Chapter 9
The Group Life Cycle and Demography of Brown Capuchin Monkeys (*Cebus [apella] nigritus*) in Iguazú National Park, Argentina

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Abstract This study reports demographic and social changes across 20 years in a population of brown capuchin monkeys living in Iguazú National Park in northeastern Argentina. Three sets of results emerge that are critical to understanding the evolution of social behavior in this population. First, patterns of age-related mortality clearly highlight certain periods of increased mortality (postnatal 6 months, onset of reproduction, late senescence) and near-perfect survival (2–6-year-old juveniles, young adult females). Second, tracking the migrations and rank-related reproductive strategies of males helps to uncover the causes and consequences of long male reproductive tenures that average 5 years. Finally, observations of relatively rare male takeovers of the alpha breeding position reveal a predictable sequence of stages in a group's life cycle that tie together female fecundity, infanticide, group size, and kinship-based group fissions. These coordinated aspects of demography and kinship in different stages set the context for understanding differences between groups in social structure and organization.

9.1 Introduction

The population of *Cebus [apella] nigritus* in the Macuco trail area of Iguazú National Park, Argentina, has been studied since 1988 (Brown and Zunino 1990). This work has included censuses at least twice a year since 1991 (Di Bitetti and Janson 2001a; Ramírez-Llorens et al. 2008), and intensive behavioral and

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ecological studies spanning over 80 months (e.g., Janson 1996, 1998, 2007; Di Bitetti and Janson 2001a; Di Bitetti 2005; Baldovino and Di Bitetti 2008; Wheeler 2009; Baldovino 2010). During this period, groups have grown, split, joined, experienced male replacements, changes in matriline dominance, dispersal of subadult males, and complete replacement of the original cohort of females by their daughters. This report summarizes data on the rates of such events and on their demographic and behavioral consequences.

Both kinds of information are needed to understand the importance of a given selective force in a particular study population (Koenig et al. 2006; Kappeler and Fichtel 2012). Short-term studies can provide excellent data on the frequencies and consequences of common sources of natural selection but may miss rare albeit important sources of selection or may estimate their impact poorly. For instance, during the 30 years prior to 2004, several groups of researchers had studied various populations of *Cebus* "*apella*" superspecies (using the old taxonomy; these are now more properly referred to as species in the genus *Sapajus*: Lynch Alfaro et al. in press). Despite such effort, none had reported direct evidence of infanticide by males (although Izawa (1980) presented suggestive evidence). In 2005, we saw a male who attacked and killed an infant, and recorded two additional infant disappearances after a male takeover of our main study group (Ramírez-Llorens et al. 2008; see also Izar et al. 2007). Retrospective analysis of long-term demographic data suggests that infanticide has been the most important single source of mortality of unweaned infants in this study population, despite the rarity of male takeovers and the difficulty in documenting the behavior (Ramírez-Llorens et al. 2008). Thus, long-term studies can provide crucial context to interpret the social structure and organization of a species (e.g., Mitani et al. 2002). An important insight emerging from our analysis is that groups may show predictable "life cycles" – coordinated repetitive temporal patterns of group size, composition, and social change – that set the context for understanding rare demographic events in our study population.

9.2   Description of the Study Population

The Macuco trail area of Iguazú National Park, Argentina, is accessed from the Centro de Investigaciones Ecologicas Subtropicales (25°40′43″ S, 54°26′57″ W), just north of the main tourist attraction of Iguazú Falls. Floristically, the study area belongs to the Upper Paraná Atlantic Forest (Giraudo et al. 2003). The climate is humid and subtropical, with marked seasonality in temperature and day length, but little seasonality in rainfall. Fleshy fruits and arthropods, the most important resources for capuchin monkeys, are scarce in winter (July–August) and most abundant during spring and early summer (October–December; Placci et al. 1994; Di Bitetti and Janson 2001a; Di Bitetti 2009).

The study area contains forest in various stages of recovery from anthropogenic disturbance. First, the entire area to the north and west of the falls was a logging concession up until 1934, when the area was designated a national park by the

federal government (Ministerio del Medio Ambiente 2005). Timber harvesting was highly selective but had considerable impact on the natural vegetation, removed the largest trees and created logging roads to bring the timber to the Iguazú River; two of these logging roads, Yacaratia and Macuco, remain as tourist trails within the study site. A dirt airstrip was created in 1937. It was abandoned in 1971, but signs of former human habituation are still evident near its remnants, along the southwestern part of the Macuco trail. An important legacy of this period was the introduction of several nonnative fruit species, primarily citrus varieties and *Hovenia dulcis* (Rhamnaceae), which have escaped cultivated areas and to greater or lesser degrees become naturalized in the forest.

Current protection efforts by the Argentine National Park service are largely effective at preventing illegal logging and poaching (Di Bitetti et al. 2008; Paviolo et al. 2009). The study area boasts a fairly complete set of likely and actual monkey predators: black hawk-eagles (*Spizaetus tyrannus*), ornate hawk-eagles (*Spizaetus ornatus*), jaguarundis (*Puma yagouaroundi*), oncillas (*Leopardus tigrinus*), margays (*Leopardus wiedii*), ocelots (*Leopardus pardalis*), pumas (*Puma concolor*), jaguars (*Panthera onca*), and tayras (*Eira barbara*). Two species of large raptors, crested eagles (*Morphnus guianensis*) and harpy eagles (*Harpia harpyja*), formerly bred in the area, but the removal of the large emergent trees that they favor for nesting, in addition to general habitat loss, has made them no more than occasional visitors. Most of the five pit viper species (Crotalinae) that are expected for the region are seen routinely in the summer months; the medium-sized rainbow boa (*Epicrates cenchria*) is rare. Current anthropogenic disturbances inside the study area are routine use of the Macuco trail by tourists, noise from nearby roads, and helicopter flights relatively low above the canopy. Since 2007, increasingly frequent interactions (mostly begging for or stealing food) between individuals of one of the study groups and tourists near the falls have become a source of concern.

The study animals live in multi-male, multi-female groups of between 7 and 44 individuals (Di Bitetti and Janson 2001a; Agostini and Visalberghi 2005). With rare exceptions, all individuals of both sexes can be arranged into a linear dominance hierarchy based on decided agonistic and approach-avoid interactions. As in other *apella* populations, each study group has a clear alpha male who tends to be centrally positioned within the group spread and has feeding and mating priority (Janson 1984, 1985). The Iguazú capuchins often feed on multiple food sources at a time, thereby reducing aggression and monopolization of food by dominants (cf. Janson 1996; Di Bitetti and Janson 2001b). Females are philopatric and form alliances based on kinship and reciprocal social grooming (Di Bitetti 1997).

The data for this study come from nine social groups in the vicinity of the Macuco trail, inhabiting an area of over 6 km^2 (Ramírez-Llorens et al. 2008). The early (1991–1992) groups were Macuco (MAC), Yacaratia (YAC), Barrio (BAR), Rubias (RUB), Silver (SIL), and Laboratorio (LAB). In 2005, MAC split, giving rise to two additional daughter groups, Rita (RI) and Gundolf (GUN); MAC split again in 2009, producing an additional daughter group Spot (SP). Individual animals were recognizable through a combination of relatively stable patterns of

fur color, tuft shape, size, healed injuries, as well as sex and group membership; altogether, 289 distinct individuals are in the database, although not all of them survived long enough to be named or even sexed. We did not capture and permanently mark the study animals, so the displacements of emigrating animals (mostly males) were recorded only opportunistically and for at most a year after their departure from one of the main study groups. The only group for which we have consistent census information throughout the 20-year study period is MAC and its daughter groups; for these groups, it is possible to state mother–infant relationships for the 147 descendants of the initial cohort of 5 adult females in 1991. Many researchers have contributed to the demographic database over the years, but nearly all of the consistent census data come from the authors for the following periods (CHJ: 1991; MSD: 1992–1996; MCB: 1997–2010). The study groups were either the subject of intensive behavioral study or were censused thoroughly at least twice per year, once late in the year (late November or December) after the major period of births and once in May–June after the period of high infant mortality.

