered squirrels at lower rates than did SR monkeys, but they were

more likely to hunt squirrels once they were encountered, and LB monkeys were more successful in their squirrel hunts than were SR monkeys. The most likely explanation for the difference in success rate between the two sites is that the LB monkeys have a different kill technique than do the SR monkeys. LB monkeys consistently kill squirrels with a rapid bite to the head or neck as soon as they catch it; in contrast, SR monkeys try to eat the squirrel before killing it, and squirrels are ultimately killed by a variety of inefficient techniques. SR monkeys also appear to engage in active search for squirrels (i.e. quiet, vigilant, stalking behavior without other forms of foraging, in areas of high squirrel abundance), which is a hunting technique not observed at LB. Aside from these differences in squirrel hunting, there are no other striking differences between sites in predatory behavior that can plausibly be attributed to social learning. Although this is the only case in which a behavioral difference (e.g. squirrel neck biting) is homogenous within a group, there are many other complex hunting techniques (e.g. drowning coati pups, baiting coati mothers off the nest, removing currawong eggs from under the mother via a hole created in the bottom of the nest) that are practiced by some but not all group members; these could conceivably be acquired at least in part via social learning. We currently lack the sorts of evidence necessary to adequately assess the role of social learning in establishing these variations in predatory behavior.

### 5.3 Predators

In general, there was strong intersite agreement about which animals were considered potential predators; boas, caiman, rattlesnakes, felids, canids, large raptors, and unfamiliar

humans were consistently greeted with alarm calls and mobbing responses (Rose et al., in prep). It is important to note that behavioral uniformity across individuals and sites does not necessarily imply that there is no social contribution to learning (see Galef, this volume; Dewar, this volume). If there is strong enough selective pressure for the monkeys to recognize a species as dangerous, they should all converge on a similar response to the species – e.g. alarm calling, fleeing, and/or mobbing from a safe distance. Given that it is very risky for young animals to discover the properties of potential predators via trial and error, it makes sense to rely heavily on social learning in this particular behavioral domain, at least in cases in which asocial cues are not necessarily reliable (see Dewar, this volume). Even if fellow group mates are overly conservative in their assessment of the danger involved in interacting closely with predators, naïve animals will be better off using social cues than asocial cues as long as exhibiting an antipredator response or giving up feeding opportunities entailed by avoiding the potential predator is not too costly.

In many animals, juveniles' response to members of other species is influenced by adults' responses. In vervets, for example (Cheney and Seyfarth, 1990), there are several different types of alarm calls, including distinct calls for leopards, eagles, and pythons, and juveniles must learn the appropriate contexts for producing these calls. The appropriate response to hearing these calls is also learned: infants who had the opportunity to observe correct adult responses responded correctly to playbacks of alarm calls more frequently than did infants who did not look at adult models. There is some suggestive evidence that call usage is also influenced by the

responses of adult models to calls (Cheney and Seyfarth, 1990). Thus far, the ontogeny of anti-predator responses in capuchins has not been investigated in great detail for *C. capucinus*. Here we present some data on the demographic patterning of alarm call responses at Lomas Barbudal, the only site for which we have detailed data on juveniles as well as adults (Table 14.3). One first step in demonstrating that social learning is taking place is to document a change in behavior developmentally; this we can accomplish in this chapter. The next step, which is more difficult, is to demonstrate that this change occurs as a consequence of social experience. We will propose some ways in which the role of social influence on the development of anti-predator responses can be assessed in the field.

- Insert Table 14.3 here -

The data in Table 14.3 suggest that juveniles initially overgeneralize their alarm calls, frequently calling in response to harmless animals. Two findings stand out in particular. First, the proportion of alarm call bouts given in response to clearly harmless stimuli (e.g. nonpredatory birds, harmless snakes or even snakeskins, primatologists, frogs, coatis and inanimate objects such as dolls) decreases with age, whereas the proportion of alarm calls given to dangerous animals (e.g. dogs, boa constrictors, rattlesnakes, felids, raptors, unfamiliar humans) increases, particularly between the younger juvenile (0-18 month) and older juvenile (18 month-puberty) stages. Rose et al's investigation of capuchins' interactions with mammals found that only juveniles alarm call in response to agoutis and anteaters, and that 83% of alarm calls directed at coatis are by juveniles.

