Chapter 7
The Lomas Barbudal Monkey Project: Two Decades of Research on *Cebus capucinus*

Susan Perry, Irene Godoy, and Wiebke Lammers

Abstract The Lomas Barbudal Monkey Project began in 1990 with the study of a single white-faced capuchin monkey (*Cebus capucinus*) group, and has since expanded to 11 groups. Social behavior has always been the primary focus of our research, with emphasis on communication, social learning, and life history strategies. Genetic analyses in the context of this long-term study have enabled research of many standard behavioral ecology topics such as kin-based altruism, reproductive skew, and inbreeding avoidance. Long-term research on numerous groups, and collaboration with researchers at other *C. capucinus* sites, has permitted the documentation of social traditions regarding both communicative rituals and foraging techniques.

7.1   The History and Infrastructure of the Study Site

7.1.1   History

The Lomas Barbudal Monkey Project began with my (SP's) dissertation work on the evolution of intelligence. I was looking for a stable country where I could begin a long-term project investigating social relationships and social intelligence in capuchin monkeys, which were known for their large relative brain sizes. Costa Rica, with its friendly policy toward researchers, excellent environmental record, superb medical system and lack of an army, was the obvious choice. Following the

S. Perry (✉) • I. Godoy
Department of Anthropology, Center for Behavior, Evolution and Culture, University of California, Los Angeles, CA, USA
e-mail: sperry@anthro.ucla.edu; godoy@ucla.edu

W. Lammers
Proyecto de Monos, Bagaces, Costa Rica
e-mail: wiebkelammers@gmail.com

advice of Colin Chapman, who had censused monkeys in Guanacaste province, I settled on Lomas Barbudal as a study site and conducted a pilot study in 1990.

Lomas Barbudal Biological Reserve is a tropical dry forest site located in Guanacaste Province, northwestern Costa Rica. It was established as a reserve by UC-Berkeley entomologist Gordon Frankie, who has described the vegetation structure (Frankie et al. 1988). The monkeys range well outside the reserve into other public and private lands. This highly disturbed forest includes riparian forest, dry deciduous forest, mesic forest, and regenerative forest. Lomas receives 1,000–2,200 mm of rain annually between the months of May–November (Frankie et al. 1988), and fires are common in the dry season. Lomas Barbudal is approximately 55 km away from the better-known Santa Rosa National Park, which also hosts a long-term study of white-faced capuchins (see Fedigan and Jack 2012). The two sites have similar ecologies and plant lists (Panger et al. 2002); however, the Lomas monkeys have plenty of access to fresh running water, whereas the Santa Rosa monkeys rely heavily on waterholes in the dry season.

In 1991, the year following my pilot study, Joseph Manson and Julie Gros-Louis joined me as field assistants for my thesis research and became co-founders of the site, assisting me in the set-up of the site and co-managing it with me until the end of 2001. For the first 4 years, we documented the social behavior of a single group, Abby's group (AA).

Following my thesis research, Joe Manson and I received half-time tenure track jobs at UCLA, and began developing plans to make Lomas a long-term project. Our UCLA startup funds allowed for the purchase of a 1977 LandCruiser and a tent, and funds from my postdoctoral fellowships purchased Psion handheld computers, to streamline data collection. From 1994 to 1998, we pitched our tents on a rice farm owned by some *campesino* friends (the Rosales family) and ran our laptop computer on a truck battery powered by solar panels. In the meantime, Julie Gros-Louis began her dissertation research and was primarily responsible for the habituation of a second study group (Rambo's, RR). Because all of us had commitments teaching or taking classes at our respective universities, there were periods of time when no one could be present at the site. We initially attempted to solve this problem by inviting graduate students from other universities to work there in exchange for contributing to the demographic database. This, however, was a failure in terms of the long-term goals of the project; visiting students were not willing to invest the time to learn the identities of young monkeys who were not their focal subjects, or to track the movements of migrating males. And it was difficult to persuade anyone to continue data collection through the worst of the rainy season. It became clear that obtaining an accurate demographic database required employing someone whose sole responsibility was to collect these data for the project during our absence.

By 2001, things were not looking good for the future of the field site. The rice farm where we lived had been sold. Julie was finishing her final field season for her doctoral research. To ensure proper management of the site and the long-term database, it was imperative that I maintain a continuous presence at the site, and this was not possible while I was employed by UCLA. At this critical juncture,

I was fortunate to be appointed director of the Cultural Phylogeny research group at the Max Planck Institute for Evolutionary Anthropology (MPI-EVAN) in Leipzig. Germany. This job allowed me to devote all of my time to research and to hire a large crew to run the project when I was in Germany for 6 months of each year. The project rented two adjacent houses in the nearby town of Bagaces (35 min from the forest where we work), which had electricity, running water, and even internet access, so that I could supervise my crew's work remotely. The modernization of the site made it possible to attract field assistants who would stay for a year or more.

During the MPI phase of the project, we employed 6–9 interns per year, plus a permanent staff of seven people. The MPI-EVAN job ended in 2006, at which time I returned to my half-time job at UCLA. Thus far we have succeeded in keeping the project running on far less funding than was available at MPI, via short-term grants from NSF, the Leakey Foundation, and the National Geographic Society. We still maintain a staff of six interns, two full-time permanent staff and two part-time permanent staff. But now that we lack the security of long-term funding from MPI, we are extremely vulnerable to funding crises that could suddenly end the project at any time. This insecurity makes it harder to retain valuable staff members.

Beginning in January 2002, we completed habituation of a third study group (Pelon, FF) and were able to monitor all of our groups for up to 25 days/month year-round. These groups grew and fissioned (see Fig. 7.1), and males migrated to new groups. Currently, we have 11 study groups, nine of which we follow for several days per month, and two of which we visit more sporadically. Since 1994, we have collected fecal samples for genetic analysis from virtually all members of the study groups (aside from infants who die before we can obtain samples), and since 2006 we have been collecting fecal samples for hormonal analysis (fecal corticosteroids and testosterone). Our genetic and hormonal work has been carried out by graduate
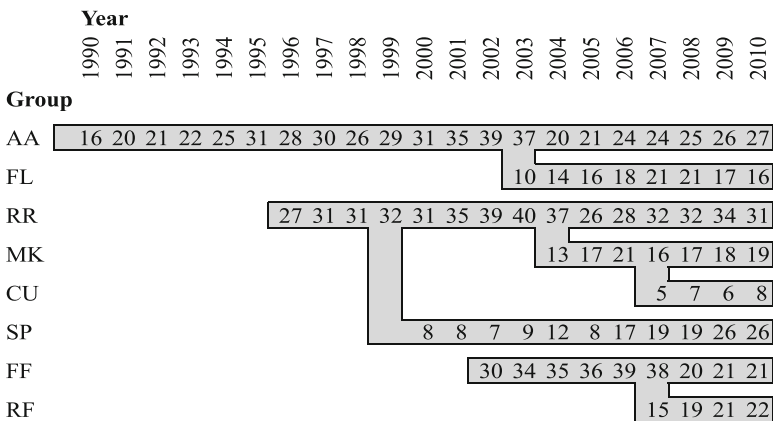
Group	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
AA	16	20	21	22	25	31	28	30	26	29	31	35	39	37	20	21	24	24	25	26	27
FL														10	14	16	18	21	21	17	16
RR							27	31	31	32	31	35	39	40	37	26	28	32	32	34	31
MK															13	17	21	16	17	18	19
CU																		5	7	6	8
SP											8	8	7	9	12	8	17	19	19	26	26
FF													30	34	35	36	39	38	20	21	21
RF																		15	19	21	22

Fig. 7.1 Maximum group sizes during each year of observation, and timing of fissions. For fission years, we report the size of the group right before the fission for the larger fission product, and the size of the group right after the fission for the smaller fission product

students working in the MPI-EVAN laboratories of Linda Vigilant and Tobias Deschner.