Like other capuchin monkeys, the study population is omnivorous, with a diet consisting mainly of ripe fruits and arthropods (Robinson and Janson 1987). Seasonal trends in diet reflect the varying abundance of these resources. In the austral winter, when neither ripe fruit nor insects are readily available, the capuchins consume large amounts of vegetation, primarily leaf bases of bamboo and bromeliads (Brown and Zunino 1990). Births are highly seasonal; nearly all occur between October and February (Di Bitetti and Janson 2001a). Because of the scarcity of ripe fruit during June through August, Janson has used this population (primarily the MAC study group) for a series of large-scale provisioning experiments using up to 27 feeding platforms to test several hypotheses about foraging cognition and feeding competition (Janson 1996, 1998, 2007; Janson and Di Bitetti 1997; Di Bitetti and Janson 2001b). Smaller-scale use of feeding platforms has enabled studies on other topics in this population (e.g., Visalberghi et al. 2003; Di Bitetti 2005; Wheeler 2009). Use of the feeding platforms has not had a detectable effect in increasing birth rates (Di Bitetti and Janson 2001a) or infant survival rates (Ramírez-Llorens et al. 2008) in MAC relative to other groups. Some nonprovisioned groups in the population experienced similar population growth during parts of this period (e.g., SIL).

9.3   Demography of the Iguazú Capuchin Study Groups, 1991–2010

Nine study groups have been followed or censused with sufficient continuity to allow tracking of life events of identified individuals. The length of study in years for each group is 1 (SP), 2.5 (BAR), 4 (RUB), 5 (RI), 5.5 (YAC, LAB, GUN), 6 (SIL), and 20 (MAC); for further details from 1991 to 2006, see Ramírez-Llorens et al. (2008). Shorter periods have provided data for demographic rates and rare

events, while longer-term observations have permitted analyses of key events in the life cycle of groups (see Sect. 9.6 below). For rare events such as adult male immigration or male replacements, the sample size is the total observation years across all groups (55 group-years). In all cases, when an event happened between two censuses, the event was attributed to the date midway between the census dates, unless other information (e.g., infant size or behavior) suggested that the true date was closer to the first or second census date.

9.3.1   Fecundity

Female capuchin monkeys give birth on average every 19.4 months, without strong effects of group size or offspring sex (Di Bitetti and Janson 2001a). Birth intervals are significantly shorter if the previous infant dies before 8 months of age than if it survives its first year (14.1 versus 20.4 months; Ramírez-Llorens et al. 2008). Because births are highly seasonal, actual birth intervals cluster around 1 year or 2 years (rarely 3 or more years). If a female's prior offspring survives past 8 months, the modal birth interval is 2 or more years (52 of 80 cases), whereas if the prior infant does not survive to 8 months, the modal interval is 1 year (27 of 34 cases).

Female fecundity increases rapidly between the ages of 5 and 8, followed by a period of highest fecundity for females between 9 and 16 years of age, ending with a period of decreasing fecundity in females above 16 years of age (Fig. 9.1). There is clear statistical evidence for reproductive senescence in the declining birth rates of older females (Fig. 9.1) but not for menopause. Three of the four females estimated to have survived beyond 22 years continued to reproduce (one had an unusually long interbirth interval of 4 years); the fourth one (GU) moved with her daughter RI to form a new group in early 2005 and has had no offspring since late 2005 (ages 24–28).

The age at first birth of 27 known-age females ranged from 47.5 to 96.2 months, with a median of 71.64 months or about 6 years. Age at first birth is significantly earlier for females of alpha matrilines than for those in lower-ranking matrilines (6 of 8 first births at about 5 years of age in alpha matrilines versus 1 of 12 first births in non-alpha matrilines, Fisher exact test, two-tailed $p = 0.0044$). The likelihood that a female gave birth in a given season, after controlling for maternal age and survival of the prior infant, did not depend significantly on matriline rank measured as modal rank for foundress females during the first decade of the study and for their daughters as their mother's rank at the time of the daughter's first parturition (logistic regression, effect of rank: $p = 0.66$).

9.3.2   Survival

Survivorship is calculated based on two distinct data sets: (1) the histories of all individuals observed to be born into study groups and followed until disappearance,
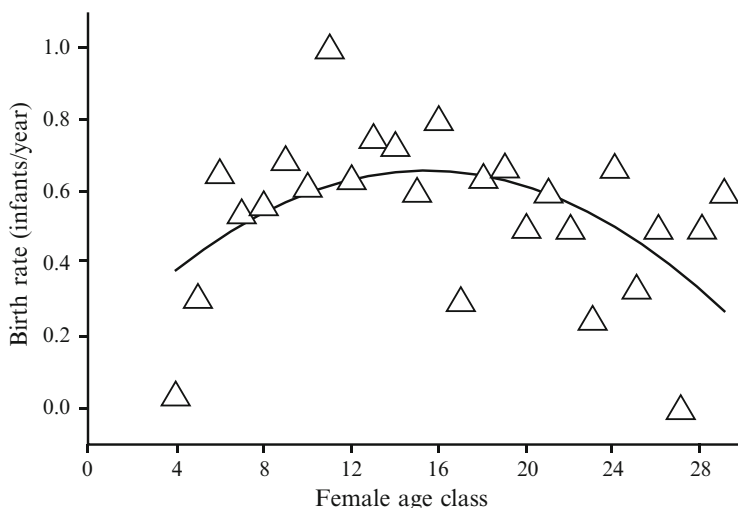
Fig. 9.1 Birth rate as a function of female age. There is a significant quadratic relationship between the fraction of females bearing offspring in a given year and the females' ages (% born = 0.73116065 − 0.0045456 × age − 0.0021112 × (age-16)^2; ANOVA $F_{2,23} = 4.0$, $p = 0.032$). These cross-sectional values are validated by a more appropriate longitudinal analysis. Using a logistic General Linear Mixed Model of the probability of giving birth in a given year within individual females, using female identity as a random effect, the effect of having a prior surviving infant is negative ($p < 0.0001$), and the effect of maternal age has a positive linear ($p = 0.006$) and a negative quadratic coefficient ($p = 0.006$)

death, dispersal, or the end of the present study period, and (2) individuals already present at the start of the study and similarly followed. Histories of individuals still alive at the end of the present study are right-censored, whereas histories of individuals alive for an unknown period prior to the start of observations are left-censored. However, because of predictable age-related changes in size, shape, and fur patterning from birth through early adulthood (10–15 years of age), we estimated the ages of all individuals present at the start of the study for purposes of estimating age-specific survivorship.

The survivorship curve for individuals in MAC shows several periods of distinct mortality rates (Fig. 9.2). First is a period of high postnatal mortality (48%/year) lasting until roughly 8 months of age. About 40% of this early mortality occurs within the first 2–3 weeks after birth and is likely due to infant weakness; there is some clustering of these deaths among females, as 9 of the 12 early infant deaths occurred in only 3 of the 12 females that bore at least six infants each (contingency table, G with Williams' correction = 25.8, $df = 11$, $p = 0.007$). The remaining early mortality is evenly spread across the first 6 months of life and includes infanticide, which accounts for at least 27.3% of all infant mortality (Ramírez-Llorens et al. 2008). Second is a period of lower mortality (10.1%/year) between about 8 and 18 months of age, during which weaning generally occurs. Third is a period of remarkably low mortality (2.75%/year) between 18 months and about
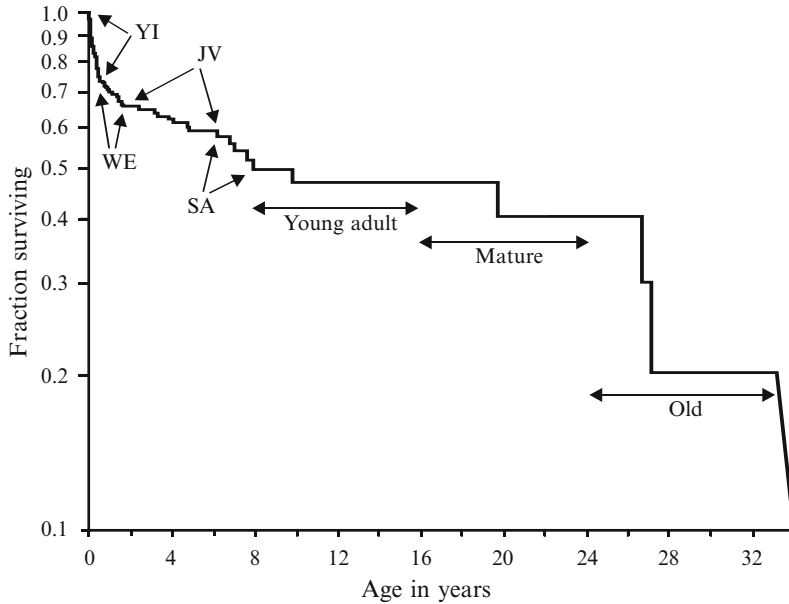
Fig. 9.2 Age-dependent survival. Survivorship graph for all individuals (male and female) born into MAC and its daughter groups in 1991–2010, combined with data on adult females categorized as young adult (YA; 8–16 years), mature (M; 16–24 years), and old (O; over 24 years) at the start of the study, for a total of 715 individual-years. Based on differences in the (log)linear slopes of contiguous regions, four periods of relatively uniform mortality can be recognized prior to adulthood (see text): YI = young infants (0–8 months old, sample size: $N = 146$), WE = weanlings (8–18 months, $N = 100$), JV = juveniles (18 months–6 years old, $N = 84$), SA = subadult (6–8 years old, $N = 37$). Sample sizes for the older female age classes are YA = 20, M = 9, O = 5. Expected lifespan at birth is 8 years, but females that survive to 8 months can expect to live another approximately 24 years on average

