Chapter 13
The 30-Year Blues: What We Know and Don't Know About Life History, Group Size, and Group Fission of Blue Monkeys in the Kakamega Forest, Kenya

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Please note the erratum to this chapter at the end of the book.

Abstract Long-term studies uniquely allow researchers to investigate phenomena that play out over long periods, as well as rare events that accumulate slowly into a respectable sample. This chapter takes both approaches in reporting on a 30-year study of blue monkeys (*Cercopithecus mitis stuhlmanni*), reviewing life-history data mainly for females, which can live up to 33 years, and presenting data related to group fission, a rare event. Compared to close relatives, blue monkeys appear to have an exceptionally slow life history, related to low levels of mortality in forest environments. Group fissions show variable patterns, occurring at variable group sizes, and usually involving the splitting of a few family units, including mothers and young daughters. Ecological factors such as feeding competition do not appear to explain why fission occurs, and females do not seem to increase reproductive rates, improve infant survival or reduce the likelihood of male takeovers after fission.

13.1 Introduction

Long-term studies of animal populations uniquely allow two kinds of investigation. First, one can document phenomena that occur over long periods; second, one can examine patterns in rare events, which accumulate slowly. This chapter takes both perspectives in reporting on a 30-year study of blue monkeys (*Cercopithecus mitis stuhlmanni*), an African forest-dwelling guenon.

Most African guenons have not been well studied even on a short-term basis. Most likely, this reflects the practical difficulties of observation in the forested habitat that most species inhabit: dense vegetation, rather small body size, hairy faces, and the fact

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that many are hunted makes field study, and especially individual identification, a significant challenge. Long-term study offers a potential solution because it permits habituation, at least in unhunted populations. Habituation allowed me to address questions and use field methods that were unthinkable at the beginning of our study.

After describing briefly some of the conditions of the study, I first summarize what we know about the life history of this species, based on records from individually identified animals monitored over three decades. This period approaches a natural lifetime. The data allow a robust understanding of basic life-history parameters, at least for females, and contribute to a comparative view of life-history variation in the primate order. Second, I address the related topics of group fission and group size, by examining aspects of the circumstances and consequences of rare fission events. Even after 30 years, the sample is small. The data suggest some common patterns, but also present puzzles that even longer-term study may help to resolve.

13.2 Study Site, Population, and Research History

13.2.1 Study Site

The study population inhabits the Kakamega Forest, western Kenya, a rainforest at 1,765 m with a gazetted area of 238 km^2 (Mitchell et al. 2009). Annual rainfall averaged 1,973 ± 310 mm over the 1979–2009 study period (unpublished KFS and BIOTA records). Combining elements of central African lowland and Afromontane forests, Kakamega is a relatively young forest (~10–12,000 years old), more isolated than many others in the East African region from similar forest patches. This history, together with decades of human influence (Mitchell 2004), has left the forest as an island amidst densely populated farmland, and diverse in the vegetative assemblages represented. Of the total gazetted area, less than half is natural forest, with the remaining portion plantation, bush- and grassland, and even farmland.

Our ~2 km^2 study site, located around the Isecheno forest station (0°14′11″ N, 34°52′02″ E), comprises mainly near-natural and old secondary forest (Fig. 13.1). This area was selectively logged in the 1930s, with enrichment planting of some indigenous species and some exotic species (which largely failed) in the 1940s (Mitchell 2004; see Watts (2012), for a similar history in another East African forest). Trees with the highest importance values ($\geq$1.4, where IV = unitless sum of relative density, relative basal area and frequency, with 3 as a maximum value; Grieg-Smith 1983) in each monkey home range include *Antiaris toxicaria* and *Trilepisium madagascariensis* (Moraceae), *Croton megalocarpus* (Euphorbiaceae), *Funtumia africana* (Apocynaceae), *Olea capensis* (*Oleaceae*), and *Polyscias fulva* (Araliaceae; Card 2010). In the last 5 years, after several group fissions and home range shifts in the study population, we have added other forest types to the areas occupied at least sometimes by certain study groups, including mature (70 year old)

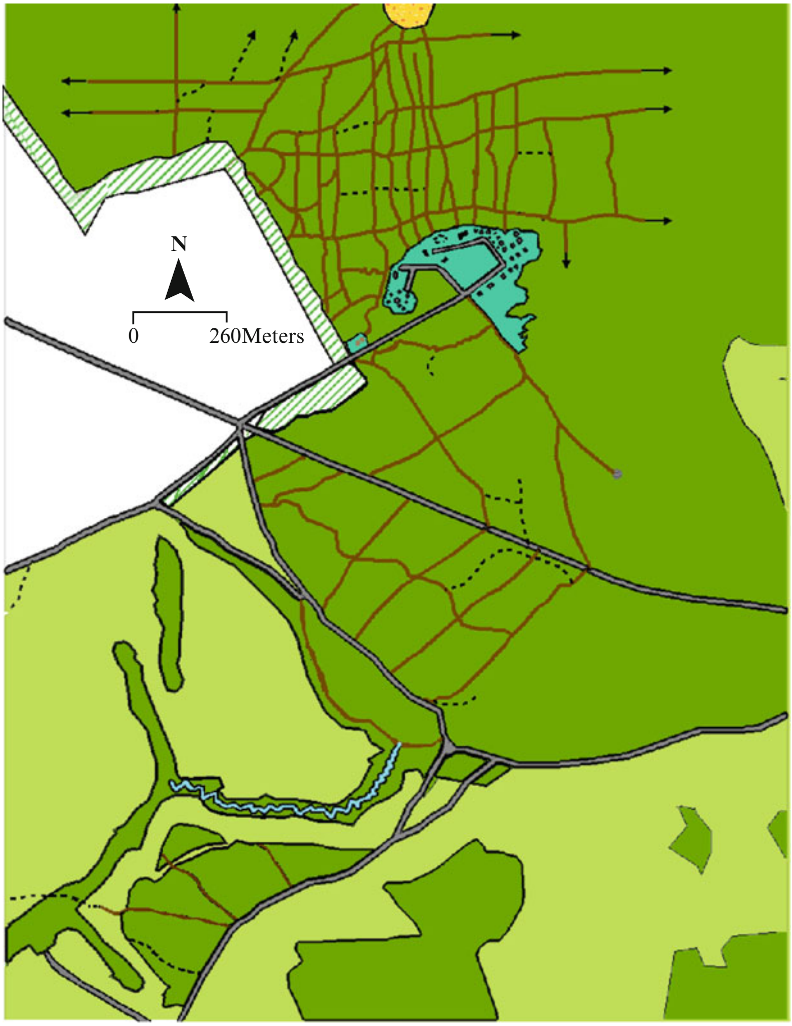

Fig. 13.1 The Isecheno study area. *Dark green* area shows forest cover (habitat used by *blue monkeys*), with footpaths used by researchers indicated in *brown*, dirt roads in *grey*. *Pale green* shows scrubland with some scattered trees, which the monkeys rarely cross; these areas of government land have varied histories, some having been plantations and/or areas of shifting cultivation. *Green striped area* represents a tea plantation ("Nyayo tea zone"), added in 1986, and white areas adjacent to tea show areas of human habitation with small-scale agriculture (private land). The forest station is indicated in turquoise. *Small yellow* area at top of the figure shows a natural grassland