The topics of investigation have always centered on social behavior. The first few years of the project were devoted to documenting basic natural history of social communication and the structure of social relationships (Perry 1996a, b; 1997; 1998a, b; 2003; Manson et al. 1999; Gros-Louis et al. 2003; Perry et al. 2004; Perry and Manson 2008). Between 1995 and 2001, we investigated communication (vocal, gestural and olfactory) in greater detail and became particularly interested in the way in which individuals negotiate their social relationships (Manson et al. 1997, 2004a, 2005; Manson 1999; Manson and Perry 2000; Gros-Louis 2002, 2004a, b, 2006; Fichtel et al. 2005; Campos et al. 2007; Gros-Louis et al. 2008; Perry and Manson 2008). Our discovery of group-specific communicative rituals launched me on a multi-year study of social learning and social traditions (Panger et al. 2002; Perry et al. 2003a, b; Rose et al. 2003; Perry and Ordoñez Jiménez 2006; Perry and Manson 2008; Perry 2009). The interest in social learning spurred me to begin a developmental study of 46 infants in 2001 that continues to the present (Perry 2009). The availability of genetic data has enabled us to answer basic questions in behavioral ecology about issues such as kin-based altruism, inbreeding avoidance, and mating systems (Muniz et al. 2006, 2010; Perry and Manson 2008; Perry et al. 2008). This knowledge contributes to our long-term study of life history strategies.

7.1.2   Data Collection Methods

In the early years of the study, a team of observers (a narrator and a spotter, to check ID's) collected data, and data were narrated directly onto microcassette recorders. This method was essential in the early days, due to the richness of the behavioral repertoire, which had not yet been thoroughly documented. In 1997, we switched to using Psion palmtop computers, and I developed an elaborate system for rapidly coding behaviors in fine detail. We still switch to microcassette recorder when the action is extremely rapid or complex (e.g., when there are coalitionary fights or multi-party play bouts, or when the animals innovate and we have no codes to describe their actions accurately). These inserts are transcribed into the data after they are transferred into Excel spreadsheets at the end of the day. During data collection, one person types and double-checks IDs while the second person narrates the action and constantly watches the focal animal. Focal follows are the top priority in data collection, and these vary in length from 10 min to 12 h, depending on the topic of investigation. During these follows, we collect activity data and proximity data during point samples every 2.5 min, and continuous data on all social interactions, vocalizations, object handling and foraging events. We also conduct group scans approximately every 30 min, in which activities, food type (for foraging activities) and proximity to other animals are recorded. *Ad libitum* data on predator encounters, fights, agonistic interactions, sex, grooming, and innovative or

traditional behaviors are also collected. Census sheets are filled out daily, reporting who was in each group, health and wounding status, and reproductive states. At the end of each year of employment with the project, each observer fills out a 26-item personality questionnaire on the animals they studied. During some years, there are special protocols in addition to these core protocols, which can include recording (audio or visual), field experiments of various types, and food processing protocols that note processing techniques, proximity between foragers, and gaze directed toward other foragers. Fecal samples are collected for both genetic and hormonal analysis. We have used a variety of methods for collection of genetic samples (Muniz and Vigilant 2008), all of which have worked: collection in (a) 96% ethanol, (b) silica, (c) RNA-later, and (d) a two-step process involving first ethanol and then silica. We dry and grind feces in the field for hormone analysis and mail them to a lab for extraction.

7.1.3 Current Infrastructure and Logistics of the Site

The bulk of the core data collection is performed by a crew of six or more interns. Most are people who have just finished a bachelor's or master's degree and are seeking fieldwork experience before continuing to a Ph.D. program or a career in conservation. Two Costa Ricans (Alex Fuentes Jiménez and Juan Carlos Ordoñez Jiménez) have been employed by the project for a number of years to help with data collection, logistics, and plant identification. Two managers aid me in the running of the site. One lives in the project house and is responsible for the training of assistants, monthly inter-observer reliability checks, scheduling, maintenance of the house and project equipment, and the running of the fecal sample laboratory. The other (Wiebke Lammers) is in charge of data organization, project purchasing and accounting, and the environmental education program. This second manager and the Costa Ricans are invaluable in coordinating conservation efforts and meeting with government officials when I am out of the country. The managers and I remain quite active in data collection, so that we can reliably identify all animals and maintain continuity in the demographic database. In addition to this core staff, who are primarily responsible for the long-term database, there are typically one or two graduate students or postdoctoral scholars who are doing independent research, and they also have field assistants. Most of the graduate students have previously served as field assistants.

In a project of this size that involves a collective attempt to produce a complex data set, inter-observer reliability is always a concern. Before anyone is cleared to collect usable data, they must pass code and syntax tests, speed typing tests on the Psion Workabout handheld computers, shadow follows (in which a trainee follows a trained team of observers and types along, and the two sets of records are compared), monkey ID tests, and vocalization recognition tests. It typically takes 6 weeks to 3 months for an intern to be considered fully trained enough to be the senior member of a two-person data collection team. Every line of data is tagged by

spotter and typist ID so that if any errors are discovered later, the relevant data can be fixed or discarded. Each month, all observers are retested on their knowledge of codes, syntax, and vocalization recognition. If there is reason to suspect that someone's typing speed has declined since the initial training, then typing speed tests are retaken as well. Because we rotate work partners regularly, and work partners constantly double-check one another's monkey IDs, there is not much chance for errors to creep into monkey IDs. Whenever there is lack of agreement about monkey IDs or about what behaviors occurred, the follow is aborted and discarded. Whenever there is doubt about plant identification, a sample is collected and brought back to the Costa Rican botanist. We have a short staff meeting every night during dinner to discuss any doubts about protocol that have arisen during the day's data collection. Vocalization tests are always the hardest for achieving inter-observer reliability, so we just keep training records regarding which observers reliably recognize each vocalization and only analyze vocal data from those observers who are reliable for that call type.

Currently the project has amassed approximately 70,600 h of behavioral data, stored in the form of Excel spreadsheets. With this amount of data, the analysis process has become unwieldy, and so we are in the process of constructing a MySQL relational database to aid in the analysis process, modeled roughly after Babase, the database created for the Amboseli Baboon Project (Alberts and Altmann 2012).

7.2 Demography

7.2.1 Dispersal Patterns

Female capuchins at Lomas Barbudal are philopatric, as at other sites where this species and genus have been studied (Fragaszy et al. 2004; Perry et al. 2008; Jack and Fedigan 2009). Although we have directly observed immigrations or immigration attempts by 85 males (many of these migrating multiple times), we have still never witnessed a migration by a female (but see Jack and Fedigan (2009) and Fedigan and Jack (2012) for a few exceptions to this pattern at Santa Rosa). There have been 90 adult females above age 5 observed in our study for a period of up to 20 years. We have witnessed females interact non-aggressively with females from other groups only three times in 20 years and have never seen females seriously attempt to join other groups. In two cases, the females were separated from their own groups briefly following an intergroup encounter, and in the third case, it appeared that an estrous female and a male wandered away from their group and temporarily joined a neighboring group for half a day, until there was an intergroup encounter between the two groups and they returned to their normal group.

Typically females only remove themselves from close proximity with female kin when their group becomes so large that coordination of group movement becomes difficult (i.e., group size of >30). In these cases, groups fission fairly neatly along

matrilines, so that the average relatedness among females is higher in the fission products than in the original group (Muniz 2008). The fission process may take up to 3 months, during which the two subgroups apparently try to stay together, but finally they decide who will be in which subgroups and adopt hostile relations toward the members of the other subgroup. For the first several months after the fission, intergroup relations are actually more hostile than is typical in intergroup encounters, and even females physically attack one another (whereas in typical intergroup encounters, active participation is almost exclusively by males). Figure 7.1 shows the history of group fissions at Lomas, with the number of monkeys that was present in each group at the time the fission occurred.