6 years, during which juveniles are sheltered from both competition for food (by the dominant male and their mothers) and from predation risk (by being able to occupy central positions in the group spread; Janson 1990; Di Bitetti and Janson 2001b).

Up to 6 years of age, the data include roughly equal numbers of males and females; there is no sex difference in survivorship for known-sex individuals (typically those that survive past 4 months of age; proportional hazards model, effect of individual's sex: $p = 0.50$). From 6 to 8 years, mortality increases (to about 8.6%/year) among females (most males have dispersed by the end of this age range; see below). This period includes the first birth and nursing for most females, and the higher mortality may be associated with the stresses of starting reproduction. After 8 years is a long period of negligible mortality among females (0.7%/ year; Fig. 9.2). This halcyon period of near-perfect survival and high fecundity (Fig. 9.1) lasts roughly from 8 to 16 years of age, a period we refer to as "young adulthood." There follows a period of about 8 years during which "mature" females (ages 16–24) retain high fecundity but begin to experience modest mortality

(2.5%/year, Fig. 9.2). After the age of 24, "old" females experience a reduction in fecundity (Fig. 9.1) and increase in mortality (to 14.0%/year, Fig. 9.2).

Maternal rank (see Sect. 9.3.1 for definition) did not significantly affect juvenile survival for any interval of infant and juvenile ages (up to 1 month of age, 1–8 months, 8–18 months, and 18–60 months) or for cumulative survival from birth to 60 months (logistic regressions of infant survival, effects of rank: all $p > 0.34$).

9.3.3 Matriline Rank Stability and Growth Rates

Once a daughter reached adulthood, her dominance rank usually closely approximated that of her mother (Table 9.1). However, while she was still a juvenile, her rank appeared to depend more on her age and size relative to other juveniles than on her mother's rank, although the protection and intervention of a high-ranking mother could allow a daughter preferred access to contested food sources. Juvenile females nearly always rank below any adult female in access to contested food sources, but sometimes, subadult females of high-ranking lineages could displace low-ranking adult females.

Matrilines maintained stable ranks as long as the matriarch was alive. Notable changes in matriline rank were observed only twice in the 15 study years that MAC did not divide (1991–2005), but these corresponded to the only two instances of mature or old female mortality in this period. The first case was that of OL and her presumed daughter SP (born prior to the start of the study, but associated with OL spatially and socially). OL was very old but still very aggressive, often initiating threats toward other females or soliciting coalitions to threaten other group members. Although an exact nondependent rank for OL is hard to estimate (due to the high frequency of coalitionary aggression), she was not a peripheral group member and fed in many contested food sources along with SP. Following the death of OL in 1992, SP was still a juvenile and almost immediately became one of the group's most peripheral members, rarely seen feeding in the main group and mostly avoiding agonism in contested food trees throughout the subsequent 14 years; she split from her natal group in 2010, following a change in the dominant male, and formed a new group with one adult male and her three youngest offspring.

The second case was that of F2. She was the clear alpha female from 1991 to her disappearance and presumed death in mid-2001. During this period, both her male and female offspring benefitted from F2's agonistic protection when entering and feeding in contested food sources. Her oldest daughter (MF) that survived to reproduce clearly ranked closely below F2 at the top of the female hierarchy but disappeared (and is presumed to have died) a few months after her mother's disappearance. F2's younger surviving daughter (UR) was still a juvenile when F2 disappeared; UR survived another 5 years yet never attained high rank and was among the lowest-ranked adult females at the time she first gave birth.

Table 9.1 Changes in matriline dominance across years of the study

Rank	1991–1993	1996	1998	2000	2003	2005–2006	2006–2007
1	F2	F2	F2	F2	YO(DO)	TH(DO)	TH(DO)
2	GR = OL	GR	GR	MF(F2)	TH(DO)	YO(DO)	EST(TH < DO)
3		WC(GR)	WC(GR)	GR	GU	GR	YO(DO)
4	GU = DO	GU	LU(GR)	LU(GR)	RI(GU)	CHI(GO < DO)	CHI(GO < DO)
5		DO	mf(F2)	MG(GR)	SP(OL)	SP(OL)	GR
6	sp(OL)	lu(GR)	GU	WC(GR)	CL(SP < OL)	EST(TH < DO)	CL(SP < OL)
7	wc(GR)	th(DO)	DO	GU	WC(GR)	CL(SP < OL)	OLI(SP < OL)
8		SP(OL)	TH(DO)	RI(GU)	GV(WC < GR)	OLI(SP < OL)	SP(OL)
9		ri(GU)	SP(OL)	DO	WE(WC < GR)	UR(F2)	eva(CL < SP < OL)
10		yo(DO)	ri(GU)	TH(DO)	GR	eva(CL < SP < OL)	bia(SP < OL)
11		mf(F2)	yo(DO)	YO(DO)	LU(GR)	jos(SP < OL)	jos(SP < OL)
12		mg(GR)	mg(GR)	GO(DO)	MG(GR)	bia(SP < OL)	maw(UR < F2)
13		go(DO)	go(DO)	SP(OL)	GRE(GR)		
14	cl(SP < OL)	cl(SP < OL)	cl(SP < OL)	CL(SP < OL)	ur(F2)		
15	we(GR)	we(GR)	we(WC < GR)	we(WC < GR)	est(TH < DO)		
16			gre(GR)	gre(GR)	chi(GO < DO)		
17				gv(WC < GR)			
18				mi(TH < DO)			
19				ur(F2)			

Sufficient dyadic agonistic data to produce female dominance hierarchies were obtained only by certain researchers, so sampling is not as uniform or complete as desirable. Early hierarchies were arranged by eye, but later ones were calculated using MatMan. The adult females present at the start of the study are considered the matriarchs and are given with no abbreviation in parentheses. Each offspring's abbreviation is followed by her genealogy in parentheses, with "<" meaning "daughter of." Juveniles are given in lowercase, and adults in uppercase; infants are not included. In 2004–2005, GR's matriline (except GR) fissioned from MAC to form the GUN group, and GU's matriline split off to form RI group. Unrelated females linked by '=' were not distinguishable in rank.
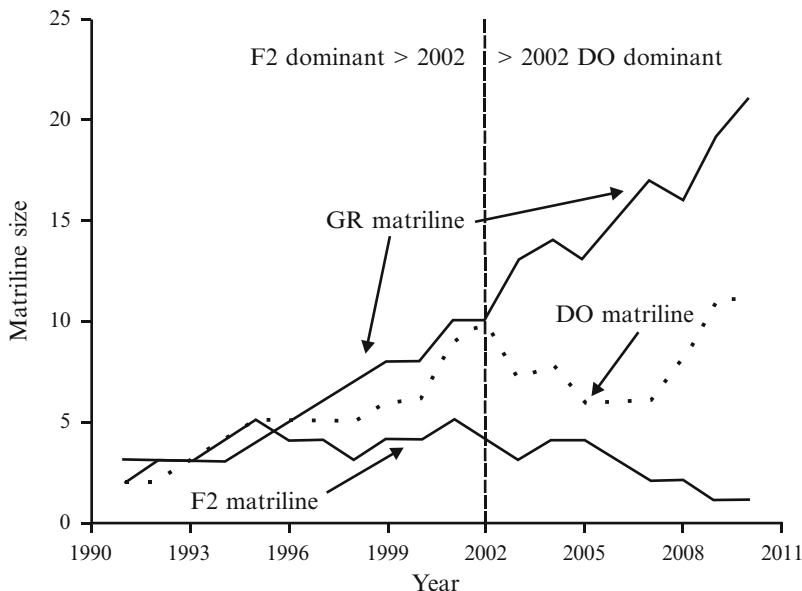
Fig. 9.3 Matriline dynamics. Growth of lineages of three of the five adult females present in the Macuco group in 1991; kinship among these females is not known. Female F2 was the alpha female during 1991–2001, GR was the beta, and DO was either delta or epsilon (depending on the year). F2 died in mid-2001, and by mid-2002, DO's matriline had moved from near the bottom of the female hierarchy to become alpha. For clarity, the growth rates of two other matrilines are not shown, but they were intermediate between GR and F2 and had net losses in only 1 of 20 observation years on average. The two dominant matrilines had losses in 4 of 20 observation years

Interestingly, after the death of the alpha female and her adult daughter, the beta female GR did not become the new alpha nor did her matriline become top-ranking, although she had three adult living daughters. Instead, the new alpha position was attained by DO's two oldest daughters of the fourth-ranking matriline (the two daughters exchanged the alpha position early in this period).

