

RESEARCH ARTICLE

Social Structure and Life-History Patterns in Western Gorillas (*Gorilla gorilla gorilla*)

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Life-history traits and ecological conditions have an important influence on primate social systems. Most of what we know about the life-history patterns and social structure of gorillas comes from studies of eastern gorillas (*Gorilla beringei* sp.), which live under dramatically different ecological conditions compared to western gorillas (*Gorilla gorilla* sp.). In this paper we present new data on western gorilla social structure and life histories from four study sites, and make comparisons with eastern gorilla populations. Data were obtained from two study sites with gorilla groups undergoing the habituation process (Lossi, Democratic Republic of Congo; and Bai Hokou, Central African Republic) and two “bai” studies (Maya Nord and Mbeli Bai, Republic of Congo). The size and structure of these groups were similar to those seen in eastern gorillas. However, differences in the occurrence of various group transitions (group formations, changes between one-male and multimale composition, and group disintegrations) exist, and western gorillas notably exhibit much higher rates of male emigration and correspondingly fewer multimale groups compared to mountain gorillas. Certain phenomena have been observed only rarely, including predation by leopards. The preliminary data show no significant differences in birth rates between western gorillas and mountain gorillas. The ecological variability across gorilla habitats likely explains the flexibility in the social system of gorillas, but we need more information on the social relationships and ecology of western gorillas to elucidate the causes for the similarities and differences between western and eastern gorillas on the levels of

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INTRODUCTION

While the main focus of socioecological models has been to elucidate the relationship between the ecological conditions and social systems of vertebrates [Isbell & Young, 2002; Sterck et al., 1997; van Schaik, 1989; Wrangham, 1979, 1980], particular emphasis is now being given to the role of life-history patterns in primate socioecology [Kappeler & van Schaik, 2002; Kappeler et al., 2003]. This approach complements previous attempts to explain social systems as sex-specific responses to ecological conditions by integrating the relationships among life-history patterns, ecological conditions, and reproductive strategies. Primates are particularly interesting study species for investigating interactions among individual behaviors, group dynamics, and population dynamics [Altmann & Altmann, 1979; Bentley, 1999; Borries et al., 2001; Dunbar, 1985, 1987; Lee, 1994; Yamagiwa, 1999] (Robbins and Robbins, 2004). Much is known about the variations in the social structure and life-history patterns of the great apes [Bentley, 1999; Boesch et al., 2002; Delgado & van Schaik, 2000; Robbins et al., 2001; Wrangham, 1979, 1986], including mountain gorillas, but the biggest remaining gap in our knowledge concerns western gorillas.

Gorillas are widely distributed across nine central-African countries (Fig. 1). A recent taxonomic reclassification now groups gorillas into two species and four subspecies (western gorillas: *Gorilla gorilla gorilla* (western lowland gorillas) and