The second striking result emerging from Table 14.3 is that the rate of alarm calling increases with age, but the rate of alarm call bouts (i.e. responses to a particular stimulus) does not. This is due to an age-related increase in the number of calls given per bout, which is more extreme for males than for females. One of the most striking aspects of antipredator behavior in capuchins is the amount of time and energy that the monkeys spend alarm calling and harassing predators, particularly snakes, when they could be devoting this time to foraging or other activities. Snake mobbings may prove to be a particularly productive context for the investigation of social learning. During a snake mobbing, the monkeys gather around the snake in response to hearing an initial alarm call by the discoverer. Each monkey looks for the snake, glancing back and forth between the alarm calling monkey and the ground, as if following the gaze direction of the caller, until the snake is localized. Typically, the newcomers do not call until they have located the snake, but sometimes they give one or two tentative-sounding calls before locating the snake, and begin calling with more insistence once they begin looking in the right place to see the snake. Because boas and rattlesnakes do not move once they have been spotted, even when pelted with broken branches, they represent no danger to the monkeys once their location has been divulged to the rest of the group. Nonetheless, the monkeys remain at the site of a snake for extended periods of time, up to 45 minutes per session, calling repeatedly and menacing the snake from a safe distance. That the monkeys are willing to give up so much foraging time to stay near the snake is remarkable given the capuchins' highly constrained activity budgets (Terborgh, 1983, p. 49).

It is possible that lengthy snake mobbing sessions are beneficial to young monkeys and their parents (whose reproductive success depends upon their offspring recognizing predators) because such sessions afford juveniles an opportunity to study the properties of snakes that elicit alarm or mobbing responses from adults and compare them with the properties of snakes that do not elicit concern from adults. Juvenile capuchins do occasionally mob nondangerous snakes. It might be worth considering the possibility that capuchins are engaging in teaching when they engage in prolonged snake mobbing sessions. According to Caro and Hauser's (1992, p. 153) definition of teaching, "an individual actor A can be said to teach if it modifies its behavior only in the presence of a naïve observer, B, at some cost or at least without obtaining an immediate benefit for itself. As a result, B acquires knowledge or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do, or that it would not learn at all." It is possible that adult capuchins modify their behavior in the presence of juveniles and predators, by increasing call rate and lengthening mobbing duration in the presence of naïve animals, thus aiding naïve animals to learn how to identify predators and respond appropriately. Field experiments can help resolve this issue.

Some naturalistic observations seem to suggest that adults do modify their behavior in such a way that they may aid the learner to learn (often termed "scaffolding," following Bruner, 1982; Wood, 1980). For example, Rose (unpubl. data) reports the following intriguing anecdote from Nancite group at Santa Rosa, which is similar to instances that have been observed at Lomas. "In 1996, the group encountered and vigorously mobbed an unusually large boa

(estimated at least 2 m long and thigh thickness) resting on the ground in a semi-clearing among mangrove roots. The mobbing monkeys had already begun to disperse when the beta male arrived on the scene. He alarm called briefly at the snake, scanned for a few moments, and then went to the edge of the clearing and picked up an infant on his back who had been hanging back from the activity. The male carried the infant to a branch well above the boa, stared at it, and again began to alarm call at it. He stayed in this position for about 5 minutes, during which time the infant also stared at the snake and alarm called at it.” The male, in effect, aided the infant to inspect a dangerous predator and to practice the correct action from a safe position.

Another approach that can be taken to understanding the role of social learning in predator recognition is Dewar’s cost-benefit model (Dewar, this volume). This approach could be useful in understanding, for example, the intersite differences in the reaction to indigo snakes that are reported in Rose et al. (in prep). Indigo snakes (*Drymarchon corais*) are quite large (>2 m) nonvenomous snakes that eat small vertebrates such as fish, turtles, lizards, frogs, rodents and birds (Janzen, 1983). They have never been observed to prey on monkeys. At SR, monkeys of all age-sex classes routinely alarm call and harass indigo snakes. The LB monkeys do not alarm call in response to indigo snakes, but juveniles did harass them in 6 out of 10 encounters. At PV, the monkeys do not exhibit any fear of indigo snakes. One adult female at PV was observed to drink from a waterhole while in physical contact with a large indigo snake that was also drinking (Rose et al., in prep). These intersite differences are perplexing, but they might make more sense if we were able to sort out the relative values of social and asocial cues at the different sites. For

example, the sites may differ with regard to variables such as the proportion of snakes encountered that are dangerous.