"mixed plantations" (Mitchell et al. 2009) where *Prunus africana* and *Zanthoxylum gilletti* are the two most important species, and exotic plantations of *Bischofia javanica*, *Cupressus lusitanica*, *Grevillea robusta* and *Pinus patula*, all of which offer food to blue monkeys.

The Kakamega Forest as a whole has undergone significant habitat change even over the 30 years of this study, with anthropogenic increases in fragmentation and forest loss in many areas, and successional recovery in others that are better protected (Lung and Schaab 2006). The actual study area used for primate research appears to have been somewhat buffered from these forest-wide trends, probably because of its proximity to the forest station and perhaps because of the long-term presence of researchers (Fashing et al. 2004). Locally, habitat change has mainly taken the form of occasional (and illegal) tree- and liana-cutting. Two more major changes during the 30-year study include the 1986 razing of 60 m of edge forest to create the Nyayo tea zone, intended as a buffer area, and the 2008 razing of 20 m of forest along two roads passing through the study area for installation of power lines. Establishment of the tea zone decimated what was likely a considerable portion of the home range of what became one of our study groups 6 years later, but details of its effect on the monkeys are unknown as this group was not being closely monitored at the time. The 2008 cutting of forest for power lines led the three affected groups to change their ranging behavior, with each expanding into areas that were seldom or never used previously.

Natural predators of blue monkeys still occur in the forest. Alarm responses to raptors are common, typically a near daily occurrence. The African crowned eagle (*Stephanoaetus coronatus*), a confirmed predator elsewhere (Lawes et al. in press), is regularly if rarely seen, most often in aerial displays. In the first years of the study, I witnessed actual eagle attacks, but these have become much less frequent; it is possible that eagles prefer to hunt monkeys that are not as close to humans. The only witnessed predation involved a Gaboon viper (Förster 2008). We have occasionally observed humans, accompanied by dogs, hunting monkeys illegally. Circumstantial evidence suggests that a few of our study animals were killed by such hunters.

13.2.2 The Primate Community and Study Population

Common members of the Kakamega primate community include blue and redtail (*Cercopithecus ascanius*) guenons, as well as guerezas (*Colobus guereza*), which are the most commonly sighted diurnal species (Fashing and Cords 2000) and pottos (*Perodicticus potto*), which are regularly seen at night (K. Davey, W. Okeka, and E. Pimley personal communication). Rare or spatially restricted species include de Brazza's monkey (*Cercopithecus neglectus*) along particular river courses (Muriuki and Tsingalia 1990; Chism and Cords 1997/1998), olive baboons (*Papio hamadryas anubis*), and the occasional vervet (*Chlorocebus aethiops*; personal observation). Of these, deBrazza's monkeys are the only species never observed in our study area, which does not contain the riverine habitat they favor. While the more common species have been the subject of detailed study (Cords 1987; Wahome et al. 1993; Fashing 2001a, b, c, 2002; Chapman et al. 2002; Fashing et al. 2007), long-term individual-based records are available only for blue monkeys (Cords and Chowdhury 2010). The study population, at 198–242 individuals per km^2, is relatively dense (Fashing and Cords 2000), and it has been holding steady, or possibly increasing slightly, over the study period (Fashing et al. in press).

13.2.3 History of the Study

Blue monkeys at Kakamega live in groups of 7–65 members, with a single adult male most of the time (although other adult males may join during the breeding season, Cords 2002a). When I began research in July 1979, I studied just one group (T) of ~45 individuals (as well as one group of redtail monkeys). The T group fissioned in 1984 (Cords and Rowell 1986), but one daughter group moved into inaccessible habitat by 1989, forcing us to truncate records for these animals. In 1992 we began working with a neighboring group (G), which fissioned in 1999. Three subsequent fissions (2005–2009), described in more detail below (Table 13.1), left us with six groups in the study population in 2009.

Several aspects of the study conditions changed gradually over the three decades. First, the animals became more habituated to human observers, with particularly noticeable changes during the first 15–20 years. Although blue monkeys are primarily arboreal, I sometimes found them in low vegetation and even on the ground during my first 12 months, but they were skittish and retreated into the canopy when I came close. After 20 years, by contrast, the presence of observers seldom had any noticeable effect on their movements or location. Second, increasing habituation facilitated individual recognition, as it allowed the close-up inspections needed to distinguish individuals based on minutiae of their physical appearance. Our study never included any kind of capture or marking for this purpose; instead, we used features such as the shape of the tail end, nose and ears, hairiness of ears, and subtle differences in skin or hair color. For adult females,

Table 13.1 Group fissions in the Kakamega blue monkeys from July 1979 to July 2010

Size of parent group (name)[a]	Date of fission	Size of larger daughter group (name)[a]	Size of smaller daughter group (name)[a]	Fraction of matrilineal family units that broke apart[b]	Ranks of matrilineal units in the smaller group[c]
46 (T)	1984	33 (Tw)	13 (Te)	–	–
49 (G)	Oct 1999	28 (Gs)	21 (Gn)	–	–
61 (Tw)	Apr 2005	44 (Tws)	17 (Twn)	2/12	1, 2*, 3*
37 (Gs)	Oct 2008	30 (Gsa)	7 (Gsb)	2/8	4*, 5*, 6, 8
31 (Gsa)	Nov 2009	22 (Gsaa)	9 (Gsc)	2/5	2*, 4, 5*