Males can either migrate singly or in groups of 2–8. Often co-migrant males are kin, and co-migration with kin can occasionally result in higher relatedness among adult males than among adult females. However, in 10 out of 11 demographic situations analyzed from three social groups at Lomas at different time periods, adult females had higher average relatedness than adult males (Muniz 2008). Males born into our three primary study groups, (AA, RR and FF) tend to make their first migration at age 92 months, regardless of whether we use a sample of 21 males from our developmental study whose birthdates and migration dates are fairly accurately known, or a sample of 44 males from the broader study whose birthdates and migration dates are somewhat less accurately estimated. The three youngest males to migrate were 4 years old, and they migrated in the context of a fission and/or an alpha male takeover in which a large all-male group composed of their male relatives formed. It is likely that they would not have migrated so early if the fission had not occurred. The seven oldest males to leave their natal groups were 11 years old. Additionally, one 11-year-old remains in a fission product of his natal group (but does not reside with either parent). This male is missing a hand, which may inhibit him from migrating, though he did accompany some of his brothers on a visit to a neighboring group once.

This mean age of migration (7.6 years) is considerably higher than that seen at the nearby site of Santa Rosa National Park, where males tend to make their first migration at a mean age of 4.17 and never remain in natal groups past age 8 (Jack and Fedigan 2004; Fedigan and Jack 2012). It is not clear why this difference between the two nearby, ecologically similar sites exists. Possibly the apparently higher rate of lethal coalitionary aggression at Lomas Barbudal (Gros-Louis et al. 2003) makes migration more dangerous, but the exact rate of such killings at Santa Rosa has not yet been reported. Males at Lomas tend to co-migrate more often than Santa Rosa males do, and so many males may spend extra years in their natal groups waiting for close kin to mature to migration age so that they can move together. Every one of the 44 males born into our study groups whom we have seen to migrate has migrated with other natal males, at least initially (though sometimes the co-migrants do not remain with their co-migration partners after one male has claimed the alpha position). In contrast, only 71% of males at Santa Rosa co-migrate (Jack and Fedigan 2004). We do see occasional solo migrations at Lomas, but thus far it has always been males from unhabituated groups who have migrated alone into our study groups; therefore, we know nothing about the migration options for these males.
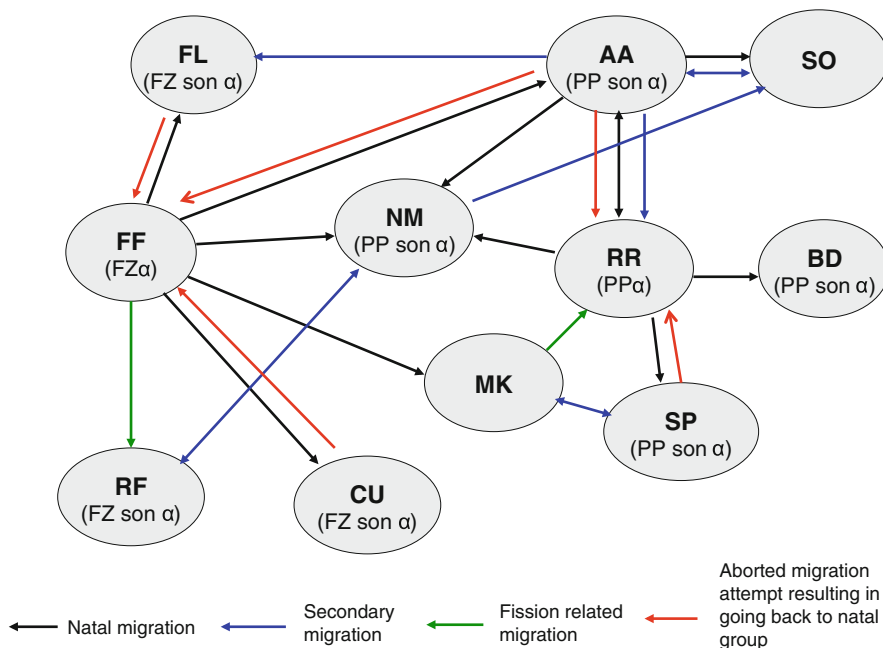
Fig. 7.2 Diagram of male migrations. Each oval represents a social group. Two long-term alpha males are noted, as are their alpha male sons. See text for the four types of migrations, which are denoted by different types of *arrows*

Figure 7.2 demonstrates the patterning of male migration. There are four basic types of migration or transfer: (a) natal transfer (i.e., transfer from the natal group to another group), (b) secondary transfer (transfer from one non-natal group to another non-natal group), (c) "fission transfer" in which males initially go with their mothers during a fission, but later move to the other fission product that has less closely related adult females, and (d) "returning home" transfers, in which males first transfer to a non-natal group and then return to the natal group.

Some males make many false starts; that is, they transfer to non-natal groups, but return to the natal group for extended periods between each transfer attempt; in these cases, we counted all emigrations out of the natal group as natal migrations for the purpose of Fig. 7.2. We only included multi-male/multi-female groups in this diagram, but there are also many all-male groups in the study area that shift composition at high rates. Males often spend prolonged periods in these groups in between periods of residency in groups containing females. Some of the secondary migrations reported in Fig. 7.2 might not have been direct migrations, but rather involved visits to all-male groups and perhaps even other multi-male/multi-female groups in between. Males typically transfer to an adjacent group with females or to an all-male group, at least initially.

It has been proposed (Schoof et al., 2009) that one of the reasons males engage in parallel dispersal is because it gives them access to willing coalition partners who can

enhance their competitive ability in within-group and between-group competition. One of the arguments for why males are expected to engage in parallel dispersal is to keep male kin together so that they can engage in kin-selected altruism (Schoof et al. 2009). Indeed, at Lomas there is a tendency for male co-migrant dyads to be more closely related than randomly selected male–male dyads from a given group (Wilcoxon signed ranks test: $Z^+ = -2.132$, $p = 0.016$, $N = 13$ migration events; Muniz 2008). At Lomas, it is definitely true that males aid one another in defending the group from intruders (Perry 1996b; Perry and Manson 2008), and that they regularly aid one another in takeovers of other groups (Perry and Manson 2008, unpublished data). It is less certain whether co-migrants aid one another in within-group coalitionary aggression in their new groups more often than do pairs of males who are not co-migrants; this topic will require further research. Certainly we do see many cases in which co-migrants side against one another in within-group coalitionary aggression. Once a takeover has been achieved, we sometimes see cases in which co-migrant males engage in fierce battles over the alpha position with their own brothers, inflicting severe wounds. Strong circumstantial evidence from Lomas indicates that males sometimes kill their brothers and their brothers' infant offspring in disputes over the alpha position, despite their close genetic relatedness (unpublished data).

7.2.2 Genetic Structure of the Population

The Lomas Barbudal capuchins are noteworthy for often having quite long alpha male tenures, lasting up to 18 years. These long tenures, combined with high reproductive skew, mean that natal individuals are often related both through the maternal and the paternal line. Out of 2,111 dyads analyzed from five social groups, 4% were full siblings, 5% were maternal half siblings, and 24% were paternal half siblings (Muniz 2008). Another unusual feature of capuchin social structure imposed by long alpha male tenures is the high frequency with which alpha males co-reside with their daughters and grand-daughters. In most mammalian populations, father–daughter inbreeding is avoided by having one sex disperse. But capuchins avoid father–daughter inbreeding even while co-residing (Muniz et al. 2006). Paternity data on 97 infants born during 15 stable alpha male tenures show that in the years before an alpha male's daughters have started to mature, the alpha males have sired 96% of all offspring (data from Godoy 2010; Muniz et al. 2010). However, subordinate males who have been helping an alpha male defend his group's females from extra-group males experience greatly increased breeding opportunities when the alpha male's female descendents finally mature. Subordinate males have sired 94% (31/33) of offspring produced by females that were the daughters or granddaughters of their groups' current alpha males (Godoy 2010; Muniz et al. 2010). Thus, the longer an alpha male remains in place, the lower the degree of reproductive skew, due to the increasing numbers of his female descendents.