Despite the lack of significant maternal rank effects on fecundity or infant survival, the long-term success of different matrilines in MAC and its daughter groups differed markedly (Fig. 9.3). Rank effects were absent largely because alpha matrilines had the lowest recruitment of all matrilines (Fig. 9.3; F2 1991–2001, DO from 2002 onwards), whereas the beta matriline (GR) had the most consistent and highest growth rate. The low effective recruitment success of the alpha female F2's matriline was due to overproduction of male versus female offspring (ratio of 5:2 compared to 44:47 for the remaining females in MAC), along with the deaths of both of her subadult (6–8 years old) daughters. After it shifted from subordinate to alpha status in 2002, the low recruitment success of DO's matriline was due mostly to low juvenile survival (survival to age 2 of 0.4 versus 0.70 for other females). The different causes for low recruitment of these two dominant matrilines do not suggest any simple cause, but the overall pattern implies that alpha status confers no strong fecundity or survival benefits for females in this population.

9.4 Male Life Histories and Strategies

9.4.1 Natal Dispersal

We documented the emigration of 27 natal males during 55 group-years of observation. Because we do not mark individuals with permanent tags, we cannot follow the fates of dispersing males beyond about 1 year after they leave their natal or current group, and even this ability is restricted to a subset of males that we are lucky enough to find again. Thus, we cannot extend the survivorship graphs of juvenile males beyond the age of dispersal (cf. Fig. 9.3 for females), although we know the fates of a few individuals. Unlike in *Cebus capucinus* (Jack and Fedigan 2004), natal dispersals in our population were isolated events. We documented only a single clear codispersal, out of 21 natal male dispersal events in well-studied groups (MAC, GUN, RI), when two males disappeared on the same day in 2006. They were found together about 16 km from their natal group in the local town (Puerto Iguazú) a few days later. The very long dispersal distance and the unusual coincidence of their simultaneous departure gave rise to the suspicion that they had been captured by local tourists and released in the town.

Dispersal events are not clustered in time. Although in five cases, two natal males dispersed from the same group within 3 months of each other, this frequency of clustered dispersals does not differ from random (given a rate of 0.688 natal male dispersals per group-year of study, we should expect 3.32 of 21 dispersals to occur at random within 3 months of a previous dispersal, $G = 0.9$, $df = 1$, $p > 0.5$). In only one of these cases of closely spaced dispersal were the two males known to have dispersed together to the same group, which was their mother's natal group. In addition to the case of simultaneous long-distance dispersal, the fates of eight dispersing natal males were known: two were seen alone in the natal territory several weeks to months after emigration and did not appear in neighboring groups, and in six cases, the males were found in a neighboring group several months after emigration. Given that we frequently observed neighboring groups, the above data suggest that male dispersal is usually (21/27 cases, across all study groups) further than one group away.

Natal males disperse across a range of ages, but most dispersal events occur between the ages of 5 and 7 years, with a mean of 5.7 (Fig. 9.4). Both cases of infant dispersal occurred when their mothers apparently left their natal group. Three cases of male dispersal at younger than 4 years of age were all from a daughter group (RI) back to the mother's natal group (MAC); none of the mother's (known) matrilineal relatives lived in the latter. Excluding these five cases raises the mean age of dispersal to 6.5 years (median of 6.1 years). At the time of dispersal, they are clearly smaller than fully adult males of 9–10 years of age.
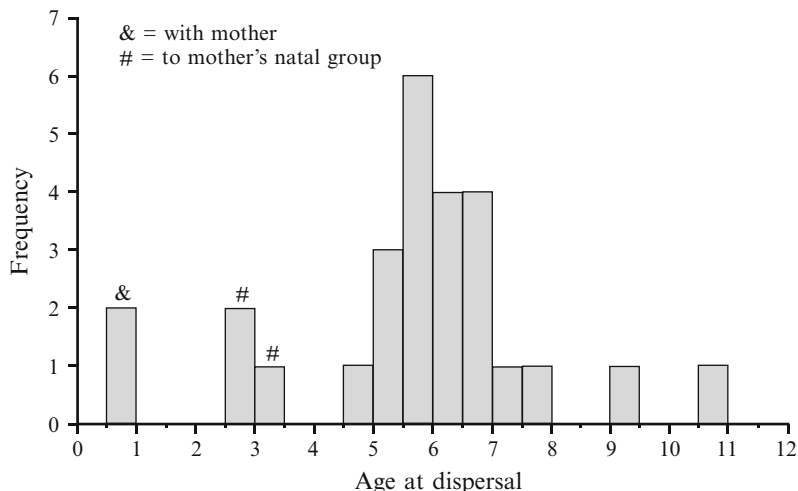
Fig. 9.4 Distribution of the ages of dispersal for natal males in all study groups 1991–2010. The two cases of dispersal at less than 1 year of age were infant males that disappeared along with the mothers and are presumed to have codispersed with them (but the possibility of coincident death cannot be excluded). The three unusual cases of dispersal between 2.5 and 3.5 years of age were from a recent fission group of Macuco (Rita) back to the Macuco group, and all occurred within 1 year

9.4.2 Immigrant Males and Their Fates

We documented the immigration of 39 subadult (5–8 years old) and young adult (9–11 years old) males into focal groups in 55 group-years; there were also 12 presumed immigrant adult males present in various study groups when we started sampling, including five that were alpha males (treated separately below). Some of the immigrant males had been seen previously alone in the home ranges of the groups that they joined, but the prior histories of most were unknown, suggesting that they did not move in from immediately neighboring study groups. Immigrant males stayed in a group until they either emigrated, challenged the dominant male for alpha status, or achieved alpha status some other way. We can assign "fates" to each of 46 non-alpha males; 17 of these were still subordinates at the end of the samples on their groups, and the remaining 29 males were involved in 35 changes in status (Table 9.2). The most striking aspect of these changes is the existence of three distinct "pathways to power": a subordinate male can become alpha by challenging the existing alpha, inheriting the alpha position if both the challenger and the alpha male are badly injured in a fight, or taking over as the alpha male of a daughter or splinter group of females that usually occurs shortly after a new male becomes established (see Sect. 9.5.1). The frequency of nonaggressive paths to power (inheritance or new group creation) is nearly as high as aggressive ones (9 versus 11 cases).

Table 9.2 "Fates" (changes in status) of 47 subordinate adult males following immigration to one of the study groups, and the mean and range (in parentheses) of values for each variable

	Challenge and replace prior alpha male	Inherit alpha role without fight	Leave as alpha male in new daughter group	Emigrate without obvious cause	Emigrate during or soon after alpha male change	Still subordinate at end of sample
N males (only complete tenures)	11 (3)	2 (1)	7 (4)	8 (3)	7 (6)	17
Mean number of years of residence prior to status change, all data	3.84 (0.02–8.49)	2.15 (1.64–2.67)	3.07 (0.41–5.0)	2.0 (0.54–5.5)	0.89 (0.22–2.36)	1.46 (0–4.64)
Mean number of years of residence prior to status change, complete tenures	3.95 (0.02–6.55)	2.67	3.92 (3.01–5.0)	2.83 (0.54–5.5)	0.85 (0.22–2.36)	NA
Mean age at status change	14.25 (10.5–21.7)	8.65 (7.6–9.6)	14.15 (10.1–18.4)	10.37 (7.8–14.5)	8.6 (6.2–12.4)	NA

Several males were assigned more than one fate, as they either changed status within a group or were tracked through more than one study group. Many of the residence durations are censored because males were already present at the start of study on each group; results are provided both for all data and only complete tenures.