[a] Group sizes exclude the resident adult male

[b] See Fig. 13.2 for details

[c] Highest-ranking matriline = 1; asterisks indicate matrilines whose members ended up in different daughter groups

nipple length and coloration, and for males, scars and stiff fingers, were also useful features, documented in recent years with digital photographs. Third, habituation allowed close following of individual animals and more continuous monitoring of their movement and activity patterns. Focal samples would have been unthinkable early on, but were possible by the late 1990s (Pazol and Cords 2005). Some of the results presented below derive from focal animal samples taken in recent years. Fourth, the observation schedule changed: after 2 years (1979–1981) of observations averaging 12 days per month, there followed 16 years in which observer presence was more intermittent, typically 2–5 months of near daily records per year. Beginning in mid-1997, however, observations occurred continually on a near daily basis (Cords and Chowdhury 2010 present further details). Fifth, the research focus shifted, reflecting what was possible logistically. Initially I studied interspecific sociality, examining associations of blue monkeys with redtails (Cords 1987, 1990a, b), and aspects of the mating behavior of adults (Cords 1988, 2002a; Cords et al. 1986). Only after 20–25 years was it possible to conduct detailed studies of social behavior of younger animals (Förster and Cords 2002, 2005; Ekernas and Cords 2007; Cords et al. 2010) and to amass rare events into an informative sample (Cords 2007; Cords and Fuller 2010). Lastly, the number of monitored groups increased throughout the study, from one in 1979 to six in 2009. This increase reflects the facts that greater habituation facilitated observational study generally and that we were motivated to continue monitoring long-studied individuals after natural group fission events.

13.3 Long-Term Data: Life History

13.3.1 Summary of Life-History Patterns

Beginning in late-1979, we collected data on births, disappearances and deaths, immigrations and emigrations of individually recognized animals. These data allowed derivation of basic life-history variables for this population (Cords and Chowdhury 2010), especially for females, the philopatric sex. Males emigrate from their natal groups at puberty (7 years; Ekernas and Cords 2007), and thereafter live for several years either alone or in loose associations with other males away from groups with females. After emigration, they therefore become difficult to monitor longitudinally. Here, I summarize the main findings of our study (details in Cords and Chowdhury 2010).

Blue monkeys have an extremely slow life history in the context of other cercopithecines (Cords and Chowdhury 2010). The mean, median, and modal age of first birth for females is 7 years. Most interbirth intervals lasted 24–36 months, averaging 25 months during the later years when observations were not intermittent; in these years, observers were not likely to miss births followed by neonatal death. This figure masks the usual strong effect of the first infant's fate on the interbirth interval, however. The mean interval increased from 18 months ($N = 53$) when the first infant died within 12 months to 31 months ($N = 193$) when it survived the first year (Cords and Chowdhury 2010). Given moderately strong seasonality in births (Cords and Chowdhury 2010), this means that most females produce a new infant after 2–3 years when the first one survives its first year.

Age-specific survivorship showed patterns common to many primates (Fig. 13.2), with higher mortality for infants (23% died, 5% were right-censored, i.e. had unknown fates) and a fairly constant rate of mortality from young adulthood onward. Annual mortality rates for juveniles (aged 2–4 years, all prereproductive) averaged $5 \pm 8\%$ ($N = 29$ years), an identical value for annual mortality of adults (aged 5 years or older, $5 \pm 5\%$, $N = 29$ years). The oldest female of known age lived to at least 33.5 years; several others that apparently died of natural causes (as opposed to a few cases in which human intervention was suspected) lived into their late 20s, and several females of this age are alive at the time of writing.

For animals with such long lifetimes, even 30 years is insufficient to document maximal lifespan with a large sample, and an estimate of average lifespan would be biased toward animals that died young. Despite sparse information on old females, our data suggest that female blue monkeys that live into their 20s and beyond may have postreproductive lifespans of several years. The female with the longest known lifespan did not give birth during the last 11 years of her life. Observations were not intermittent, so the long nonreproductive period cannot be attributed to undetected births followed by neonatal death. Other females also had long periods (8.0, 6.4, and 3.7 years) between the birth of their last offspring and their own deaths but intermittent observations, at least in the first two cases, make it impossible to ascertain that intervening births (followed by neonatal death) did not occur. Some other individuals, however, showed no evidence of reduced reproductive

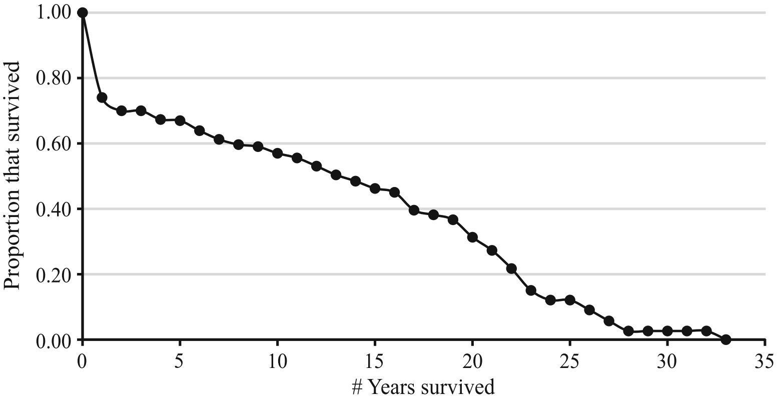

Fig. 13.2 Age-specific survivorship curve, based on minimum survival data from 418 individuals. Age class 0 refers to newborns, 1–0–1 year olds, and so forth. For further details, see Cords and Chowdhury (2010). Reprinted with kind permission from Springer Science + Business Media, Cords and Chowdhury (2010; Fig. 2)

rates even though they lived into their late 20s. Two females lived to ≥27 years and each gave birth for the last time within 2 years of her death.

We evaluated reproductive termination using Caro et al.'s (1995) criterion, by which a female is considered to have terminated reproduction if the difference between age at death and age at last birth exceeds the mean of her interbirth intervals by ≥2 standard deviations. Only 14 females with known or estimated ages died after giving birth at least three times, allowing calculation of mean birth intervals and standard deviation. Two of the 14 terminated reproduction, according to Caro et al.'s criterion. One of these females had the longest recorded lifespan at Kakamega and the other died at about 21 years. However, included in this analysis were four females who we suspected were victims of poaching; if their deaths were thus untimely, they may inflate the number of females that did not show slowdowns at the end of their lives.

Age-specific fecundity rose fairly steeply during years 5–8, and appeared to decrease gradually from about age 13 years (Fig. 13.3). The most advanced age at which a female gave birth was 26 years when we included only females whose ages were known to the nearest year. The fecundity curve shows nonzero values at ages 27 and 28 because there was some probability of a female being 27–28 years old at the birth of an offspring in cases where maternal age was estimated with greater uncertainty (see Cords and Chowdhury 2010 for further details on age estimation). Even though our data spanned a 29-year period, sample sizes for these old females were small.