#### 5.4 Feeding competitors

Dewar's approach might also illuminate intersite differences in capuchins' decisions as to how to treat feeding competitors (such as coatis, howling monkeys and spider monkeys) or species that are ecologically neutral. In the case of feeding competitors, the costs and benefits of ignoring the other species are different from the predator case. By ignoring the competitor when it is in a feeding tree, the capuchin may acquire less food, even if the capuchin is continuing to forage while ignoring the competitor. Most likely, asocial cues (such as whether the animal is currently feeding on a preferred food of capuchins) would be more useful than social cues for determining the optimal way to interact with allospecifics; but this is an empirical question.

Rose et al. (in prep) documented some fairly striking differences between SR and LB regarding interactions with howling monkeys. At Lomas, 80% of interactions between capuchins and howlers were aggressive, compared with 59% of interactions at SR. The LB capuchins were more vicious in their attacks on howlers, sometimes inflicting quite severe wounds on them.

Almost all of the aggression was by capuchins against howlers, but howlers reciprocated in a few instances. To the extent that encounter rate between the two species can be used as a crude proxy for level of feeding competition, the higher levels of aggression at LB relative to SR can not be attributed to greater feeding competition at LB (Rose et al., in prep); however, encounter rate is a fairly crude means of measuring feeding competition. The SR monkeys exhibited affiliation (in

the form of play) towards howlers in 10% of interactions, whereas the LB monkeys only exhibited affiliation towards howlers in 0.5% of their interactions with them. This result is a bit more difficult to explain in terms of ecological costs and benefits to the monkeys. Even more striking is the tendency of some monkeys at SR to groom and otherwise affiliate with spider monkeys, a species not present at LB. With one exception, all 10 of the monkeys who groom spider monkeys had originally come from LV group. It seems possible that the tendency to groom spider monkeys is a socially transmitted trait (Rose et al., in prep).

### 5.5 Unfamiliar humans

Rose et al. (in prep) also reported some interesting variation in the ways in which capuchins interact with unfamiliar humans. At PV, the monkeys rarely alarm-called at humans, whereas the SR monkeys alarm-called more frequently (25-75% of encounters), and the LB monkeys alarm called at humans the most frequently. Interestingly, however, the LB monkeys alarm-called almost exclusively to local farmers who were either traveling down the road bisecting the monkeys' home range or poaching in the reserve and they virtually never alarm called at tourists. Although they often harassed tourists, they very rarely harassed farmers. Clearly the monkeys were using some asocial cues from the humans to decide whether they were dangerous or not. However, the monkeys may be using some social cues as well, either by observing how other monkeys interact with the unfamiliar humans, or by observing how the primatologists interact with them.

## **6. Longevity and biological significance of traditions**

No doubt the longevity of traditions depends not only on the demographic characteristics of the population, but also on the behavioral domain in question. For example, if the precise form of the behavioral trait is well-suited to solving a particular and persistent problem, then it is likely that the tradition will be maintained with good fidelity for long periods of time. For example, anti-predator responses to a predator or a particularly clever way of processing a desirable food are behaviors that would be expected to persist for generations. We do not yet know with absolute certainty that foraging or anti-predator traditions exist in capuchins; nor do we know the durability of such putative traditions with any degree of certainty. We have better data on the longevity of traditions in the domain of social conventions. If our hypothesis about the function and design of these behaviors is correct, i.e. that the flexibility in form of such traditional social conventions is what makes them useful bond-testing signals, then it is no surprise that these traditions are short lived, lasting only a few years (approximately 7-10 years, though this may be a slightly low estimate due to censoring biases). Demographic considerations also affect the durability of traditional social conventions. Because capuchins live in small social groups, and because these conventions are practiced by only a subset of the group, the loss of one or two avid practitioners of a convention can cause the behavior to drop out of the repertoire entirely, even if many remaining group members know how to perform the behavior.

Another issue that is frequently raised is whether traditions lasting less than a generation time are biologically significant (e.g. Avital and Jablonka, 2000; McGrew, 1992, p. 77, 1998; Whiten et al., 1999). It is important to note that even short-lived traditions (“fads,” as some

would call them) can have fitness consequences for their practitioners. For example, let us assume for the moment that the traditional social conventions described in this chapter aid the monkeys enough in forming social bonds that they have positive fitness consequences. A monkey who has the capacity to develop these sorts of idiosyncratic bond-testing signals will have an advantage over monkeys who are less skilled at this form of social learning. Regardless of whether the particular traditions s/he forms survive into the next generation, practicing this behavior during his/her own lifetime will have increased her fitness.