Replacement of the alpha male position is associated with predictable emigration of the group's remaining non-natal males. In 6 of the 7 well-observed replacements of the alpha male in groups with three or more non-natal males, most or all of the group's non-natal males who did not obtain the alpha position left the group within days to 8 months, accounting for 10 of the 15 total individual emigrations recorded in the whole study. Even counting each bout of postreplacement emigrations as a single event, the frequency of such emigration bouts within 8 months of a male change is much higher than expected by chance (6 versus 1.33, out of 11 total bouts of emigration, $G = 11.9$, $df = 1$, $p < 0.001$).

Bouts of immigration are also more likely following alpha male replacements. In 13 of the 33 cases that could be scored, the arrival of new males to a group occurred within 6 months after the replacement of the group's alpha male. This frequency is much greater than the 3.6 immigration cases expected at random, given only 12 alpha male replacements in the same 55 group-years ($G = 17.97$, $df = 1$, $p < 0.001$). Thus, it appears that newly vacated "slots" for subordinate males are rapidly filled. In most (10/13) cases, the new males came into large groups with over eight adult females, suggesting a preference to join large female groups. Potential immigrants may take into account the number of males already in a group before moving: in the most closely monitored study group, the number of males lost and gained per year was well correlated (excluding the 11 years with neither losses nor gains, $N = 9$ years, $r = 0.95$, $p < 0.0001$).

Once a male joins a new group, his subsequent fate (Table 9.2) depends on his age and chance. Males less than 9 years old are not of full adult size and do not challenge adult males for high rank. They typically remain for shorter periods, emigrating predictably after 2–3 years of residence or when the alpha male is replaced, unless they happen to inherit the alpha status, a rare event over which they have little control. Fully adult male immigrants of at least 9 years of age take positions in the higher ranks of the male hierarchy, sometimes (three cases) challenging the alpha male within 5 months of immigrating but more commonly waiting long periods (an average of 5.2 years, $N = 8$) for successful opportunities to challenge the alpha or to become the alpha male of daughter or splinter groups of females at group fission (associated with alpha male replacement – see below). Males that took the alpha position in fission groups were of the same age on average as males that challenged the alpha (14.15 versus 14.25 years old), and spent nearly the same average time in residence before assuming an alpha role (3.92 versus 3.95 years, Table 9.2). Beta males can be very "patient" waiting for an opportunity to defeat the alpha male, which may take over 8 years to arrive (the case of GE in MAC, 1991–1999). These long waits for a beta male to take over the dominant position may provide opportunities for the beta male to reproduce, as the beta male had preferential access to females that happened to be in estrus at the same time as a more dominant female (Janson 1984) and to the daughters of the dominant male, who did not solicit their fathers as mating partners (Di Bitetti and Janson 2001a).

9.4.3 Tenure and Replacements of Alpha Males

Unlike many other primates in large multi-female groups in which the dominant male of a group may change frequently, sometimes more than once per year (e.g., Palombit et al. 2000), the alpha males in all known populations of *Cebus apella* superspecies tend to have long tenures. Figure 9.5 shows the survival plot of all tenure lengths (including censored durations) documented in the alpha males of the Iguazú population. Very short tenure lengths (less than 4 months) occurred when a male challenged the alpha successfully but the challenger was seriously injured (one case), failed to kill the former alpha male who returned to claim the alpha role (one case), returned to beta status following a group fusion (one case), or inherited alpha status and was subsequently challenged for the alpha position by an older male (one case). Tenure lengths for males that acquire alpha status by challenge versus group fission did not differ in our study (ANOVA, $F_{1,14} = 0.001$, $p = 0.98$). If a male retained alpha status past the first 4 months, tenure lengths were typically long, with a median duration of 5.01 years and a 0.76 chance of lasting at least 3 years. One male, Pecoso, was documented to be the alpha (in Silver group) for at least 11.6 years.

One case of failed male replacement revealed a likely cause of the relatively long tenures of dominant males in this population. Dedos, who had been the dominant male of MAC for over 6 years, was attacked and injured, but not killed, by Gendarme on about September 8, 1997. Dedos withdrew from MAC but remained
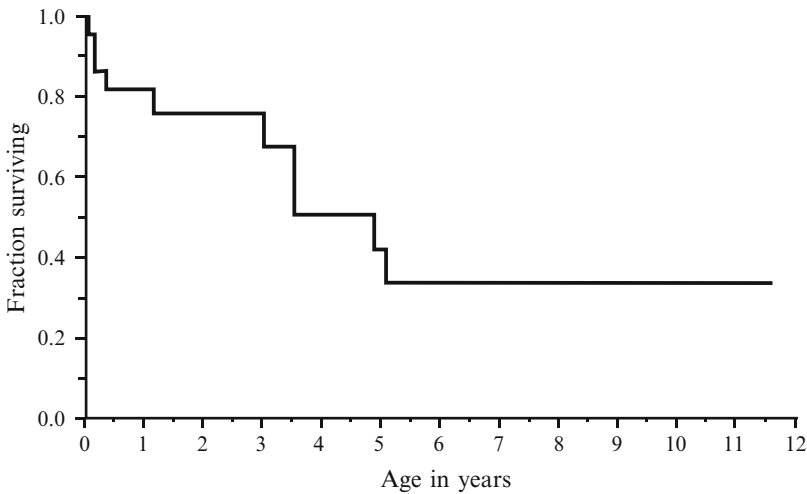

Fig. 9.5 Alpha male tenure duration across all study groups ($N = 23$ males). A tenure length was calculated as the number of days from the date of a male's first appearance as alpha to midway between his last known date as alpha and the date of the next census on his group. About 18% of alpha males held their rank for less than 4 months, but if they made it past this initial period, their expected tenure was 5 years. All four tenure lengths above 5.1 years (5.3, 5.9, 8.5, 11.6) were censored and thus represent minimal estimates of true tenure lengths

in the group's home range for over a month following his injury. Dedos then returned to MAC in late October 1997, and the two males faced off against each other. Dedos was backed up by a cohort of females, including all but one of the group's adult females, whereas Gendarme was backed up only by one female, WC, a putative daughter of Dedos. Dedos and his supporters won this encounter, whereas Gendarme suffered additional wounds during a series of fights. Dedos returned as the dominant male for another nearly 2 years until being badly injured by Gendarme in July of 1999. That the support of Dedos by other group members was more than symbolic is suggested by the fact that in the 1997 series of fights, both the dominant female, F2, and an older natal male, DF, were injured; similar injuries of natal males and adult females occurred during some other male takeover periods. Thus, the dominant male appears to enjoy support by most existing adult females and his sons in conflicts against male challengers, perhaps allowing him to maintain his breeding position in the group far longer than would be the case without this support.

9.5   Changes in Group Size, Group Fission, and Group Fusion

We have detailed data on composition, births, deaths, and migrations for all individuals in MAC and its descendant groups GUN, RI, and SP, from February 1991 through the end of 2010. During this 20-year period, numbers of individuals in these groups increased at a steady rate of about 4% per year (Fig. 9.6), regardless of alpha male changes, infanticides, and two group fissions.

Group counts from other groups span at most six continuous years and are less informative about long-term growth rates. Most groups grew in numbers over the period of observation, but four groups either went extinct or moved entirely out of the known study area and were not seen again. Two of these were small splinter groups (one from the breakup of YAC in 2009; one from the fission of MAC in 2009); in both cases, the group composition was one adult male, one adult female, and one or two juveniles. Two other groups (BAR, RUB) were not seen after 1996 and are presumed to have gone extinct or moved out of the study area; the BAR group partially occupied an area of regenerating forest that was cut down to provide new tourist facilities starting in 1998.