Figure 7.3 shows the breeding histories for the males in Rambo's group from 1991 to 2008. This pattern is similar to what we observed during two other long-term tenures. At the start of the study, alpha male Pablo (PP) co-resided with two other immigrant
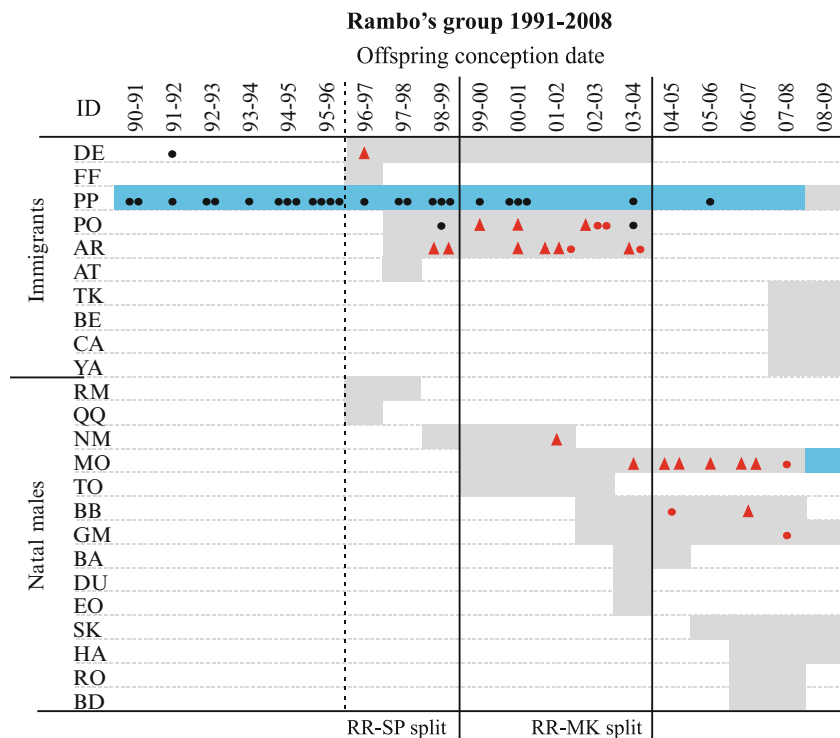
Fig. 7.3 Distribution of paternity over time in Rambo's group. All males residing in a group during a particular year are shaded in grey, with the alpha male having *blue* shading. Offspring of the current alpha males' daughters are represented by *red triangles*, and offspring of the alpha male's granddaughters are represented by *red circles*, while offspring of all other females are represented by *black circles*. Vertical dashed lines indicate the beginning of direct observations

males with whom he had non-antagonistic relationships. In 1997, a trio of migrant males immigrated relatively peacefully and did not attempt to overthrow PP. Again in 2008, four migrant males who had known one another in AA group immigrated peacefully. At the end of 2008, PP was overthrown by MO, who was the offspring of PP's former ally DE. Aside from MO, RM and QQ, all other natal males in the group were PP's sons or grandsons. PP remained in RR group after losing alpha status.

PP sired 25 out of 30 offspring (83% of offspring) born to females who were not his direct descendants; the remainder were sired by immigrant males. Of those offspring born to PP's daughters and granddaughters, 12 were sired by immigrant males, 4 were sired by PP's sons (i.e., his sons bred with their paternal half sisters or nieces), and 7 were sired by MO, a natal male who was unrelated to PP and only distantly related to most of the females with whom he bred. Thus, PP did not breed with any of his daughters or granddaughters.

Long-term alpha males have far more reproductive influence in the population than is apparent just by examining the patterns of reproduction in the groups in which they reside. This is because long-term alpha males have ample opportunity to produce sons,

who then migrate and often become alpha males themselves, monopolizing reproduction in other groups. Figure 7.2 shows which adjacent groups have alpha males who are sons of the long-term alpha males PP (of RR group) and FZ (of FF group). These males may have additional sons who are alpha males in groups outside our study area. To the best of our knowledge, PP has sired at least 25 offspring, 83 grandoffspring, and nine great-grandoffspring at the present time (and of course the numbers of his second and third generation descendents will continue to increase after his death).

7.2.3 Sources of Mortality and Ages at Mortality

Although white-faced capuchins can live to 55 years of age in captivity (Hakeem et al. 1996), maximum life span is in the wild is unknown because no field study has come close to spanning that amount of time. Certainly, however, it is rare for capuchins to live that long. Based on genealogical data, we estimate that our oldest living monkey is 36 years old. Of the 24 monkeys who were members of AA group during the first 3 years of our 20-year study, only 2 females are still living.

Mortality rates at Lomas Barbudal were calculated using individuals with birthdates known to an accuracy of plus or minus 3 months ($N = 262$). We assigned two values for age at death to those individuals presumed dead ($N = 108$); these incorporated inaccuracy in both birth and death dates. We used these values to generate two curves for mortality rates across time (Fig. 7.4a), one using the lowest possible value for age at death and second curve using the highest possible value. Since birth dates were relatively accurate, the two curves produced similar results. We also included in this analysis stillborn infants and obvious miscarriages (when it was clear that a female was pregnant based on the size and shape of her abdomen, and then she suddenly decreased in size). Because mortality was highest in the first year (26–30%), we generated a separate graph to describe mortality rates within that year in four 3-month increments (Fig. 7.4b).

The principle cause of mortality for infants under 1 year of age seems to be infanticide. The mean interbirth interval for those cases in which the first infant lives until the next infant is born is 749 days $\pm$ 145 ($N = 41$ IBI's for which birthdates were known to an accuracy of 1 week). This is slightly shorter than the 2.25-year (~821-day) interbirth intervals reported for Santa Rosa (Fedigan and Jack 2011). However, when the previous infant dies or is abandoned before the second is conceived, the mean interbirth interval is 444 days $\pm$ 168 ($N = 21$), i.e., significantly shorter than when the previous infant lives (two-sample t-test with unequal variance, $t = 7.09$ (37), $p < 0.0001$). The mean time to conception following an infanticide was 478 days $\pm$ 212 ($N = 6$), or 271 days shorter than in cases where infanticide was not committed.

We analyzed the effects of adult male migrations and alpha male turnovers on infant mortality rates using a sample of 210 births for which we had accurate birthdates. For each birth, we scored whether a male migration or a turnover in the alpha male position occurred within 6 months before or 1 year after the infant's
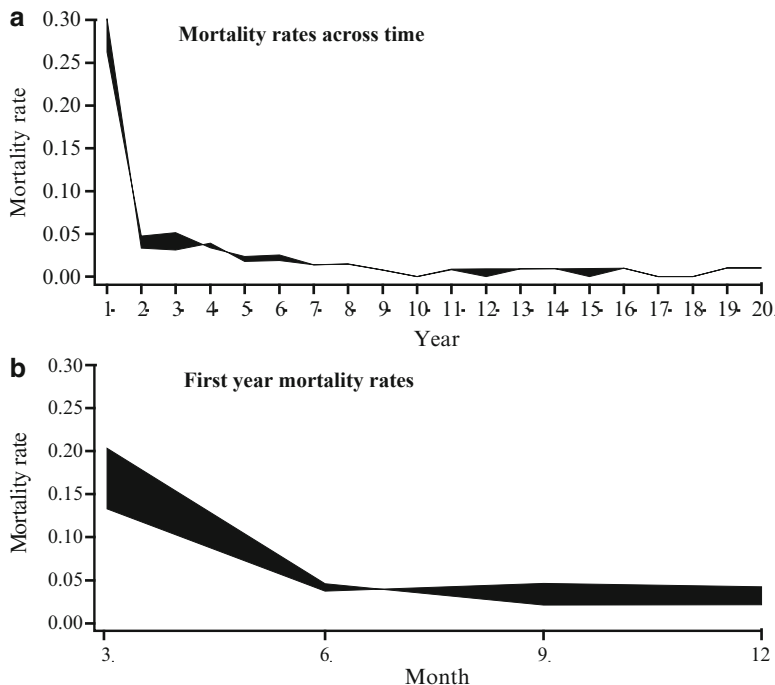
Fig. 7.4 Mortality rates over the life span. (**a**) Shows the mortality rates over the first 20 years of life; (**b**) shows the timing of deaths during the first year of life. *Shaded areas* in both graphs denote the upper and lower bounds of mortality rates