The heuristic model of "traditions space" in chapter one of this volume provides a useful framework for thinking about how the properties of traditions vary across behavioral domains in capuchins. Regarding social conventions, we can safely assume that social contribution is absolutely essential to the production of the behavior. Not all group members acquire the behavior: it is performed by members of cliques consisting of approximately 30-60% of all group members in most cases. We cannot accurately measure tradition duration in most cases, but they appear to last about 7-10 years (i.e. less than a generation time). For the behavioral domain of food processing, we have some limited evidence that social contribution is a factor affecting the distribution of foraging techniques within groups, at least for some food species; however, it may be the case that social contribution is fairly minimal. Our data on extractive foraging at LB indicate that there is heterogeneity within groups regarding processing techniques. For example, 29% of monkeys at LB scrub their *Luehea* fruits to extract the seeds, whereas the remaining 71% pounds the fruits. Likewise, only about 77% of monkeys at LB tap branches when foraging for

insects, and only 17% of LB monkeys rub the hairs off their panama fruits when foraging. Thus far we have no data on the duration of food processing traditions (in fact, we consider it premature to label these foraging variations "traditions" until we have more evidence regarding the social contribution to the acquisition of these behaviors). Likewise, we lack data on social context necessary to discern the social contribution to predator-prey interactions and thus label them as traditions, though these data can be collected in the future. There is extreme homogeneity both within and between groups in the reactions of capuchins to potential predators, and slightly less homogeneity in their responses to potential prey and feeding competitors. These patterns of behavior are stable over long periods of time (i.e. multiple generations), presumably because they are highly adaptive.

## **7. Conclusions**

Many capuchin groups exhibit social conventions (e.g. hand-sniffing, sucking of body parts, or "games") that are specific to a large subset of a particular group. In some cases it was possible to document the social transmission process from the time of innovation until the "extinction" of the behavior. Some conventions sprang up in virtually identical form at multiple sites. Such social conventions are hypothesized to serve as tests of social bonds, and we speculate that the lability of these behaviors is a useful design feature for bond testing.

Numerous inter-site and intra-group differences in food processing techniques have been documented. In some cases it is possible to demonstrate that those animals who spend the most

time together also use the same foraging techniques, thus suggesting a role of social learning in the production of food processing techniques.

There is considerable intersite homogeneity regarding the quality of monkeys' interactions with other species, particularly when they are interacting with potential predators. However, intergroup homogeneity does not necessarily imply lack of social contribution to the behavior pattern, and we propose some ways to assess the role of social learning in predator-prey interactions.

## **8. Acknowledgements**

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 Ramon de Bagaces, Hacienda Pelón, Rancho Jojoba/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 Carnegie, Alisha Steele, Matthew Duffy, Maura Varley, Ryan Crocetto, Hannah Gilkenson, Jill Anderson, Craig Lamarsh, Sasha Gilmore, Dale Morris, Dusty Becker, 3 expeditions of Earthwatch volunteers, and 7 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, Filippo Aureli, Eva Jablonka and Andy Whiten commented on the manuscript, providing many helpful comments. Members of the UCLA Behavior, Evolution and Culture group and the contributors to the "Traditions 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 authors.

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 Leakey Foundation (3 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 (4 grants), the University of Michigan Alumnae Society, and UCLA (2 Faculty Career Development grants). MB thanks the University of California-Riverside Graduate division (3 grants), Earthwatch, UREP, and NIH-MIRT (grant to E. Rodriguez). LF's research is funded by an on-going 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, Natural Sciences and Engineering Research Council of Canada (post-graduate scholarship), Alberta Heritage Scholarship fund (Ralph Steinhauer Award), Ruggles-Gates fund for Biological Anthropology (Royal Anthropological Institute), Sigma-Xi, Faculty of Graduate Studies and Research/Department of Anthropology at the University of Alberta, and the above-mentioned NSERC grant to LF. KM's fieldwork was supported by an

NSF dissertation improvement grant (#SBR-9732926), and a UC-Berkeley Social Sciences and Humanities Research Grant. JM was supported by a UCLA 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 (3 grants) for helping to make her research possible. LR was supported by an NSERC post-graduate scholarship, NSF, National Geographic Society, the L.S.B. Leakey Foundation, Sigma Xi, and Ammonite Ltd.