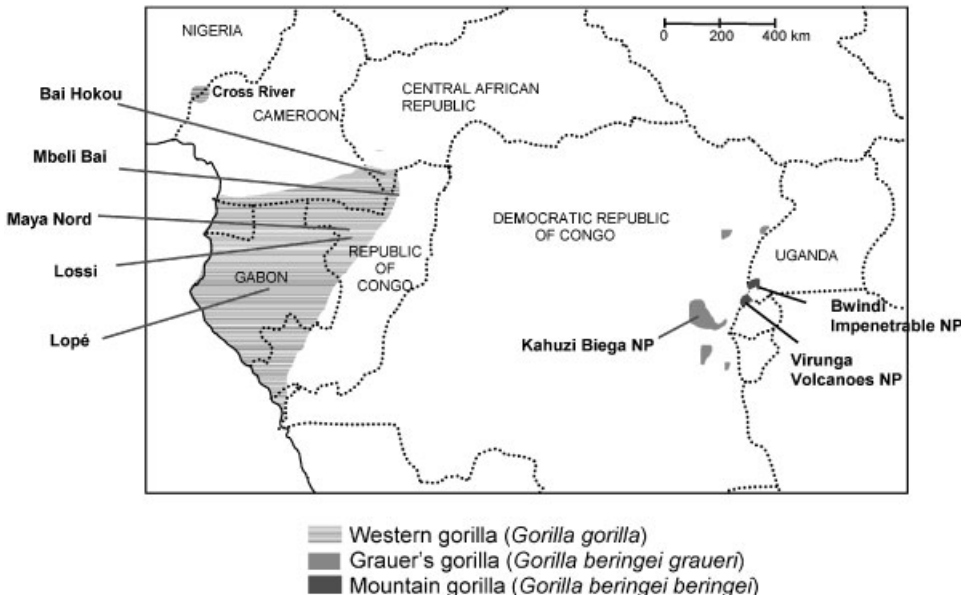


Fig. 1. Map of Africa indicating all the study sites discussed in this paper.

G. g. diehli (Cross River gorillas); eastern gorillas: *G. beringei graueri* (eastern lowland or Grauer's gorilla) and *G. b. beringei* (mountain gorillas) [Groves, 2001]). Most of what we currently know about the ecology, social behavior, life-history patterns, demography, and population dynamics of gorillas comes from detailed, long-term studies at the Karisoke Research Center, and routine censuses in the Virunga Volcanoes of Rwanda, the Democratic Republic of Congo (DRC), and Uganda [Kalpers et al., 2003; Robbins et al., 2001]. However, the small, isolated Virunga population, found at the altitudinal extreme of gorilla habitats, cannot represent the entire genus.

The Karisoke gorillas feed extensively on terrestrial herbaceous vegetation and eat almost no fruit, because fruit is rare in their habitat [Watts, 1984]. Western gorillas, Grauer's gorillas, and Bwindi mountain gorillas live in markedly different habitats, eat much more fruit, experience greater seasonal variation in food availability, have longer daily travel distances, and have larger home ranges than the Karisoke gorillas [Doran & McNeilage, 1998, 2001; Doran et al., 2002; Nkurunungi, 2003; Robbins & McNeilage, 2003; Yamagiwa et al., 1996] (Rogers et al., 2004; Ganas et al., 2004).

The impact of predation and disease on mortality rates may also vary among gorilla populations [Freeland, 1976; van Schaik, 1989]. For example, respiratory diseases that are often fatal for mountain gorillas [Mudakikwa et al., 2001; Watts, 1998] have not been reported for western gorillas. Ebola, which is known to have affected one of the study populations discussed in this article, can have devastating effects on ape populations (e.g., at Lossi [Boesch & Boesch-Achermann, 2000; Huijbregts et al., 2003; Walsh et al., 2003]). Predation by leopards also has a greater impact on western gorillas [Fay et al., 1995; Watson, 1999–2000] than it currently does on mountain gorillas, who probably now have no predators other than humans [Sholley, 1991].

Western gorillas form stable, cohesive groups that are similar in size (average = 10 individuals) and composition to those of eastern gorillas [Tutin, 1996; Parnell, 2002a]. However, groups with more than 20 individuals are known only for western gorillas at Odzala National Park and in eastern gorilla populations [Bermejo, 1999; Kalpers et al., 2003; Magliocca et al., 1999; Yamagiwa & Kahekwa, 2001]. Multimale groups are rare in western gorillas [Bermejo, 1999; Remis, 1997; Magliocca et al., 1999; Parnell, 2002a; Tutin, 1996] and Grauer's gorillas [Yamagiwa et al., 1993], but are common in mountain gorillas (8–50% of groups [Kalpers et al., 2003; McNeilage et al., 2001]). While female primary and secondary dispersal are universal in gorillas [Harcourt et al., 1976; Sicotte, 2001], female western gorillas appear to prefer smaller groups [Stokes et al., 2003; Tutin, 1996]. In contrast, although female mountain gorillas, which face low feeding competition, show no group size preference, they do prefer multimale groups over one-male groups and solitary males [Watts, 2000].