birth. Only 18% of infants died in periods characterized by stable alpha males, whereas 49% of those infants born in alpha male turnover periods died before reaching 1 year of age. This is a significant difference (Pearson's $\chi^2 = 23.38$, 1df, 1-tailed $p < 0.001$), and replicates similar findings from the Santa Rosa capuchins (Fedigan 2003; Fedigan et al. 2008). We witnessed 20 peaceful immigrations, i.e., migrations in which no alpha male turnover occurred. The mortality rate for infants born during times of peaceful male immigration (25%) did not differ significantly from that for infants born during periods in which no male immigrated (23%) (Pearson's $\chi^2 = 0.038$, 1df, 1-tailed $p = 0.845$). We do not always witness infant deaths, so we cannot be certain what proportion are due to infanticide. We directly observed six infanticides, and in five other cases we witnessed the alpha male stalking the infant for days previously, and/or the mother alarm-calling at the alpha male right after the infant was killed (Manson et al. 2004b; Perry and Manson 2008). In another four cases, infants disappeared in the middle of an infanticide spree when a new alpha was seen to kill other same-aged infants. In another 11 cases, a female was pregnant on the last day of observation during one month, but when next seen was no longer pregnant and had no infant; it was impossible to know whether there was a miscarriage or an infanticide. Thus, although we cannot give a precise rate, infanticide is clearly the biggest source of infant mortality at our site.

7.2.4 Age at First Reproduction for Each Sex

Females at Lomas Barbudal give birth for the first time at a mean age 6.22 years (SD = 0.58). This sample is based on 30 females for whom the age of their own birth and the age of their first infant's birth is known to an accuracy of ±3 months. It includes three miscarriages. If we look only at the age of first live birth, then the mean age of first birth increases to 6.30 (SD 0.62). The youngest female to give birth was 5.50 years old.

Determining the age of first reproduction for males is much more difficult because there is such high reproductive skew that very few males actually reproduce. Only 27 males in our population are known to have sired offspring, and we only had reasonably accurate birthdates (+3 months) for two of these, since it is primarily the older males who reproduce. Of these two males, one conceived his first offspring at 7.3 years of age, and the other conceived his first offspring at 9.0 years. Based on our much rougher age estimates for other sires, we suspect that the typical age at which males first conceive an offspring is much later, however.

7.2.5 Birth Seasonality

67.1% of births at Lomas Barbudal ($N = 173$ births, during years for which we have continuous demographic monitoring) occurred between April and July, though some births occurred during all months but October. Thus, the birth season straddles the end of the dry season and the start of the rainy season, which typically begins in mid-May. Figure 7.5 shows the distribution of births across years, using
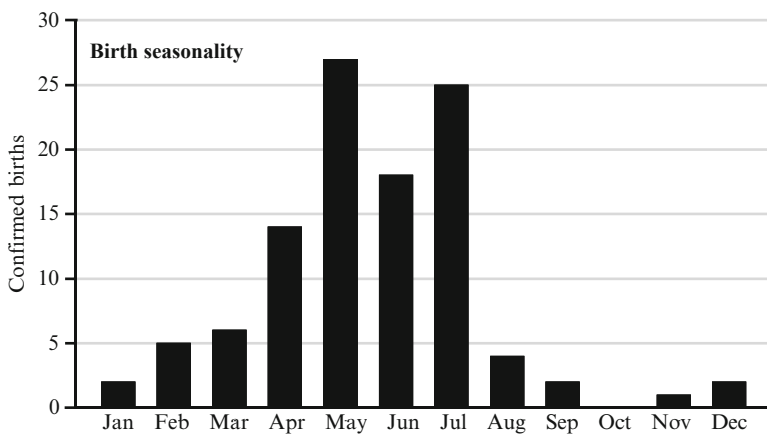
Fig. 7.5 Number of births in each month in a sample of 106 births for which birth date was known accurately enough to assign it to a particular month

only those births for which we knew the precise month ($N = 106$). The timing of this birth season corresponds roughly to that of Santa Rosa (see Fig. 8.2 in Fedigan and Jack 2011), where 40% of births occur in April–June.

7.3 Topics We Could Not Have Studied Without Long-Term Research: Social Learning and Traditions

Lack of temporal depth in datasets from wild animal populations usually prevents researchers from identifying *traditions*, defined as "enduring behavior patterns shared among members of a group that depend to a measurable degree on social contributions to individual learning, resulting in shared practices among members of a group" (Fragaszy and Perry 2003). Simply knowing that a behavior pattern varies across sites in cross-sectional samples is insufficient to conclude that the behavior is a tradition, because many factors, including between-site genetic and ecological variation, can affect behavioral variation. To determine whether a behavior pattern is a true tradition, it is useful to know whether and how it varies over time. Two forms of long-term temporal patterning strongly suggest that social learning affects the acquisition of a behavior. First, a behavior may appear suddenly in an individual (i.e., as an innovation) and then spread, in a transmission chain, through that individual's social network. Second, a general behavior pattern may occur universally in a population, but exhibit discrete variant forms, and immature individuals may preferentially acquire the variants favored by their close spatial and social associates. We have documented both patterns over multi-year periods at Lomas Barbudal, the first with respect to dyadic social rituals and the second with respect to foraging techniques.

7.3.1 Social Conventions

Early in the history of the project, SP began visiting other field sites and communicating with the researchers who worked at these sites. It soon became apparent that some of the more bizarre behaviors we witnessed were not common features of the repertoire of capuchins everywhere, and we decided to coordinate our methods so that we could more rigorously investigate the hypothesis that capuchins exhibit social conventions – i.e., dyadic communicative rituals that are unique to particular cliques or social groups. We made a list of candidate traditions by identifying forms of social behavior that were practiced in some social groups at a rate of at least once per 100 h of observation, but were absent in others that had been studied for at least 250 h. We also kept track of which individuals practiced the behaviors and of how long the behaviors persisted in each group's repertoire, for all cases in which the timing of the field seasons permitted documentation of the innovation event and included the periods during which it could have spread and, where relevant, when it became extinct.

In our original study, which included 19,000 h of behavioral observations on 13 social groups from four sites in Costa Rica over a 13-year period, five behaviors qualified as traditions according to our operational criteria (Perry et al. 2003a). One of these, handsniffing, involved the insertion of a finger into the nose of another monkey; this behavior was often mutual and exhibited many minor variations in form. Handsniffing was common for a period of 1–7 years in five out of the 13 groups we studied and at three of the four study sites. The sucking of body parts (ears, tails or fingers) was common in two of our study groups for periods of 6 months or more. Three "games" were invented by a single monkey (Guapo of Abby's group at Lomas Barbudal) and had roughly the same format, in which one monkey has something in its mouth that the partner tries to remove from the mouth (a finger or a tuft of hair from the partner, or an inanimate inedible object such as bark or a stick). The mouth is pried open using hands, feet, and perhaps the mouth, and the object is passed back and forth from mouth to mouth.