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Table 14.1: Periods of data collection on social behavior at each study site

Site and study group	Time period (months/yr)	Observation hours	Principal investigators during each time period	Uses of data (S=social conventions F=food processing; I=inter-specific interactions)
LB: Abby's	5-8/90	337	SP	S*,F,I
	5-12/91	619	SP	S*,F,I*
	1-12/92	1850	SP	S*,F,I*
	1-5/93	1234	SP	S*,F,I*
	2/94	72	SP,JM	S*,F,I
	7-8/95	282	SP,JM	S*,F,I
	12/96	48	SP,JM	S*,F,I
	1-8/97	914	SP,JM,JGL	S*,F,I
	2-5/98	381	JGL	S*,F,I
	1-7/99	356	SP,JM,JGL	S*,F,I
	1-6/00	372	JGL	S*,F,I
	1-6/01	784	SP,JM	S*,F*,I
LB: Rambo's	1-8/97	964	SP,JGL	S*,F,I
	1-5/98	315	JGL	S*,F,I
	1-7/99	759	SP,JGL,JM	S*,F,I
	1-5/00	542	JGL	S*,F,I
	1-6/01	655	SP,JM	S*,F*,I
SR:Sendero	1-6/86	69	LMF	S*
	5-9/92	10	KM	S*,F,I
	1-4/93	35	KM	S*,F,I
SR:CP	1-6/86	123	LMF	S*
	1-7/91	285	LR	S*,F,I*
	5-9/92	150	KM	S*,F,I
	1-4/93	120	KM	S*,F,I
	1-9/95	405	LR	S*,F,I*
	12/95-8/96	327	LR	S*,F,I*
	1-12/98	770	KM,KJ	S*,F,I*
	1-4/99	168	KJ	S*,I*

SR: LV	1-7/91	260	LR	S*,F,I*
	5-9/92	170	KM	S*,F,I
	1-4/93	200	KM	S*,F,I
	1-9/95	656	LR	S*,F,I*
	12/95-8/96	341	LR	S*,F,I*
	1-12/98	1332	KM,KJ	S*,F,I*
	1-4/99	204	KJ	S*,F,I*
SR:Nancite	12/95-6/9	408	LR	S*,F,I*
SR: Cuajiniquil	2-12/98	264	KJ	S*,I*
	1-2/99	1	KJ	S*,I*
SR: Cafetal	3-4/99	56	KJ	S*
SR: Bosque Humido (BH)	2-12/98	588	KJ	S*,I*
	1-4/99	240	KJ	S*,I*
PV: Station Troop (ST)	4-12/95	852	MP	S*,F*,I*
	1/96	36	MP	S*,F*,I*
PV: Water Hole Troop (WHT)	3/95	84	MP	F,I*
PV: Lagoon Troop (LT)	3-7/95	228	MP	F,I*
Curú: Bette's group	8-9/91	189	MB	S*,F
	1-6/93	692.5	MB	S*,F
	7-8/94	147.5	MB	S*,F
	1-4,6-9/95	665	MB	S*,F
	7-9/96	226	MB	S*,F

\*=used for quantitative analyses presented or summarized in this chapter; otherwise, these data were used as a source of descriptions and anecdotes only

Table 14.2: Processing techniques (Tech.) that vary across sites and their use patterns (U.P.)