Temporary changes in group size occurred (see also Lynch Alfaro 2007). Very large groups (over 30 animals) tended to show signs of subgrouping behavior, which is not reflected in the total counts, but could lead to subgroups of defined composition ranging independently of other subgroups for several hours up to several days, even on occasion sleeping in different areas. Such subgrouping behavior appeared especially in the Argentine winter, the period of greatest food scarcity (Di Bitetti and Janson 2001a). When these large groups eventually split, the resulting descendant groups were not necessarily well-predicted by the composition of the previous subgroups, except that one fully adult male from the original large group tended to join each descendant group as the alpha (see Sect. 9.4).
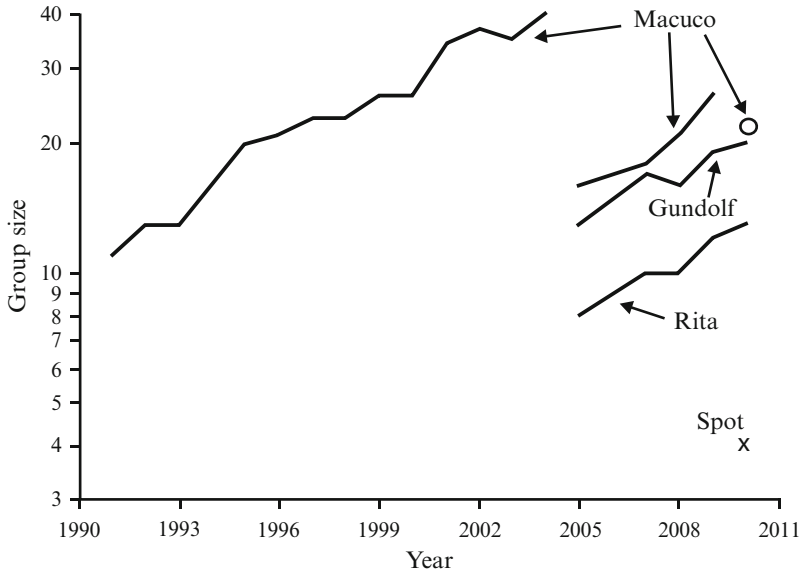
Fig. 9.6 Group sizes (excluding non-natal males) of MAC group and its daughter groups during the study period. The *y*-axis uses a log scale, so a straight line of numbers versus time represents a constant rate of growth. For the entire period, the best estimate of the growth rate is 0.04, and it does not differ before and after the group fission, nor among the daughter groups. The numbers for Rita group include the three juvenile males that emigrated back to their mother's natal group at unusually young ages (see Fig. 9.4)

9.5.1 Processes of Group Fission

We observed the detailed process of group fission in two study groups (three fission events: YAC 1991; MAC 2004–2005; MAC 2009–2010) and monitored the results of fission in a third group (SIL 1994–1995) via periodic censuses. In the first three cases, group splitting occurred in the largest groups known to us in the population at the time: YAC had 34 individuals (9 adult females) just prior to the split, and 2004–2005 MAC had 48 (14 adult females), and 2009–2010 MAC had 33 (10 adult females). In all four cases, splits occurred in association with a replacement of the dominant male in the original groups. However, not every male replacement led to group changes (see Sect. 9.4). In all of the well-observed cases, the clear establishment of the new alpha male was associated quickly with the disappearance of a majority of infants of less than 6 months of age, most likely by infanticide (Ramírez-Llorens et al. 2008). At least one group split (Rita from MAC 2004–2005) may have been the direct consequence of an adult female seeking to avoid infanticidal behavior by the new dominant male (Ramírez-Llorens et al. 2008); the same may be true of OLI's departure with her infant from MAC in late 2009, which preceded the eventual wave of infant disappearances in February–April 2010.

The fourth case of group fission occurred about 1 year following the fusion of the neighboring RUB and SIL groups, producing an enlarged SIL group in 1993. Between mid-1994 and mid-1995, the alpha male in the SIL group (LF) was replaced by a new immigrant adult male (PEC). During the same period, the two subordinate adult males in the SIL group (IN, BI) left the group with two of the three females from the original RUB group, plus one of the females formerly resident in the SIL group. One of the original RUB group females remained in the SIL group. This new RUB group remained as a separate social group, with IN as the alpha male, at least through the end of 1996. In neither SIL nor RUB did any of the infants of the 1994–1995 birth season survive to the mid-1995 census.

Group splits usually produced daughter groups of quite different sizes. In three of the four cases of group splits, the majority of the adult females remained in the original home range whereas the two new daughter groups were in each case composed of a few adult females (numbers of females for YAC 1991 = 6:2:1, MAC 2004–2005 = 8:4:2, and MAC 2009–2010 = 7:2:1) and their immature offspring. In the fourth case (Silver 1994), three females went with each daughter group.

In two well-observed group splits, smaller descendant groups were not at a demographic disadvantage compared to larger ones. There was no marked difference between the per capita growth rates of small versus large descendant groups in the 3 years following a group split, either for MAC (Fig. 9.6) or the YAC group (e.g., the Silver group increased from an initial size of about 9 animals with only two adult females in late 1991 to at least 23 individuals by 2000, an average annual increase of 10%). Because group splits were associated with a change in the dominant male and attendant infanticide, the year after a split was a year of high birth rates, as nearly all the females in a group produced offspring in the year following a male replacement.

When genealogies were known, daughter groups were found to be composed of individuals from single matrilines but did not contain complete matrilines. In the 2004–2005 MAC breakup, GUN contained all the daughters of GR and their offspring but not GR herself, who remained in MAC. Likewise, when Rita left with her offspring, her mother, GU, did not leave with her, although she joined her daughter within a couple of days. The 2009–2010 MAC split produced two splinter groups composed of portions of the matriline of SP (1 = OLI and infant; 2 = SP, BIA, DAN, FRA), yet three other adult daughters of SP (CL, EVA, JOS) stayed in MAC with their offspring, as did one of OLI's subadult daughters (OFE). Thus, the process of group fission in this population appears to produce new groups in which females are likely to be very closely related yet might well have some equally close kin in adjoining groups.

The process of group fission could take any period from 1 day to 6 months. In the case of YAC, it took about 3 months following the change in the dominant male for subgroup composition to stabilize into a close resemblance of the resulting daughter groups, during which time the group went from foraging as a single unit nearly all the time to increasing periods of 2–3 subgroups foraging separately from each other. After the fourth month, the subgroups (ST, SIL) were not seen to rejoin YAC to form the entire original group, and by the fifth month, they occupied largely

distinct but adjacent core areas. In the case of MAC 2004–2005, one of the group's adult males (GUN) formed part of several spatially distinct subgroups before the alpha male (GEN) was replaced, but after GEN was removed, GUN became more independent, and within 4 months, he and a subgroup moved to a new home range adjacent to, but not overlapping with, the original range. In contrast, the second split (RI) in MAC 2004–2005 occurred over 1 day with the dispersal of Rita and her daughters to a peripheral area in MAC's home range, where she was later joined by her mother and two of MAC's former subordinate males. In the MAC 2009–2010 split, one female (OLI) and her new infant started to stay away from MAC after the first intense male–male fights in early November, and she was last seen about 1 month later in the company of one of the adult males of the group (JE). Following the death of MAC's alpha male on November 20th, 2009, continued aggression and unstable ranks among MAC males lasted until late January 2010; during December, the group showed indeterminate cohesion, some days moving as a single group and on other days dividing into at least two distinct foraging parties that sometimes even slept in different areas. After one male (ERN) assumed the alpha role starting in February, 2010, 4 of the 7 infants in the group disappeared within 2 months; by May 2010, another subgroup (SP with BIA, DAN, FRA) had left MAC.

9.5.2 Group Fusion

One case of group fusion was documented. In early 1993, RUB was composed of two adult males (NA, SO), three adult females, and several immatures. At this time, the neighboring SIL group had two adult males (LF = alpha, IN = beta), one subadult male (BI), three adult females, and several juveniles. On the 5th of June, 1993, MD discovered SO alone and with deep wounds to his hands, elbow, and shoulder. On the 14th of June, 1993, NA was also no longer with RUB, and instead, the group had only the two subordinate males from SIL, IN, and BI. These two males stayed with RUB until at least the 28th of June as the only adult males in that group. Meanwhile, on the 21st of June, SO was seen as a subordinate male in SIL, but on the 27th of August, he was back with RUB, along with IN and BI. SO had fresh wounds on his face and at the base of his tail. That same day, RUB had an intergroup encounter with SIL, during which MD saw LF (the alpha male of SIL) with deep wounds on the face. After more chases and a fight during this encounter, SO followed and gave submissive facial gestures to LF. From that date until the middle of 1994, covering seven separate censuses of the group, SIL and RUB comprised a single unit, with LF as the alpha male, IN, SO, and BI as subordinate males, and all the females and juveniles of both groups. NA, the former alpha male of RUB, was not seen again. Thus, it appears that he was displaced as the alpha male of RUB by the two subordinate males of SIL, who then rejoined SIL with the RUB females. SO and all the other known individuals of RUB stayed with SIL for about 1 year. After mid-1994, RUB and SIL fissioned (see above).