In the case of the three games ("finger-in-mouth", "hair" and "toy"), we could construct social transmission chains. The "toy" game was invented in 1991, and the other two were invented in 1992. The "toy" game had 13 practitioners and three links in the transmission chain and lasted 9 years. The "finger-in-mouth" game and hair-passing games both lasted for 10 years and had 11 and 14 practitioners, respectively. The finger-in-mouth game had two links in its transmission chain, whereas the hair-passing game had three. In the games, adult male-juvenile males were the primary participants. The games persisted in group repertoires for 2–3 years after the innovator (a subordinate male) became alpha male and stopped participating. Some of the main practitioners continued to play these games together even after co-emigrating.

In subsequent years, we have continued to document the innovation and spread of social conventions. The larger the data set grows, the more often we find that similar innovations occur. For example, the males in Flakes group have independently invented all three of the games that were previously played in Abby's group. Despite the fact that Flakes is a fission product of Abby's group, none of the current game players were resident in the group at the time these games were played in Abby's group, so we believe them to be independent inventions. We have also observed the invention of a rare, new variant of handsniffing that includes the insertion of the partner's finger deep into the eye socket, up to the first knuckle in some cases. This variant has been slower to spread than most traditions and also not quite common enough to meet all of our operational criteria for tradition in the original study, but it nonetheless appears to be socially learned.

As the study continues and the cumulative number of observation hours per group increases, we are discovering that (a) there are more observations of groups that exhibit temporal variation in their behavioral repertoires, and (b) many groups that formerly exhibited a total absence of particular traditional behaviors now have an occasional observation of a behavior thought to be unique to another group, even if it does not spread to other group members or become common in the repertoire. The longest-studied group, Abby's group, has exhibited particularly interesting variation in the expression of handsniffing over the past 20 years. This behavior was not observed in 1990. From 1991 to 1997, it was commonly practiced by up to

12 individuals and 13 dyads in any given year. From 1998 to 2001, it was never seen, but females often sniffed their own hands. During 2002–2003, when there were frequent migrations, dyadic handsniffing was practiced at low frequency by 14–16 individuals and 15–16 dyads per year. The practice dwindled until by 2008, dyadic handsniffing had once again vanished from the group's repertoire, though solo handsniffing remained. The solo handsniffing in Abby's group and its fission product (Flakes) is never seen in three of our other study groups (MK, CU, NM) and occurs roughly an order of magnitude less often in the neighboring RR group.

7.3.2   Social Learning About Foraging Techniques

Short-term studies of *C. capucinus* have demonstrated between-site differences in the ways foods are processed (Panger et al. 2002). Providing conclusive evidence for a substantial role of social learning is impossible in such cross-site studies, although the fact that all of the sites in this study were tropical dry forest sites in northwestern Costa Rica makes a major role for ecological or genetic variation unlikely. Within-site studies are highly suggestive of a role of social learning of food-processing techniques. White-faced capuchin monkeys are more prone to observe group-mates foraging at close range when they are foraging on foods that require multiple steps to process before ingestion (Perry and Ordoñez Jiménez 2006). However, showing that monkeys observe one another does not mean that they necessarily learn from the observations. At Lomas Barbudal (Perry and Ordoñez Jiménez 2006), Palo Verde (Panger et al. 2002) and Santa Rosa (O'Malley and Fedigan 2005), pairs of monkeys who frequently associate are more prone to share the same food-processing techniques than pairs who associate less often, but the results of these comparisons are generally only marginally significant.

A longitudinal approach is preferable to a cross-sectional approach to this issue because it allows researchers to document the association patterns at the time when young animals are acquiring their food-processing techniques and are most subject to social influence, rather than simply measuring association patterns in adulthood and assuming that these represent the patterns that held when the monkeys acquired their current techniques. It is time-consuming and costly to conduct longitudinal studies of the development of large numbers of juvenile primates in the wild, so such studies are rare. We have conducted the largest such study to date, focusing on the acquisition of techniques for processing *Luehea candida* fruits, a staple item that contributes up to 15.4% of the diet during the peak fruiting period (Perry and Ordoñez Jiménez 2006). This fruit consists of a woody capsule with five cracks, from which small but nutritious wind-dispersed seeds can be extracted either by pounding or scrubbing the fruit. Both techniques are approximately equally efficient (Perry 2009). The lack of difference in efficiency means that individuals are probably less likely to select a technique on the basis of individual trial and error learning, as opposed to social learning.

All of the social groups included in the study (three groups and three of their fission products) had some group members who were primarily pounders and others

who were primarily scrubbers. However, some between-group differences in the tendency to pound or scrub existed, particularly for the philopatric sex. For example, currently nine of the 10 adult females in AA group are scrubbing specialists (the youngest female still combines pounding and scrubbing), whereas in RR group, all of the six adult females are pounders.

During the first developmental year (i.e., the first year in which the infants have exposure to *Luehea* fruits and are off the mother's back during part of *Luehea* season), most infants do not regularly process *Luehea* fruits, although they handle them and eat the seeds protruding from the ends. In their second year of exposure to the fruits, they employ a variety of techniques (about four per monkey), including both pounding and scrubbing (Perry 2009). As juveniles mature, they select a preferred technique and use it increasingly until they reach adulthood (Fig. 7.6). By 3 years, inefficient techniques have largely been eliminated from individual repertoires, and individuals use their dominant technique 82% of the time ($N = 49$ individuals), and by age 7 years, they use the dominant technique 95% of the time ($N = 27$).

Infants remain on their mothers' backs for most of the first 3 months of life. During months 4–6, they spend increasing amounts of time with alloparents, and by 6–9 months of age, they are within 40 cm of their mothers only 10% of the time (Perry 2009). Even after becoming largely independent of their mothers, they spend much time within observation range of other monkeys, and by age 5 years, they still spend 73% of their time within 4 m of at least one other monkey. Juvenile males and females do not differ significantly with regard to the amount of time they spend in proximity to their mothers, time spent alone, or time spent observing other foragers (Perry 2009).
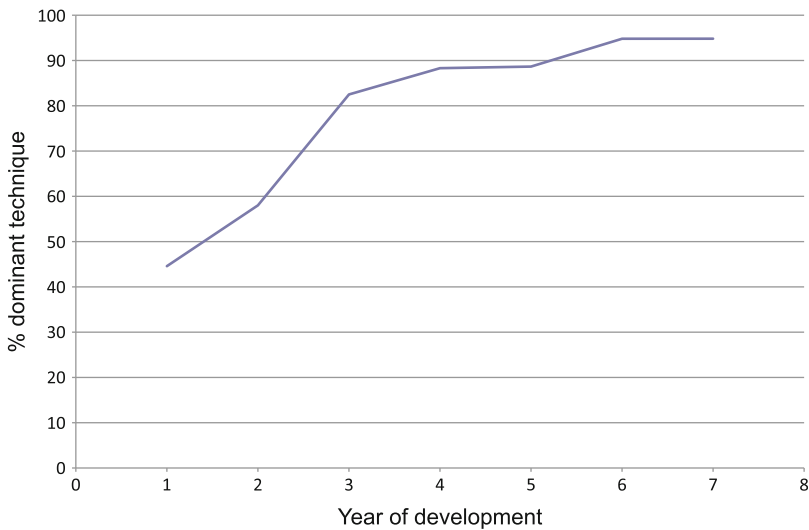
Fig 7.6 Percentage of Luehea processing incidents in which the individual's dominant (favored) processing technique is used during each year of development

We collected data on the *Luehea* processing techniques of all members of our study groups over a period of 7 years, which allowed us to follow 48 immature monkeys (21 females and 27 males) during the first 5 years of their lives. In many cases we had to drop particular monkey-years from the data set due to inadequate sample sizes for (a) number of fruits processed by the focal monkey, or (b) opportunities for the focal animal to observe others' foraging techniques. Once these cases were eliminated, we had 79 cases (i.e., monkey years) in the sample (see Perry 2009 for further details). Whenever a monkey entered a *Luehea* patch, we recorded the technique(s) used to process each fruit, the distance between the focal animal and other individuals who were processing *Luehea*, the gaze directions between animals, and the techniques being used by other animals in the same patch.