Food species	Lomas Barbudal		Palo Verde		Santa Rosa	
	Tech.	U.P.	Tech.	U.P.	Tech.	U.P.
<i>Acacia</i> spp. (fruit)	Eat	C	***		Rub	H
<i>Acacia</i> spp. (thorns)	Eat	C	Eat	C	Rub	H
<i>Annona reticulata</i>	Eat (rare)	H	Pound Rub	H P	Pound Rub	H H
<i>Apeiba tibouru</i>	Rub	P	***		Pound Rub	H H
<i>Bactris minor</i>	Eat (rare)	C	Pound	H	***	
<i>Cecropia peltata</i>	Eat	C	Eat	C	Pound Rub	C C
<i>Genipa americana</i>	Eat	C	***		Pound Rub	C C
<i>Mangifera indica</i>	Pound Rub Tap	H H H	Rub Tap	H H	***	
<i>Manilkara chicle</i>	Eat	C	Pound	P	Eat	H
<i>Pithecellobium saman</i>	Tap	P	Fulcrum	H	Rub Fulcrum	C H
<i>Quercus</i> spp.	Eat	C	***		Pound	H
<i>Randia</i> spp.	Pound	H	Pound Rub	H P	Eat	H
<i>Sloanea terniflora</i>	Rub	C	***		Leaf wrap Rub	P C
<i>Stemmadenia donnell-smithii</i>	Pound	P	Pound	H	Pound Rub Tap	C C C
<i>Sterculia apetala</i>	Rub (fruit inside of husk)	H	Rub (husk of fruit)	H	***	
<i>Tabebuia ochracea</i>	Pound Rub	H C	Pound Rub	H H	Eat	H
<i>Automeris</i> spp. Caterpillar	Leaf wrap Rub	H C	Rub	H	Leaf wrap Rub	H H
Insects in branches	Tap	C	Tap	C	Tap	H

			Pound	H		
Vertebrate prey (squirrels and coatis)	Pound Rub	H H	Eat (rare)	H	Pound Rub	H H
Army ant following	No		No		Yes	H

\*\*\* = food not consumed at this site

C=customary (exhibited by all members of at least one age/sex class)

H=habitual (not customary, but exhibited by multiple individuals)

P=present (exhibited by one monkey)

Table 14.3: Demographic patterning of alarm calls at Lomas Barbudal, 1991-1993.

Alarm Calls	Adult Males (n=4)	Adult Females (n=5)	Older Juveniles <sup>a</sup> (n=7)	Younger juveniles (n=5) <sup>b</sup>
calls/hr <sup>c</sup>	>>0.70	0.44	0.28	0.30
bouts/hr <sup>d</sup>	0.16	0.20	0.15	0.21
Calls/bout	>>4.45	2.22	1.85	1.44
% bouts to harmless stimulii <sup>e</sup>	5.2%	4.5%	10.6%	19.4%
% bouts to dangerous referents <sup>f</sup>	31.7%	20.2%	29.5%	14.7%

<sup>a</sup> Juveniles at least 1.5 years old that have not yet reached reproductive age

<sup>b</sup> Juveniles and infants <18 months old

<sup>c</sup> Number of calls per focal data hour, including multiple calls within a single alarm bout (i.e. response to a single stimulus). Note that adult male calls are underestimated due to frequent rapid calls within a single bout

<sup>d</sup> Number of calling bouts (in response to a single stimulus) per focal data hour

<sup>e</sup> % of bouts clearly directed toward harmless stimulus (e.g. non-predatory birds, harmless snakes, primatologists, frogs, coatis)

<sup>f</sup> % of bouts clearly directed toward potentially dangerous referent (e.g. dogs, boa constrictors, felids, raptors, unfamiliar humans)

Note: some stimuli could not clearly be assigned to either the harmless or the dangerous category (e.g. medium-large birds).

List of Figures:

Figure 1: Map of the study sites.

Figure 2: Distribution of social conventions across sites and groups. C=behavior is common (i.e. observed at least once per hundred hours of observation); R=behavior seen extremely rarely; X=behavior never seen in >250 hours of observation; ? =behavior not seen, but there is inadequate data to be confident of its absence.

Figure 3: 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 those dyads in which one member has never previously been seen to play with other partners. Dotted lines connect 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.

Figure 4: Social transmission chain for the “hair game.” See Fig. 3 for explanation.

Figure 5: Social transmission chain for the “toy passing game.” See Fig. 3 for explanation.