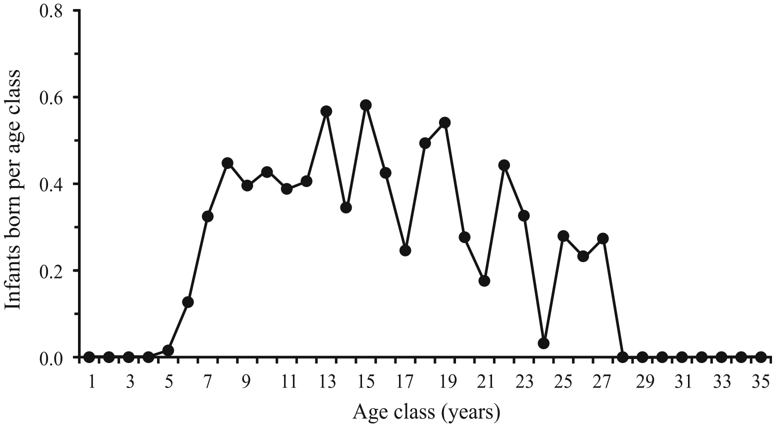

Fig. 13.3 Age-specific fecundity. Data include male and female infants born to 65 females. Greater fluctuations at later ages likely reflect reduced sample sizes. Reprinted with kind permission from Springer Science + Business Media, Cords and Chowdhury (2010; Fig. 3)

13.3.2 Blue Monkey Life History in a Comparative Context

The extreme slowness of the blue monkey life history is apparent when one compares these data with reports from other taxa. Ross (1992a) compiled data from multiple primate species on age at first reproduction, birth rate (interbirth interval), and maximal longevity to estimate $r_{\max}$, the maximum potential rate of population increase. Data came from both captive and wild animals, but it is noteworthy that she identified blue monkeys as the second slowest breeding cercopithecid, after the closely related *C. ascanius*. Only apes had $r_{\max}$ values lower than these two forest-dwelling guenons.

Isbell et al. (2009, 2011) examined Ross' values in the context of body size variation to emphasize the extremely fast life history of patas monkeys relative to their body size. I repeated their analysis, using my data to calculate $r_{\max}$ for blue monkeys ($r_{\max} = 0.11$). As Fig. 13.4 shows, among guenons some species breed considerably faster than expected for their body sizes, and others breed slower. Isbell et al.'s (2009) conclusion about the extraordinarily fast patas monkey is robust: among haplorrhines, only callitrichines have even higher $r_{\max}$ values relative to body size. Blue monkeys join *C. ascanius* and *Miopithecus talapoin* in having $r_{\max}$ values that deviate most negatively from the haplorrhine regression line, i.e. that are the lowest relative to expectations (Fig. 13.4). Thus the guenon tribe of cercopithecines includes both the fastest- and slowest-breeding Old World monkeys in this sample.

Cords and Chowdhury (2010) examined comparative data as well, but limited their consideration to *wild* cercopithecines. Even uncorrected for body mass (and *C. mitis* are among the smaller animals in this clade), blue monkeys had the latest age at first reproduction and were among three species with the longest mean

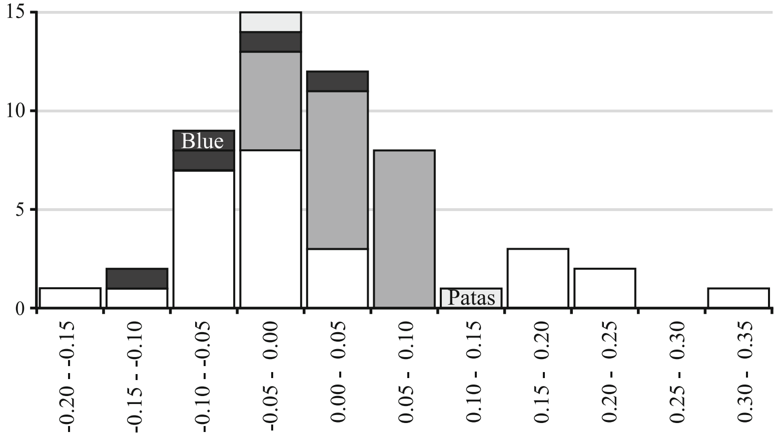

Fig. 13.4 Histogram of residuals of regression between ln body mass and ln $r_{\max}$ for haplorhine primates, using data from Ross (1992a). Forest guenons shown in *black*, open-country guenons in light *grey*. *Dark grey* represents other cercopithecoids, *white* shows noncercopithecoids, i.e., platyrrhines and apes

interbirth interval. Data on mortality after infancy require long-term study and are therefore scarce for wild populations, preventing a thorough analysis. However, a smaller-scale comparison within the guenon (Cercopithecini) tribe, which is thus more phylogenetically controlled, supports theoretical predictions (Promislow and Harvey 1990; Reznick et al. 2002) in relating life-history "speed" to levels of juvenile and adult mortality (Cords and Chowdhury 2010). When adult mortality is relatively high, selection should favor individuals breeding relatively early and often. Savanna-woodland guenons (vervets and patas monkeys) have annual juvenile and adult mortality rates three to six times higher than those of forest-dwelling blue monkeys: for example, Isbell et al. (2009) reported average annual adult mortality of 15% for vervets and 22–33% for patas, while the equivalent figure for Kakamega blue monkeys is only 5%. Similarly, maximal lifespans are very different, with vervets and patas living only into their teens (Isbell et al. 2009), while blue monkeys live into their 20s and sometimes into their 30s. Vervet and patas females first give birth much younger than blue monkeys (3 years patas, 4.5–5.7 years vervets), and interbirth intervals are considerably shorter (13–14 months). Finally, it is worth noting that these differences in life-history characters appear to be evolved ones: Rowell and Richards (1979) compared the same three guenons held in a single captive location and found the same relative patterns of age at first reproduction, interbirth interval and longevity as data from the wild provide.

Environmental variables are expected to affect life-history speed through their effects on mortality rates, but analyses of primate life histories in the context of environmental variation have been somewhat contradictory, perhaps reflecting limitations on both the data (both on the animals and their habitats) and the analytical methods (Ross and Jones 1999). The guenons are an excellent primate group in which to consider how habitat-related variation in mortality drives life-history speed, as this group includes both obligate forest dwellers, such as blue monkeys, and species that inhabit more open savanna-woodland environments. Mortality levels appear to be very different in these environments, even though very little information is available on causes of mortality in forests (Cords and Chowdhury 2010). It would be valuable to corroborate the preliminary cross-species comparisons with data from additional forest-dwelling guenons, but to my knowledge, there are no ongoing long-term studies that include individual-based life-history records. Replicating such analyses with data from wild populations of other primates may occur sooner: the macaques, a similarly species-rich group whose members inhabit a wide variety of habitats, would be good candidates. Indeed, Ross (1992b, but see Ross and Jones 1999), using data largely from captive macaques, found interspecific variation in life-history speed consistent with expectations from variation in the habitats characterizing wild populations. Long-term data from multiple wild populations are not yet available, but should provide an informative comparison.