I analyzed the data using a Poisson regression model, adjusting the standard errors for within-subject correlation (see Perry 2009 for details of measurement and analysis). The primary predictor variable was the technique to which the focal subject was exposed, which is a measure of the relative exposure to pounding as opposed to scrubbing in foraging neighbors (see Perry 2009 for details of measurement and analysis). Sex was also a predictor variable. The outcome variable was the proportion of *Luehea* fruits that the focal monkeys processed by pounding them (i. e., number of fruits pounded, divided by the sum of number of fruits pounded and number of fruits scrubbed). Developmental years were control variables.

Figure 7.7 shows the effect of observed technique on the practiced technique for males vs. females across the first five developmental years. In Fig. 7.7a, only observations of maternal foraging are included in the independent variable. Figure 7.7b includes only observation of non-maternal foraging in the independent variable. In both cases, the impact of observed techniques on practiced techniques was greatest in the second year of development. Females were more strongly influenced by observed technique than were males, across all years of development. Non-maternal influence is slightly greater than maternal influence for both males and females.

In a separate analysis (Perry 2009), I used a broader data set ($N = 106$ monkeys) in which I also included adults and included all cases for which we had adequate behavioral data to characterize individuals' techniques during the most recently available processing season and also knew the mothers of the subjects. Females were significantly likely to use the same technique as their mothers (Fisher's exact $p = 0.002$, $N = 48$), but males were not ($p = 0.18$, $N = 58$). This result parallels findings by Lonsdorf et al. (2004) at Gombe, in which the acquisition of termiting techniques was studied in 14 immature chimpanzees over a period of 4 years. In their study, daughters were more likely than sons to adopt a termiting tool length similar to the mother's; daughters acquired the technique earlier than sons and were more efficient termite-fishers. Lonsdorf et al. found that this sex difference could be explained by the fact that sons paid less attention to the mothers than the daughters did when the mother was termiting. However, in the Lomas capuchins, there are no differences between sons and daughters with regard to time spent in proximity to the mother (or other group members) or in the tendency to visually focus on the model during demonstrations of the *Luehea* processing technique. It may be that
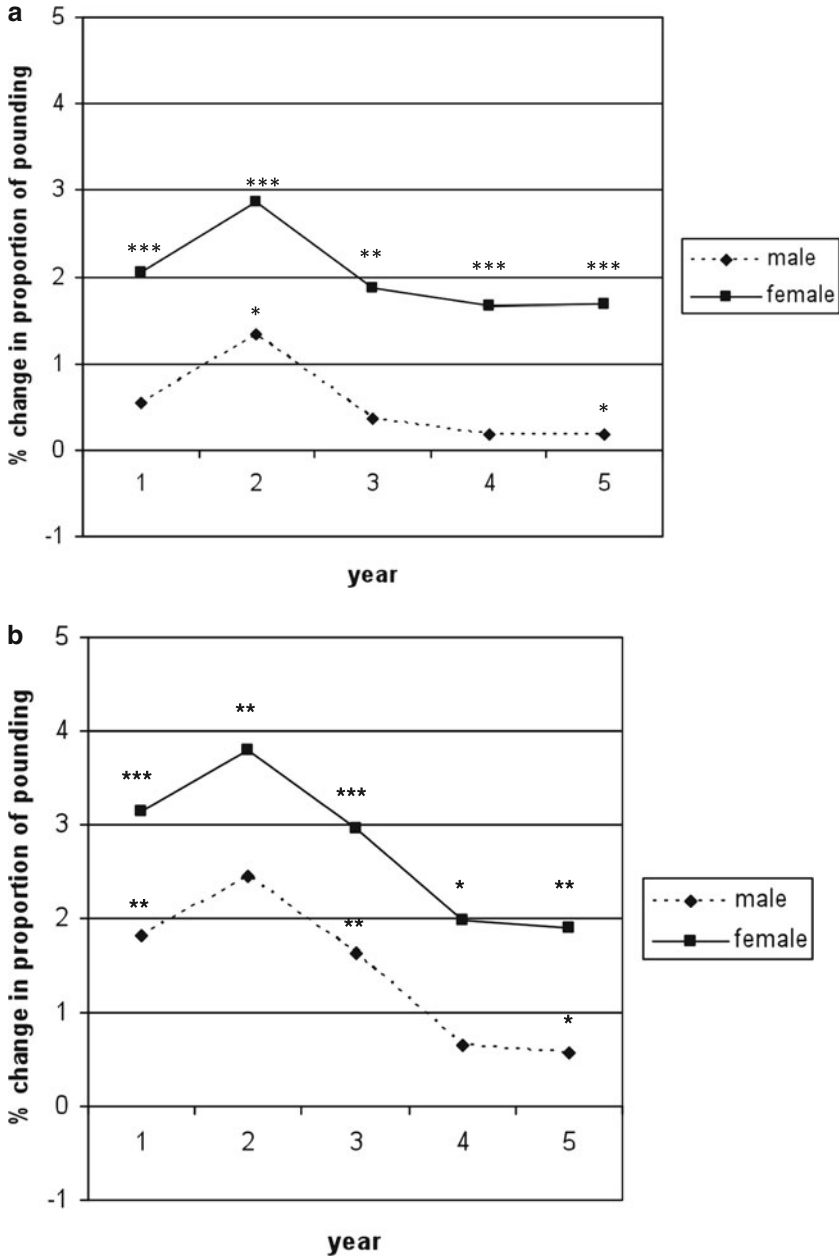
Fig 7.7 Impact of (**a**) maternal influence and (**b**) non-maternal influence on practiced technique for processing *Luehea* fruits. Y-axis is "% change in proportion of pounding practiced" resulting from a 1% change in observed technique. These two figures are slight modifications of Fig. 3b, c in Perry (2009) *=p≤0.05; **=p≤0.01; ***p≤0.001

female capuchins, being the philopatric sex, are more inclined to identify with their closest associates in the group, and hence conform to their techniques, in accordance with de Waal's "Bonding and identification-based learning model" (de Waal 2001).

7.4 Conclusions

The most interesting pieces of information that have emerged from our project are findings that were only possible to obtain via long-term study and extensive inter-site collaboration. To gain a deeper understanding of the social strategies of these long-lived animals, we needed to integrate data from multiple social groups and sites for hundreds of individuals over a period of 20 years, and even now, we are far from having complete life histories for many individuals in our sample. The discovery of father–daughter and grandfather–granddaughter inbreeding avoidance was possible only by obtaining genealogical data for multiple generations. Migration strategies can only be documented by knowing the natal groups of males and following them for multiple decades as they migrate repeatedly under changing demographic circumstances. The role of social learning in acquiring foraging skills was documented by collecting extraordinarily detailed observations at high density for a 7-year period in multiple groups. Finally, the documentation of group-specific communicative rituals was possible only by collecting long-term data on transmission chains, changes in groups' behavioral repertoires over multi-year periods, and comparative data from multiple sites.