Figure 1

**FIGURE 1: Map of the Main Capuchin Study Sites Discussed in this Volume**

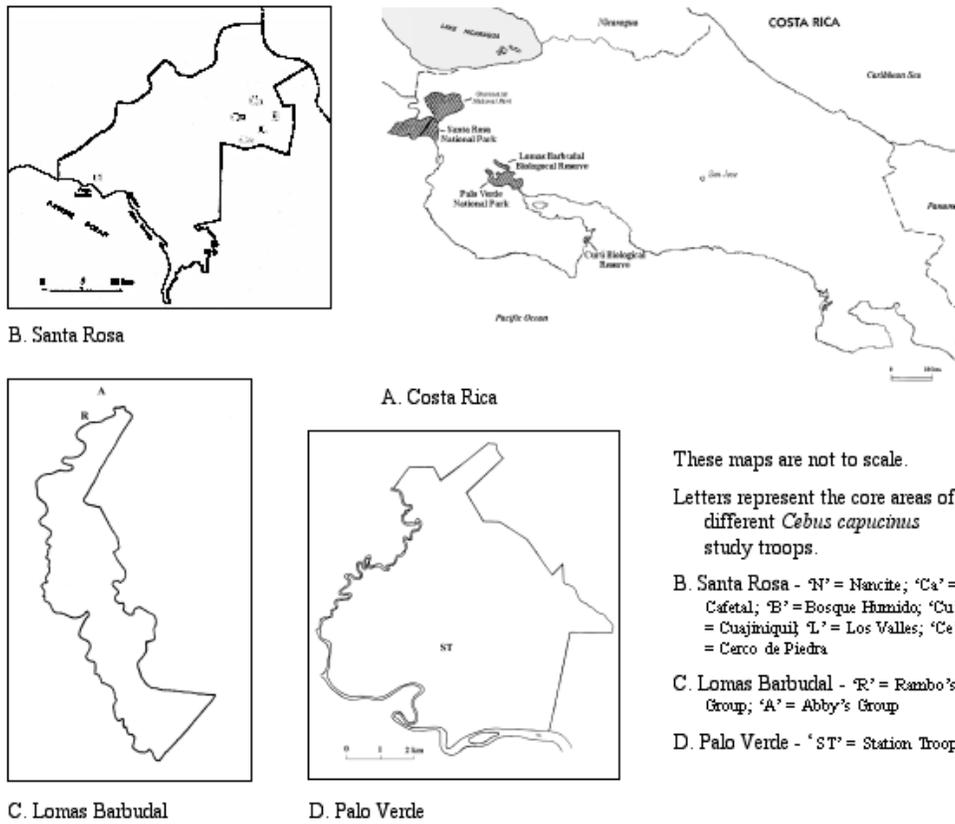


Figure 2

	Hand-sniffing	Sucking	Finger game	Hair game	Toy game
<i>Santa Rosa</i>					
Sendero	C	?	?	?	?
Cerco de Piedras	C	X	X	X	X
Los Valles	R	R	X	X	X
Nancite	X	X	X	X	X
Cafetal	?	C	?	?	?
Cuajiniquil	C	C	?	?	?
Bosque Humido	X	R	X	X	X
<i>Lomas Barbudal</i>					
Abby's	C	C	C	C	C
Rambo's	R	C	X	X	X
<i>Palo Verde</i>					
Station Troop	C	R	X	X	X
<i>Curú</i>					
Bette's group	X	R	X	X	C

Figure 3 [note: View figures at 400% for full resolution.]