13.4 Rare Events: Group Fission and Group Size

For social animals that spend their entire lifetimes in single groups, studying the adaptive benefits of group-living is difficult: one cannot experimentally manipulate the variable of interest, and even natural variation may be nonexistent. In blue monkeys, for example, females remain in their natal groups for life, never spending time alone or transferring to new groups. A female's group identity changes only during group fissions and fusions. These events offer a potentially revealing window through which to consider the costs and benefits of group-living (Dittus 1988; Van Horn et al. 2007), as both the circumstances surrounding the fission or fusion, and the way in which individuals realign themselves in new groups, may indicate what makes a group successful or not for its members. Such events are typically uncommon, however, and gathering even a modest sample of occurrences from which to generalize patterns can be a challenge. In 30 years, only five fissions occurred in our study groups, and the first example of a fusion occurred in the 30th year. Here I report on the fission events, and how they may inform an understanding of blue monkey society.

13.4.1 Basic Features of Blue Monkey Fissions

Group fissions occurred episodically over the 30-year period (Table 13.1). The rate of fission would be entirely different if one compared the first vs. last few years of the study. In addition, the critical group size at which fission occurs appeared to be 45–50 animals after the first two fissions (agreeing with reports from another wild guenon, *C. ascanius*; Struhsaker and Leland 1988; Windfelder and Lwanga 2002), but then group Tw grew to 61 animals before it split in 2005. By contrast, the two most recent fissions occurred in groups that were considerably smaller than in previous cases (Table 13.1), suggesting that the processes driving fission are not simple consequences of group size.

A common feature of all group fissions was that the parent group split unequally (see also Perry et al. 2012). The larger daughter group averaged 70% of original group members (Table 13.1). In all cases, the larger daughter group claimed the larger portion of the original group's territory. Another common characteristic of fissions was that one of the daughter groups expanded its territory within a year after the fission, engaging in a series of aggressive intergroup encounters with neighboring groups that had previously occupied the new area. In four of five cases, it was the smaller daughter group, relegated to the smaller portion of the original range, that did this, suggesting that an insufficient supplying area for food drove the territorial expansion. Territory boundaries remained remarkably stable except after fissions: indeed, some boundaries between groups have involved the very same trees over 30 years (Cords 2007). Similar range changes have been reported for redtail monkeys, with range expansion sometimes involving the larger and sometimes the smaller fission product (Struhsaker and Leland 1988; Windfelder and Lwanga 2002).

Unfortunately we had little background knowledge of neighboring nonstudy groups, which would assist a more detailed understanding of how these range expansions come about. A new group that is too small may face particular challenges. For example, 6 months after the most recent fission (2009), the ten-member Gsc group had managed to secure only a very small area of forest (approximately 3 ha) where it had priority over its neighbors. In contrast, other groups typically have areas of exclusive use that are five to ten times larger. The addition of nine new group members to Gsc (two adult females, seven mixed-sex juveniles), in the first fusion ever witnessed in blue monkeys, had not changed this situation 14 months later. Gsc seemed to move through the forest at the mercy of other groups, usually retreating from any they encountered. Struhsaker and Leland (1988) reported a similar consequence for an unusually small (~15 member) group formed after a redtail monkey group fission.

Females appeared to engineer the process of group fission in every case: over a period of days to months, they formed temporary subgroups with unstable membership, with no noticeable increase in aggression (see also Perry et al. 2012). Eventually, they settled into parties that remained apart from one another and aggressively defended their portion of the original group's territory against the new sister group. We have taken the date of the first aggressive territorial encounter between new sister groups as the date of fission in our study. Females also sometimes appeared to take an active role in deciding how the original groups divide. This was most obvious when they directed aggression at one another, seemingly trying to deter a former group-mate from joining their new sub-party. In contrast, no aspect of male behavior suggested that males attempted to influence the process of fission. The adult male resident in the original group joined the larger daughter group twice, and the smaller group three times.

Female cercopithecine monkeys typically remain with their female kin for life. One would thus expect fission to occur along kinship lines, as reported for baboons and several macaques (Dittus 1988; Oi 1988; Ménard and Vallet 1993; Okamoto and Matsumura 2001; Widdig et al. 2006; Van Horn et al. 2007). The three most recent fissions in our study population occurred when we had sufficiently deep pedigree records to evaluate whether close maternal kin (grandmother–granddoffspring, mother–offspring and sibling pairs) remained together after fission. While matrilines generally did stay together, each fission included 2–3 matrilineal units that broke apart (Table 13.1; Fig. 13.5). In six of these seven cases, mothers ended up in different groups than some or all of their daughters, and all six involved the separation of a mother and at least one *juvenile* daughter, even though juveniles are socially close to their mothers as indicated by frequent grooming (Cords 2000a; Cords et al. 2010). The seventh case involved three sisters whose mother was no longer alive at the time of group fission: the youngest (aged 4) did not join her older sisters after the split. A particularly puzzling observation was that one adult female (indicated by an asterisk in Fig. 13.5), abandoned her mother, sisters and 2.4 year old daughter (who was occasionally seen to suckle just weeks