References

Alberts SC, Altmann J (2012) The Amboseli Baboon Research Project: Forty Years of Continuity and Change. In: Kappeler PM (ed) Long-term field studies of primates. Springer, Heidelberg

Campos F, Manson JH, Perry S (2007) Urine washing and sniffing in wild white-faced capuchins (*Cebus capucinus*): testing functional hypotheses. Int J Primatol 28:55–72

de Waal FBM (2001) The ape and the sushi master: cultural reflections of a primatologist. Harvard University Press, Cambridge, MA

Fedigan LM (2003) Impact of male takeovers on infant deaths, births and conceptions in *Cebus capucinus* at Santa Rosa, Costa Rica. Int J Primatol 24:723–741

Fedigan LM, Jack KM (2012) Tracking Neotropical Monkeys in Santa Rosa: Lessons from a Regenerating Costa Rican Dry Forest. In: Kappeler PM (ed) Long-term field studies of primates. Springer, Heidelberg

Fedigan LM, Carnegie SD, Jack KM (2008) Predictors of reproductive success in female white-faced capuchins (*Cebus capucinus*). Am J Phys Anthropol 137:82–90

Fichtel C, Perry S, Gros-Louis J (2005) Alarm calls of white-faced capuchin monkeys: an acoustic analysis. Anim Behav 70:165–176

Fragaszy DM, Perry S (2003) The biology of traditions: models and evidence. Cambridge University Press, Cambridge

Fragaszy DM, Visalberghi E, Fedigan LM (2004) The complete capuchin: the biology of the genus *Cebus*. Cambridge University Press, Cambridge

Frankie GW, Vinson SB, Newstrom LE, Barthell JF (1988) Nest site and habitat preferences of *Centris* bees in the Costa Rican dry forest. Biotropica 20:301–310

Godoy I (2010) Testing Westermarck's hypothesis in a wild primate population: proximity during early development as a mechanism of inbreeding avoidance in white-faced capuchin monkeys (*Cebus capucinus*). Master thesis, University of California, Los Angeles

Gros-Louis J (2002) Contexts and behavioral correlates of trill vocalizations in wild white-faced capuchin monkeys (*Cebus capucinus*). Am J Primatol 57:189–202

Gros-Louis J (2004a) The function of food-associated calls in white-faced capuchin monkeys, *Cebus capucinus*, from the perspective of the signaller. Anim Behav 67:431–440

Gros-Louis J (2004b) Responses of white-faced capuchins (*Cebus capucinus*) to naturalistic and experimentally presented food-associated calls. J Comp Psychol 118:396–402

Gros-Louis J (2006) Acoustic analysis and contextual description of food-associated calls in white-faced capuchin monkeys (*Cebus capucinus*). Int J Primatol 27:273–294

Gros-Louis J, Perry S, Manson JH (2003) Violent coalitionary attacks and intraspecific killing in wild white-faced capuchin monkeys (*Cebus capucinus*). Primates 44:341–346

Gros-Louis J, Perry S, Fichtel C, Wikberg E, Gilkenson H, Wofsy S, Fuentes A (2008) Vocal repertoire of *Cebus capucinus*: acoustic structure, context and usage. Int J Primatol 29:641–670

Hakeem A, Sandoval GR, Jones M, Allman J (1996) Brain and life span in primates. In: Birren JE, Schaie KW (eds) Handbook of the psychology of aging, 4th edn. Academic, San Diego, pp 78–104

Jack KM, Fedigan LM (2004) Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 1: Patterns and causes of natal emigration. Anim Behav 67:761–769

Jack KM, Fedigan LM (2009) Female dispersal in a female-philopatric species, *Cebus capucinus*. Behaviour 146:471–497

Lonsdorf EV, Eberly LE, Pusey AE (2004) Sex differences in learning in chimpanzees. Nature 428:715–716

Manson JH (1999) Infant handling in wild *Cebus capucinus*: testing bonds between females? Anim Behav 57:911–921

Manson JH, Perry S (2000) Correlates of self-directed behaviour in wild white-faced capuchins. Ethology 106:301–317

Manson JH, Perry S, Parish AR (1997) Nonconceptive sexual behavior in bonobos and capuchins. Int J Primatol 18:767–786

Manson JH, Rose LM, Perry S, Gros-Louis J (1999) Dynamics of female-female relationships in wild *Cebus capucinus*: data from two Costa Rican sites. Int J Primatol 20:679–706

Manson JH, Navarrete CD, Silk JB, Perry S (2004a) Time-matched grooming in female primates? New analyses from two species. Anim Behav 67:493–500

Manson JH, Gros-Louis J, Perry S (2004b) Three apparent cases of infanticide by males in wild white-faced capuchins (*Cebus capucinus*). Folia Primatol 75:104–106

Manson JH, Perry S, Stahl D (2005) Reconciliation in wild white-faced capuchins (*Cebus capucinus*). Am J Primatol 65:205–219

Muniz L (2008) Genetic analyses of wild white-faced capuchins (*Cebus capucinus*). PhD thesis, Universität Leipzig, D

Muniz L, Vigilant L (2008) Isolation and characterization of microsatellite markers in the white-faced capuchin monkey (*Cebus capucinus*) and cross-species amplification in other New World monkeys. Mol Ecol Res 8:402–405

Muniz L, Perry S, Manson JH, Gilkenson H, Gros-Louis J, Vigilant L (2006) Father-daughter inbreeding avoidance in a wild primate population. Curr Biol 16:R156–R157

Muniz L, Perry S, Manson JH, Gilkenson H, Gros-Louis J, Vigilant L (2010) Male dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*) at Lomas Barbudal, Costa Rica. Am J Primatol 72:1118–1130

O'Malley RC, Fedigan LM (2005) Evaluating social influences on food-processing in white-faced capuchins (*Cebus capucinus*). Am J Phys Anthropol 127:481–491

Panger MA, Perry S, Rose L, Gros-Louis J, Vogel E, MacKinnon KC, Baker M (2002) Cross-site differences in foraging behavior of white-faced capuchins (*Cebus capucinus*). Am J Phys Anthropol 119:52–66

Perry S (1996a) Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. Am J Primatol 40:167–182

Perry S (1996b) Intergroup encounters in wild white-faced capuchins (*Cebus capucinus*). Int J Primatol 17:309–330

Perry S (1997) Male-female social relationships in wild white-faced capuchins (*Cebus capucinus*). Behaviour 134:477–510

Perry S (1998a) Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. Behaviour 135:139–172

Perry S (1998b) A case report of a male rank reversal in a group of wild white-faced capuchins (*Cebus capucinus*). Primates 39:51–70

Perry S (2003) Coalitionary aggression in white-faced capuchins, *Cebus capucinus*. In: de Waal FBM, Tyack P (eds) Animal social complexity: intelligence, culture and individualized societies. Harvard University Press, Cambridge, MA, pp 111–114

Perry S (2009) Conformism in the food processing techniques of white-faced capuchin monkeys (*Cebus capucinus*). Anim Cogn 12:705–716

Perry S, Manson J (2008) Manipulative monkeys: the capuchins of Lomas Barbudal. Harvard University Press, Cambridge, MA

Perry S, Ordoñez Jiménez JC (2006) The effects of food size, rarity, and processing complexity on white-faced capuchins' visual attention to foraging conspecifics. In: Hohmann G, Robbins MM, Boesch C (eds) Feeding ecology in apes and other primates. Cambridge University Press, Cambridge, pp 203–234

Perry S, Baker M, Fedigan L, Gros-Louis J, Jack K, MacKinnon KC, Manson JH, Panger M, Pyle K, Rose L (2003a) Social conventions in wild white-faced capuchin monkeys: evidence for traditions in a neotropical primate. Curr Anthropol 44:241–268

Perry S, Panger M, Rose L, Baker M, Gros-Louis J, Jack K, MacKinnon KC, Manson JH, Fedigan L, Pyle K (2003b) Traditions in wild white-faced capuchin monkeys. In: Fragaszy DM, Perry S (eds) The biology of traditions: models and evidence. Cambridge University Press, Cambridge, pp 391–425

Perry S, Barrett HC, Manson JH (2004) White-faced capuchin monkeys show triadic awareness in their choice of allies. Anim Behav 67:165–170

Perry S, Manson JH, Muniz L, Gros-Louis J, Vigilant L (2008) Kin-biased social behaviour in wild adult female white-faced capuchins, *Cebus capucinus*. Anim Behav 76:187–199

Rose LM, Perry S, Panger MA, Jack K, Manson JH, Gros-Louis J, MacKinnon KC, Vogel E (2003) Interspecific interactions between *Cebus capucinus* and other species: preliminary data from three Costa Rican sites. Int J Primatol 24:759–796

Schoof VAM, Jack KM, Isbell LA (2009) What traits promote male parallel dispersal in primates? Behaviour 146:701–726