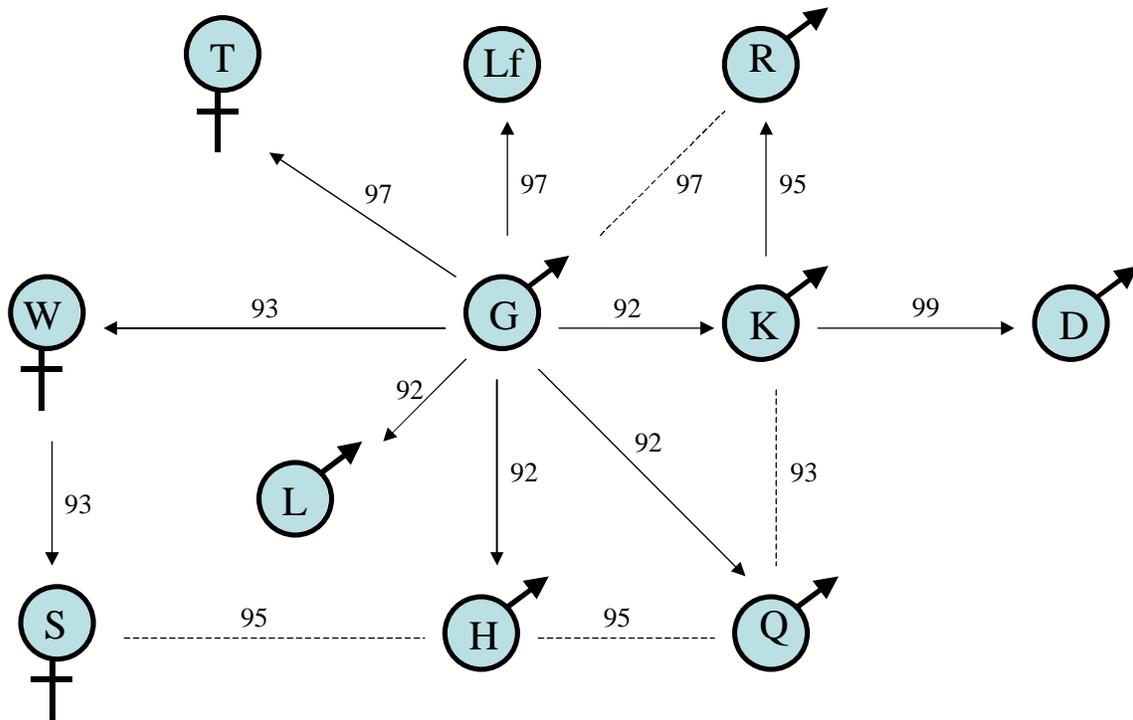


Figure 4

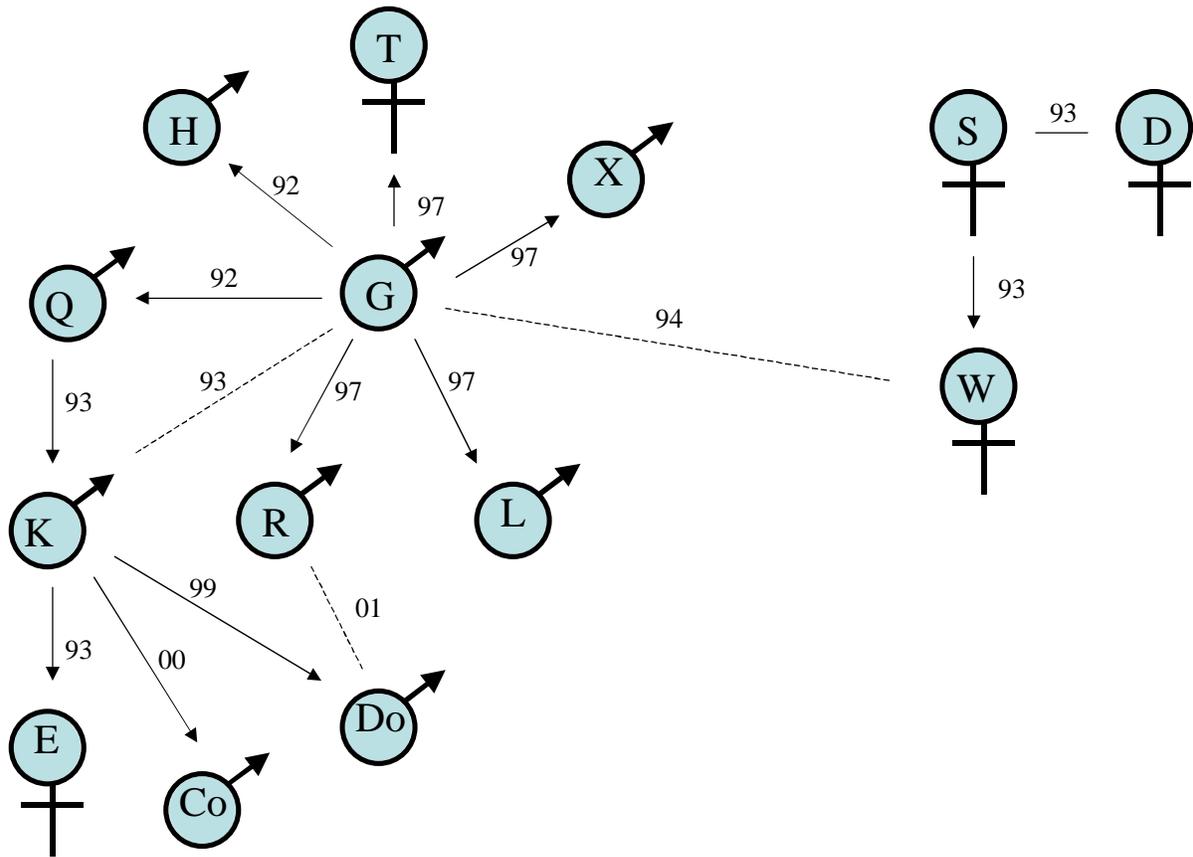


Figure 5