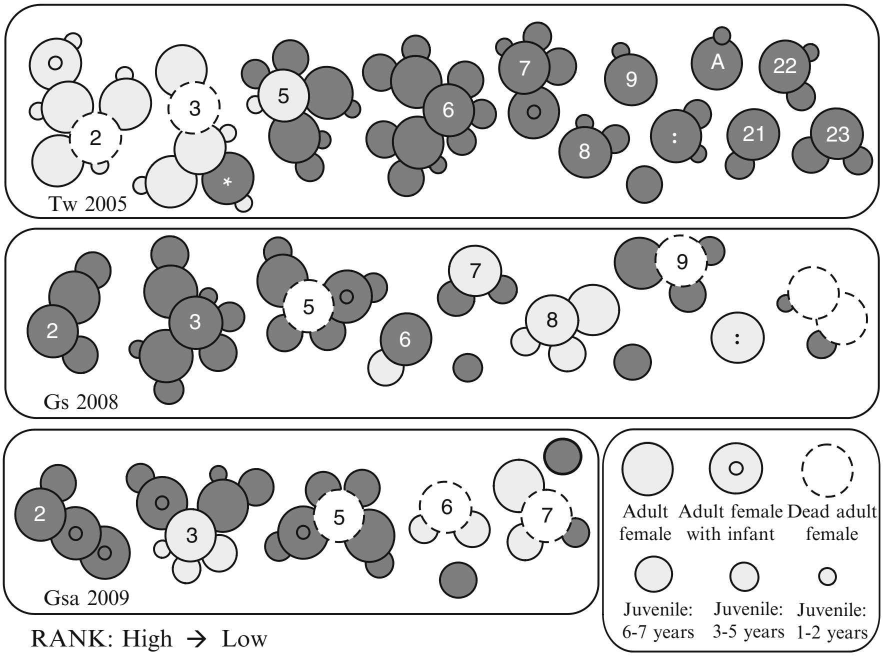

Fig. 13.5 Maternal kinship, rank, and group fission. For each of three fissions, individuals are represented as *circles*, with *shading* (*light vs. dark grey*) indicating group membership after fission, and size proportional to age (see legend). To indicate maternal relatedness, a large circle (mother) overlaps the circles representing her offspring. Matriline rank decreases from left to right, indicated by integer values (1 = highest). Matriline rank was derived from dyadic agonistic interactions among adult females, 9–12 months before fission; matrilines represented only by juveniles therefore have no rank and are randomly placed. Individual marked by *asterisk* is discussed in text

before the split) to become the sole member of her matriline in her new group. Although her family was second-ranking in the original group, and retained this position in their new daughter group, this female sunk to the bottom of the hierarchy in her new group, where she was regularly harassed. She seemed highly motivated to join this group, despite social obstacles and disadvantages. Most oddly, as the two daughter groups engaged in aggressive territorial fights, thus dividing up their former joint territory, this female crossed back on six occasions to fight with her family against the group in which she now lived.

Exceptions to the rule of kin remaining together after fission have been noted in rhesus and Japanese macaques (also capuchins, Perry et al. 2012), and attributed to paternal kinship and social bonds (Van Horn et al. 2007). Analyses now in progress may allow us to evaluate these factors as explanations for the severing of bonds with close kin in our study population.

13.4.2 Group Fission and the Costs of Feeding Competition

Primatologists often interpret group fission as an ecological necessity, inevitable when a group is too large for its individual members to move and forage efficiently because competition for food is too high (Koenig 2002; Sussman and Garber 2007). To see whether data from Kakamega support this interpretation of group fission, I compared movement and time budgets of adult females in groups of different size, and rates of aggression and reproductive output for the same females before and after fission.

As more animals in one place are likely to exhaust the food supply more quickly, larger groups should move farther and faster than smaller ones, or cover larger areas to meet their resource demands, assuming equal food density and abundance (Snaith and Chapman 2007). We examined these predictions using data on group travel, in which an hourly "center of mass" was plotted on a map of the study area, and all 50 × 50 m^2 quadrats used on a given day were noted. We found no difference in the area occupied per day among groups whose sizes differed up to twofold (Table 13.2a). Furthermore, while the group's daily travel distance varied significantly among three groups, the pattern was opposite the expectation, with the smallest group moving farthest. This pattern was not caused by variation in habitat quality, estimated as the basal area of food trees (m^2/ha), which would lead one to predict even longer routes in larger groups (Table 13.2a).

I also examined travel distances of individual females, as opposed to a center of mass of the entire group, to provide a higher-resolution analysis of foraging effort. Contrary to expectation, however, females in larger groups did not cover longer distances (Table 13.2b). Feeding activity – along with associated movement – has a diurnal rhythm, with peaks in the morning and afternoon hours (Cords 1987). When I analyzed the travel data separately for the morning, midday and afternoon hours, weak group effects emerged for morning and afternoon, but these were opposite those expected, with smaller groups moving farther than larger ones (Table 13.2b). Differences in habitat quality (measured as basal area of major food trees, Table 13.2b) could not explain these results: for example, females in larger groups might in principle reduce travel if they occupied better-quality habitat, but this was not the case. A possible explanation for greater travel in the two smaller groups (TWN, GN) relates to the attractiveness of particular resources at the edges of their home ranges: GN ate soil at a particular spot while TWN used exotic fruiting trees in the forest station.

To examine changes in time budgets, I compared females present both before and after two fissions (Gs group fission in October 2008, $N = 13$ females and Gsa group fission in October 2009, $N = 9$ females). We conducted focal samples (averaging 32 h per female in the 4 months before and in the 4 months after the 2008 fission, and 34 h per female in the 4 months before, 24 h per female in the 4 months after the 2009 fission) in which activity (moving, feeding, resting, social) was noted at 1-min intervals. I conducted before-vs.-after comparisons and present results separately for females in the two daughter groups, since fission might benefit

Table 13.2 Ranging variables and habitat quality for groups of different size

(a)	Gn: 23	Gs: 33	Tw: 46	Comparison
Area used by group (ha/day)	4.12 (2.75–5.73, 35)	4.25 (3.61–5.02, 29)	3.47 (2.62–4.88, 18)	Kruskal–Wallis, $p = 0.302$
Daily travel path of group (m)	733 (590–853, 39)	639 (536–761, 31)	583 (495–646, 17)	Kruskal–Wallis $H = 8.15$ $p = 0.017$
Habitat quality: basal area of food trees[a] (m^2/ha)	49.0	48.4	43.2	–

(b)	Twn: 16.5	Gn: 30.5	Tws: 43	Gs: 47	Comparison
Individual travel: estimated marginal means ± SEM	20.0 ± 1.2	18.8 ± 1.1	17.3 ± 2.5	19.1 ± 2.3	GLMM[b] Group: $F = 0.36$, $p = 0.75$; Period: $F = 6.28$, $p = 0.002$; Month: $F = 14.35$, $p < 0.001$
Individual travel AM (m per 10 min)	20.4 ± 2.2 (98)	23.8 ± 3.9 (130)	11.4 ± 1.7 (55)	16.8 ± 1.9 (23)	GLMM[c] Group: $F = 2.26$, $p = 0.093$
Individual travel MD (m per 10 min)	18.5 ± 2.3 (86)	16.6 ± 1.2 (119)	14.9 ± 3.6 (21)	14.0 ± 3.1 (29)	GLMM[c] Group: $F = 1.02$, $p = 0.383$
Individual travel PM (m per 10 min)	23.3 ± 1.9 (112)	23.1 ± 2.8 (117)	16.3 ± 5.2 (19)	10.7 ± 1.8 (13)	GLMM[c] Group: $F = 2.20$, $p = 0.090$
Habitat quality: basal area of food trees[d] (m^2/ha)	44.0	57.0	54.5	34.3	–