9.6   Discussion

9.6.1   Slow Life Histories

This population of *apella*-like capuchins illustrates one of the slower life histories known among monkeys. With an age at first reproduction of 6 years for females, this population would not persist without high juvenile and adult survival, which leads to a relatively high expected (at birth) lifespan of 8 years. There is some evidence that starting reproduction is stressful for females: their survival declines at age 6, and female fecundity is lower at age 5 than later (Fig. 9.1). Once a female reaches full maturity at 8 years, she has a long future life expectancy of 19 years. Although fecundity and survival begin to decline notably as a female surpasses the age of 24, there is no evidence for menopause, and even the oldest females in our study population continued to come into estrus.

Most likely because of slow infant development (Charnov and Berrigan 1993), mothers typically produce an offspring only once every other year, if the previous infant survives. This alternation of birth years sets up the conditions for sexually selected infanticide by males to be adaptive (Ramírez-Llorens et al. 2008), despite the fact that the Iguazú capuchin population is highly seasonal in its breeding (Di Bitetti and Janson 2000), which would make infanticide of little benefit to a newly dominant male in an annual breeder (van Schaik 2000). Although the great longevity and slow life history found in this population is surely assisted by the lack of large eagles preying upon adult capuchins, the reproductive parameters of Iguazú (high age at first birth, alternation of birth years) are commonly found in other capuchins (e.g., Robinson 1988; Fedigan and Rose 1995), even in areas with relatively high adult predation risk (Janson 1984). If the current notion is correct that these slow life histories are a direct result of the relatively large brain size of capuchins (Barton and Capellini 2011), then the cost of large brain size is extreme – the theoretical intrinsic rate of population growth (a rough measure of maximum fitness) in our population (from Figs. 9.1 and 9.2) is 0.1/year, a full order of magnitude less than the r_{max} of about 1 expected of mammals of equivalent body mass (Calder 1996). It is difficult to imagine what benefits of larger brains might repay such a tenfold fitness cost!

The survival of males, far more so than of females, is dictated by events related directly to their reproductive strategy, principally dispersal from their natal group and challenging an established alpha male for the dominant position in a social group. Natal dispersal is an apparent consequence of generalized incest avoidance (Di Bitetti and Janson 2001a). Prior to dispersal (typically by age 6), there is no statistical difference in survival between the sexes in natal animals in MAC. As we rarely can track dispersing males after they leave their natal group, their mortality during dispersal is not easily measured. However, we can estimate the extent of such mortality by examining group adult sex ratios, knowing the survivorship of adult females and the sources and extent of male mortality once they join established groups. Assuming the population as a whole is not growing and using

the results from Fig. 9.1 and Table 9.2, the difference between the adult sex ratio expected based on postimmigration patterns of male mortality and that actually observed implies that at least 38% of dispersing males do not survive to show up in social groups. This mortality is likely spread across 2 or more years, reflecting the difference in average age between the ages of natal dispersers (6 years old; Fig. 9.4) and the estimated ages of immigrant males (typically 8 years old or older; Table 9.2). This is a high rate of mortality for capuchins in this population and may reflect the reality of risks associated with solitary living. By comparison, females from ages of 6–8 experience a total of 15.8% mortality, which itself is markedly higher than just before or after this period (Fig. 9.3). If the estimated dispersal phase male mortality of 38% is accurate, then the life expectancy of a male at birth is only about 7 years, somewhat less than that of a female; nearly 2/3 of males born will die without ever reaching dominant status, whereas only about 40% of females born will die before giving birth at least once.

After a male migrates into a social group, attaining the alpha status may entail both mortality risks and large reproductive rewards. Although a slim majority (11 of 20) of males that attain alpha status do so by challenging the group's dominant male in one or more bouts of contact aggression, nearly half of all males attain the alpha position indirectly (Table 9.2). It is not easy to calculate the real frequency of alpha challenges and their chances of success because if a challenge does not succeed, no change in the social structure occurs and both the dominant and the challenger may sustain only minor wounds. If a successful challenge occurs, the challenger is always wounded, sometimes (2 of 11 cases) severely enough that he cannot immediately assume the alpha status even if he mortally wounds the dominant. In one case (MAC, 2009), the putative challenger (HOM) appears to be have been so severely wounded that he died a few weeks later – none of the other males in the group was severely wounded and none quickly took on the alpha role after the dominant was deposed.

After achieving the dominant status, a male can expect to retain it for 5 years; once he is deposed, it appears that he usually dies (although we can absolutely confirm the death in only two cases). In two cases, the former dominant survived the challenge; in one of these (DE), he recovered from his wounds and won back the dominant position after about 6 weeks, and in the other (ST), he left with one female as a fission product of the group after his deposition, but this daughter group was last seen 3 months after the dominant was defeated. The net result of the these challenges and their attendant mortality is that male life expectancy after immigrating to a social group at age 8 is estimated to be only an additional 10.9 years (Janson et al. unpublished data), roughly half the remaining life expectancy of 19 years of an adult female that reaches 8 years of age. Based on these differences in survival rates, life history theory predicts that male capuchins from this population should show more rapid senescence than should females, even under conditions of low environmental and social stress (e.g., captive breeding colonies).

9.6.2   Female Philopatry, Matrilines, and Group Membership

Capuchin monkeys in this population conform to some but not all of the generalities about matrilineal group structure derived from Old World primates. Like baboons and macaques, capuchin females and their kin in this population tend to support each other in aggressive interactions, daughters come to rank close to (although sometimes above) their mother, and group fissions tend to follow matrilineal divisions (but one or more members of a matriline may stay behind in the natal group). However, despite clear feeding priority and central positioning of the alpha female F2 (e.g., Di Bitetti and Janson 2001a), recruitment success into her matriline was notably lower than that of lower-ranked females (Fig. 9.3); likewise, when DO's matriline became dominant in 2002, it began actually to decline in size, whereas previously, it had been increasing. In both cases, low recruitment into the matriline was seemingly due to lower survival of offspring, and in F2's case, this was compounded with a male-biased sex ratio among her offspring. The low recruitment success of the dominant matriline does not appear to occur in recently founded daughter groups, perhaps because agonistic relationships among these related females are relatively infrequent and of low intensity. Whatever the reason for the low recruitment success (and given the small sample size of matrilines for which we have long-term data, it could be coincidence), F2's small matriline was vulnerable to marked rank change when the matriarch died; a year after F2's death, the lone surviving female of that matriline (UR, Table 9.1) was the lowest-ranked adult female.

The ability of low-ranking adult females to grow their matrilines in the face of contest competition for food may be an unusual feature of this population. Low predation risk on adult capuchins because of a lack of large monkey-eating eagles means that low-ranking subordinates may have the ability to avoid contest competition by foraging at the periphery of the group on alternative resources that might yield one or a few monkeys as much food *per capita* as do the larger and more productive food sources favored (and contested) by the dominants (Di Bitetti and Janson 2001b). Although not easily amenable to an experimental test within this population, this hypothesis makes clear predictions: the relative reproductive success of subordinate females compared to dominants should be negatively correlated with the predation rate on adult females if the major predators preferentially attack animals at the periphery of a prey group.

If the lability of matriline dominance observed in MAC is a more general feature of other groups and populations of *Cebus apella*-like monkeys, this could also explain some general features of their social behavior. For instance, even though they squabble frequently at food sources, *apella*-like capuchins have been shown to be relatively socially tolerant compared to rhesus macaques (de Waal 1986; Brosnan and de Waal 2003). Second, females have not been observed to fight over rank (nearly all agonism is clearly in the context of access to food, or defense of kin or offspring against males) or to engage in the kinds of aggressive tactics expected of animals using aggression to maintain rank position (e.g., Silk 2002).