Each group indicated by name and total membership at time of data collection. (a) Area used and travel distance by group on days with ≥10.5 h observations, March–August 2001. Values reported are medians, with inter-quartile range and *N* of days in brackets. (b) Travel distance of individual females in 10 min samples (means ± SEM for each of *N* (in brackets) females). Row 1 shows estimated marginal means for each group as derived from full dataset; rows 2–4 show observed values from each of three periods, morning (AM: 0700–1030), midday (MD: 1030–1430) and afternoon (PM: 1430–1800)

[a] Trees included were the top 30, according to plant feeding records made over an annual period (Cords 1987), and including *Maesopsis eminii* which was identified later as a major feeding tree. These species accounted for 89% of all feeding records

[b] Data from 822 10-min focal samples collected from 54 females in four groups over 8 months (July 2005–May 2006). GLMM included group ($N = 4$) and period of day ($N = 3$) as fixed factors, month as covariate, and individual as random effect

[c] GLMM with auto-regressive covariance structure included group as fixed effect, date as repeated effect, and individual as random effect. Pairwise comparisons distinguished TWS from TWN and GN groups in the morning ($p \leq 0.024$), and GS from TWN and GN groups in the afternoon ($p \leq 0.02$), although these differences became insignificant with Bonferroni correction

[d] Trees included each accounted for ≥0.1% of annual plant feeding records, as per Cords (1987). Together, they constituted 92% of all feeding records

one new group but not the other. In 2008, the five females that ended up in the smaller group showed no significant change in time budgets; for the eight that joined the larger group, moving time increased after fission from 18 ± 6% to 22 ± 8% of point samples (Wilcoxon matched-pairs signed-ranks test, $W = -34$, two-tailed $p < 0.02$), while other activities showed no significant changes. To the extent that moving time varies positively with energetic costs, an increase in smaller groups is just opposite to expectations. In 2009, the smaller group contained only two females, whose shifts in activity did not coincide. The seven females in the larger group increased feeding time (from 44 ± 2% to 48 ± 2%, $W = -24$, two-tailed $p < 0.05$) and decreased resting time (from 26 ± 2% to 23 ± 3%, $W = 28$, two-tailed $p < 0.02$) after fission. If food is harder to find in larger groups, and thus requires greater foraging effort, these changes are also opposite to expectations.

The relationship of contest competition to group fission can be evaluated by mapping dominance ranks onto fission dynamics and by comparing rates of aggression before and after fission. Neither approach suggests a clear relationship between fission and direct competition. We could evaluate dominance relationships for adult females for the four most recent fissions. In two cases (2005, 2008), fission separated higher-ranking from lower-ranking females (Fig. 13.5), although high-ranking matrilines formed the smaller daughter group in 2005 and the larger one in 2008. In the 1999 and 2009 fissions, high- and low-ranking females in the original group did not separate cleanly from one another: daughter groups included both high- and low-rankers, who generally maintained their relative positions in the new groups (Klass 2010; Fig. 13.5; n.b. the 1999 fission is not shown because kinship was not well known).

The lack of a consistent rank-related fission pattern agrees with the observation that the behavioral process of fission did not seem to involve one subgroup (presumably of low-ranking individuals) *seceding* from the main group, as has been reported in other cercopithecines where dominance rank is generally a more important predictor of social behavior (Malik et al. 1985; Dittus 1988). In blue monkeys, high- and low-ranking individuals seem to differ little socially, ecologically and reproductively (Cords 2000b; Pazol and Cords 2005, but see Förster et al. 2011); the lack of clear rank-stratification in group fissions is consistent with this general pattern, and agrees with the report of a single fission in relatively tolerant moor macaques (Okamoto and Matsumura 2001).

Blue monkeys generally exhibit low rates of aggression, but most aggressive acts – more than expected by chance – occur in a feeding context (Cords 2000b; Pazol and Cords 2005), suggesting that females compete directly for food. Therefore we also checked whether rates of aggression received decreased after fission for individuals in our study groups; such a pattern would suggest that fission reduces contest competition. Again we used focal animal data for 4 months before and after two group fissions, in which all aggressive interactions of focal subjects were noted. In one case (Gs fission in 2008), rates of aggression received did not change significantly (Wilcoxon matched-pairs signed-ranks test, two-tailed $p > 0.05$). For the eight females in the larger group, the average rate (±SEM) actually increased from 0.084 (±0.033) to 0.165 (±0.037) acts per hour, but this difference was not significant. Females that ended up in the smaller group received aggression at higher rates than those in the larger group, but the rate did not decrease significantly for them after fission either (before: 0.334 (±0.079), after: 0.309 (±0.092) acts per hour, $N = 5$). Altogether, 9 of 13 females received aggression at higher rates after fission. The results did not change if we considered all aggression, both received and given (data not shown).

In the second case (Gsa fission in 2009), the females that ended up in the larger group received aggression at lower rates after fission (before: 0.100 (±0.032) vs. after: 0.039 (±0.021) acts per hour; $W = 21$, $N = 7$, $p \leq 0.031$), suggesting that contest competition was reduced. Six of seven individuals received less aggression. The two females in the smaller group showed an inconsistent pattern, with one receiving aggression at a higher rate, and one at a lower rate, after fission. For all individuals, results were very similar if we considered all aggression, both received and given (data not shown).

The decrease in rates of received aggression that occurred in one new group after the second fission likely reflected changes in the monkeys' feeding behavior from the pre- to postfission periods. In 2009 only, the proportion of time spent feeding on fruits was lower after fission (median: 7% of observation time) than before fission (11% of observation time; Wilcoxon matched-pairs signed ranks test, $N = 9$, $W = 41$, $p \leq 0.027$); no such decrease occurred in 2008. Aggression occurs disproportionately when blue monkeys feed on fruit (Cords 2000b), so this change in diet might have driven changes in aggression rates. Indeed, rates of aggression relative to time spent feeding on fruit were not different before vs. after fission in either 2008 ($W = 44$, $N = 13$, $p \leq 0.946$) or 2009 ($W = 21$, $N = 9$, $p \leq 0.910$). Overall, then, analyses of aggressive rates did not support the hypothesis that rates of contest competition decreased after fission.

13.4.3 Group Fission and Female Reproduction

Ultimately, behavioral costs and benefits should be reflected in measures of reproductive output. In some cercopithecine monkeys (e.g., redtails: Windfelder and Lwanga 2002; baboons: Altmann and Alberts 2003), but not all, females have shown higher reproductive rates after fission. For three of the later fissions we observed, life-history data allowed us to examine whether reproductive success improved for individual adult females after fission. Figure 13.6 shows the birth rate for females that were monitored 4–6 years before and after three group fissions (1984, 1999, 2005). We deliberately chose a fairly long multi-year window before and after the fission to dampen effects of random variation in a species with interbirth intervals of 2–3 years. None of these comparisons revealed a significant difference (Wilcoxon test, all $p > 0.05$). We also compared rates of infant survival before vs. after fission (2005, 2008), but there were also no differences (Fig. 13.7). Overall, the results from these measures of reproductive success agreed with our behavioral measures in showing no advantage to females living in smaller groups after fission.

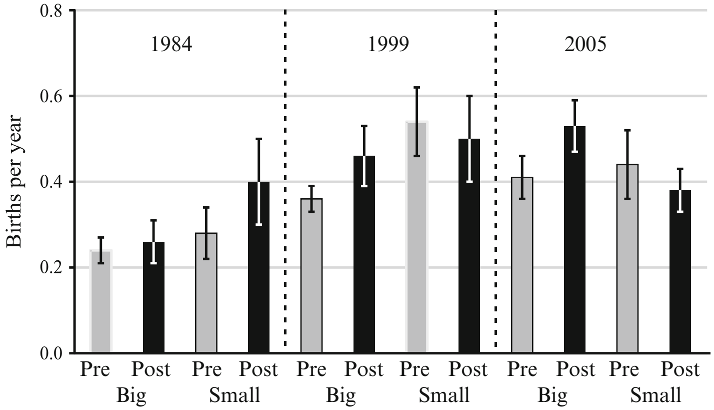

Fig. 13.6 Birth rate of females in big and small daughter groups before and after three group fissions. Females were included only if present both before and after fission for 4–6 years. No differences were statistically significant (see text)

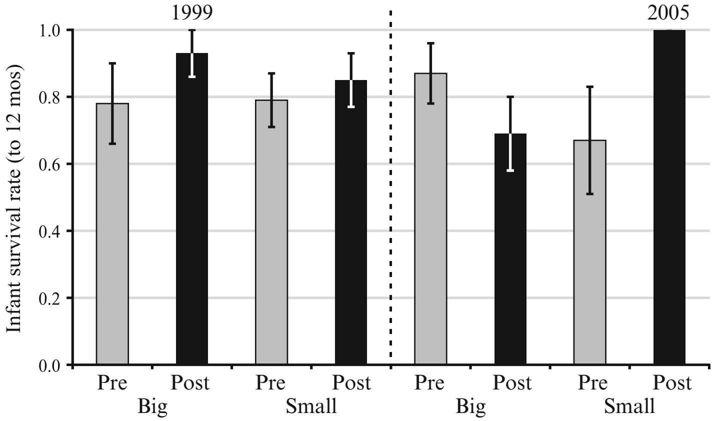

Fig. 13.7 Infant survival (to 12 months) for females in big and small daughter groups before and after two group fissions. Females were included only if they gave birth to at least one offspring within 4–6 years both before and after fission. No differences were statistically significant (see text)

13.4.4 Group Fission and Male Group Membership Changes

However, group size may affect reproductive success in other ways. In some primates, for example, infanticide risk is greater in larger groups (Crockett and Janson 2000). Blue monkey males in this population and others sometimes kill infants when they take over groups (Butynski 1982; Fairgrieve 1995; Cords and Fuller 2010). If group fission reduces the risk of infanticide, male takeovers should occur less often after fission than before. To date, however, there is no evidence that

Table 13.3 Dynamics of adult male group membership before and after group fission

Group and fission date	Parent group	Larger daughter group	Smaller daughter group	Years of observation
(a) Rate of male replacement (# singular resident males per year)[a]				
T 1984	0.2	0.2	0.25	5
G 1999	0.6	0.6	0.6	5
Tw 2005	0.2	0.2	0.4	4.5
(b) Number of breeding season male influxes per breeding season				
T 1984	0.4	0	0	5
G 1999	0.6	0	0	5
Tw 2005	0.8	0.2	0.6	5

[a] Singular male residents lived in the group for some period with no other adult males present, in contrast to some male influx participants who were never the *only* male present

the rate of male takeovers or the occurrence of male influxes during the breeding season (which also introduce unfamiliar males to the group) declines after fission (Table 13.3). Reports of fission in other (redtailed) guenons actually showed increased rates of male membership changes after fission (Struhsaker and Leland 1988; Windfelder and Lwanga 2002).

13.5 Conclusions

Clearly 30 years is not enough to understand fully the group dynamics in a study population like ours. Five fissions is still a small sample. Furthermore, making inferences about the effects of group size based on comparisons of groups that vary in size can be difficult when groups are large and animals are hard to see and habituate. In such cases, the number of groups that researchers can monitor at once is limited. When our study began, we were also unaware that group size varied extensively, given that occasional counts of neighboring groups suggested numbers like those in our single study group. The process of fission, along with background demographic processes influencing age and sex composition, has actually expanded the range of variation in a small cluster of neighboring groups, and raised questions that were not even apparent early on. It took 30 years for us to detect a group with only ten members.

Further research should resolve some of the unanswered questions. While current evidence does not seem to support within-group competition for food as a factor stimulating fission or regulating group size, the advantages of smaller group size might be apparent only episodically or when evaluated over a longer period. The immediate stimulus for group fission may not be ecological disadvantage, but the disorganized and uncoordinated movement that typifies the largest groups (also Perry et al. 2012), or less connected social networks within groups that fission. Also, we have not thoroughly documented the extent of between-group competition, and its relationship to group size. Frequent aggressive intergroup encounters over feeding trees or feeding areas suggest an important role for between-group contest competition. We know already, however, that success in individual inter-group encounters depends primarily on where the encounter occurs rather than on relative group size, with even a single animal from the "home" group able to evict a larger party of intruders from its territory (Cords 2002b). This pattern raises a different question: how are territorial boundaries established, and when do they change? For blue monkeys, group fission is apparently an important part of the answer. Relative group sizes are set at the moment of fission, and group sizes in turn seem to determine territory sizes of the new groups; thus fission provides an opportunity for individuals to reconfigure their distribution – as groups – on the landscape.

Our ongoing study will address such possibilities, as well as the ways in which life-history variables respond to variation in group size. Ultimately, some signal in life history is expected to reflect the benefits that females gain from living in relatively small groups, hence to explain the propensity of groups to fission when they become large. Only long-term data offer the possibility to detect group size effects on fitness in a species with a life history as slow as that of blue monkeys.

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