Both these features could be expected outcomes of a social system in which matrilineal support in contest competition is real, but high matrilineal rank is not easily preserved and thus not worth risking escalated contests to acquire. High matriline rank might still be worth acquiring if the breeding success of males from high-ranking matrilines is markedly higher than that of sons from low-ranking matrilines, but we have no data to test this question. A further outcome of increased mobility of matriline rank and its lack of correlation with fecundity is that females, while preferring to be "philomatric" (staying with their matriline), can take a chance to establish or join a new social group, as illustrated by the fusion and subsequent fission of the RUB group in 1993–1995 and the frequent association of group fission with male replacement.

9.6.3   Group Life Cycles

Despite some variation in details, there is an overriding pattern in group changes that profoundly affects their composition, demography, and behavior. The resulting cyclical sequence of events can be described as a group "life cycle" (cf. colony life cycles of social insects, e.g., Oster and Wilson 1978). This is summarized in a "stage" diagram (Fig. 9.7) in which each distinct configuration of group size and recency of dominant male is represented as a "stage" in the cycle, with stages connected by probabilities of moving from one stage to another. The probabilities are not shown in the diagram but could be entered into a matrix of transition probabilities based on our data. Not all the connections or possible outcomes are encompassed in this diagram, but it is a way to visualize the regularities of change in group structure that emerge from predictable individual-level behaviors. As such, it provides a way to connect natural selection on individual behaviors with their consequences at the level of group structure (cf. Hemelrijk 2002). Note that Fig. 9.7 is based on a small sample and may represent only the life cycle of MAC, which contributed most of the data; nonetheless, it provides a hypothesis against which to compare long-term demographic data from other capuchin and monkey populations.

In our study, cyclical change is driven by replacement of the group's alpha male and the attendant almost inevitable infanticide that follows (Fig. 9.7; see also Fedigan 2003). If a male attains the alpha role (by whatever means) and survives the first 6 months in that role, he is extremely likely to remain as alpha for about 5 years, although a minority can last considerably longer, even over 11 years. The lack of opportunity to replace the alpha during this period is the apparent reason that other non-natal males in the group at the time nearly always migrate away within days to months of the replacement; they are not driven out by invading males, as occurs in white-faced capuchins (Gros-Louis et al. 2003; Fedigan and Jack 2004). The lack of adult males in the group appears to attract immigration from non-natal males, especially into groups with large numbers of females. In the meantime, the alpha male will have eliminated most or all of the infants less than 8 months of age
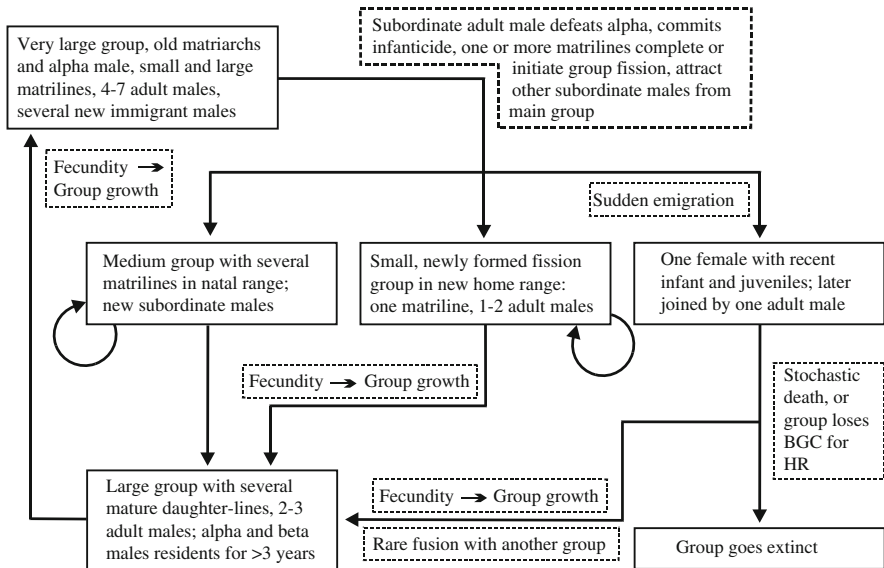
Fig. 9.7 Schematic diagram of group life cycle. Each box with a solid border is a distinct group size or composition, connected by *arrows* representing possible future outcomes of processes that are described in boxes with *dashed outlines*. These processes include net fecundity (exceeding mortality), male replacement, group fission, and risk of infanticide. *Circular arrows* pointing back to the same box represent the likelihood that a group stays in the same state from 1 year to the next. In our population, we did not observe the decline of well-established groups toward smaller sizes and extinction, but this possibility would be easy to include using *arrows* leading from larger groups to smaller ones

within 1–2 months of his having established himself as the undisputed alpha male (a process which may take up to 6 months, depending on his injuries, the presence of challengers, etc.).

Some females use the male replacement to initiate permanent group splits, either by leaving the core area of the natal group as individuals with their offspring ("splinter" groups: three cases) or by forming first temporary, then increasingly durable, foraging subgroups attended by one or two adult males from the natal group. These "daughter" groups, typically (but not always) composed of females from a single matriline, eventually move to areas that are adjacent to or slightly overlapping the natal group's home range. Splinter groups typically contain a female with her infant of the year and appear to be one way for a female to avoid infanticide by the new alpha male in her natal group. Two of the three known such splinter groups were never found again, so it may be that these females eventually join some other group far from their natal group or die as isolated individuals. The new matriarchs of fission groups experience higher birth rates in the period following the group's establishment, although the overall growth rates of fission groups are not distinguishable from that of the natal group. In typical groups where the alpha male lasts at least 5 years, group size can increase quickly, doubling within a

decade, thus providing a more attractive target for new male immigration and sowing the eventual seeds of the next male replacement. If the group is still relatively small at the time of a male replacement, the group may stay together for another "round" until the following replacement. Thus, there is an overall cycle to group size and alpha male stability that is coordinated by the events that attend the replacement of a group's alpha male (Fig. 9.7).

Understanding the group life cycle not only illuminates the importance of rare sources of selection, such as infanticide, but also is necessary to place any short-term study of a particular group into a proper perspective. Given the dynamic and cyclical nature of group size and composition, observers cannot hope to study a "typical" group or even a typical set of groups. For instance, much of the variation that we observed between groups at the start of our study in 1991 was likely an effect of observing them in different stages of their life cycles. Acknowledging and documenting group life cycle should allow researchers to detect group-specific traits that reveal potentially important relationships between extrinsic traits (e.g., habitat quality) and group characteristics. Failure to understand group life cycles may lead to the false rejection of hypotheses relating within-population variation of group size to food availability, predation risk, patchiness, or other variables thought to affect sociality.

9.7 Conclusions

Long-term studies of animal populations have been important in revealing rare sources of strong natural selection, long-term demographic cycles or epidemics, and effects of slow habitat change. For slowly maturing, long-lived animals like most primates, long-term studies are also essential to document important events or phases of individual life histories that are critical to explaining variation in individual reproductive success. In our study, the rarest and most dramatic event in individual life histories is the assumption of the alpha position by males; only about 1/3 of all males survive long enough to challenge for the alpha position; the outcome of such challenges is usually fatal for one of the participants, and the consequences of a successful takeover ramify through the group via infanticide, high turnover in non-natal males, and likely group fission (Fig. 9.7). The result of these social upheavals is that male takeovers essentially "reset the clock," often producing daughter groups with all new immigrant males, females and offspring that are of a single matriline, an immediate loss of most infants followed by a year in which nearly all females have babies, and a relatively young adult alpha male that is likely to remain as alpha for 5 or more years, long enough for incest avoidance to become an important part of mating strategies. Subsequent growth of groups is associated with lower average kinship among females, greater aggressive competition between the descendants of the original adult females, larger group size, and increased attraction of immigrant males to the group, which in turn sets the stage for new male challenges to the alpha male and possible group

fission. Recognizing this group life cycle places a different interpretation on differences in group size. Rather than interpreting these differences as stochastic variation around a stationary mean (e.g., Cohen 1971), or reflecting differences in habitat quality (e.g., Gillespie and Chapman 2001) or group competitiveness (Robinson 1988), various groups may simply be at distinct points in relatively predictable life cycles. The coordinated changes that accompany transition through the stages of a group's life cycle should predictably affect social behaviors (female–female agonism, existence of juvenile cohorts, female mating preferences). If predictable group life cycles emerge as a feature of other primate populations, documenting and understanding these life cycles should help to clarify the differences in social organization and structure between species, how these differences relate to ecological variables and fundamental life-history traits, and help to integrate male and female social strategies in a broader understanding of primate social systems.

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