Given that life-history patterns and social systems are shaped by ecological conditions and reproductive strategies [Kappeler & van Schaik, 2002; Kappeler et al., 2003; Sterck et al., 1997], we can expect to find further differences between western and eastern gorilla populations. For example, if western gorillas face stronger ecological constraints and greater female–female competition than eastern gorillas, the age at first reproduction should be later and interbirth intervals should be longer in western gorillas [Doran & McNeilage, 2001]. While the overall nutritional profits of western gorillas compared to mountain gorillas are not yet known, the female transfer preference for smaller groups is consistent with greater intragroup feeding competition due to greater reliance on clumped food resources [Doran & McNeilage, 2001; Stokes et al., 2003].

Regardless of why female western gorillas prefer smaller groups, their dispersal patterns may in turn influence male reproductive strategies [Sterck et al., 1997; van Schaik, 1996]. In eastern gorillas, males either emigrate to become solitary and then attempt to form their own one-male groups, or they are philopatric and eventually take over leadership from within a multimale group [Robbins, 1995, 2001; Watts, 2000; Yamagiwa, 1987a; Yamagiwa & Kahekwa, 2001]. Since female western gorillas prefer smaller groups, males may attain greater reproductive success by forming their own group instead of queuing for breeding positions in existing groups. Such male reproductive strategies would explain the scarcity of multimale groups in western gorillas [Parnell, 2002a; Tutin, 1996]. Group fissions and all-male groups have been reported only for eastern gorillas, and group takeovers by outsider males have not been reported for any gorilla population.

The low occurrence of multimale groups in western gorillas could lead to higher rates of group disintegration. Group disintegration, in which the silverback dies in a one-male group, and all females then transfer to another group or solitary male, has been observed in both western and eastern gorillas [Parnell, 2002a; Robbins, 1995; Sicotte, 2001; Stokes et al., 2003; Tutin, 1996]. The new silverback may kill unweaned offspring (infanticide), which could explain why females prefer multimale groups over solitary males and one-male groups in mountain gorillas [Watts, 1989, 1990a, 2000; but see Yamagiwa & Kahekwa, 2001]. Infanticide has been inferred in western gorillas twice when the infants disappeared following the mother's transfer after the death of a silverback; however, infants survived in two other cases under similar circumstances [Stokes et al., 2003].

The goal of this study was to compile new, unpublished data from four western gorilla field sites and to use this information, along with published data, to compare the social structure and life histories of western gorilla and eastern gorillas. In particular, we examine differences in 1) female reproduction, possibly due to differences in feeding ecology, and mortality patterns; 2) male emigration, possibly in response to female transfer preferences; and 3) group composition and transitions due to differences in the percentage of multimale groups. Finally, we discuss key questions to be addressed utilizing information from sites representing a variety of ecological conditions to develop a better understanding of how these conditions shape the social structure and life-history patterns of all gorillas.

MATERIALS AND METHODS

Data on births, deaths, emigrations, immigrations, and group transitions (group formations, changes between one-male and multimale composition, and disintegrations) were obtained from four study sites of western gorillas (Table I, Fig. 1). At two of these sites, researchers habituated the groups by contacting and following them almost daily. These sites were Bai Hokou, Dzanga-Sanga Reserve, Central African Republic, where data were collected from the Munye group from August 1998 to July 2003; and Lossi, Odzala National Park, Republic of Congo, where two groups were monitored several times per month from 1995 to 1996, and one group was monitored from 1995 to 1998. Most of the Lossi data are from a fourth habituated group, Apollo's group, spanning 1995 to mid-2002.

The other two study sites were "bais" or swampy open clearings, where researchers observed the gorillas from platforms placed at the edge of the clearings. The gorillas were habituated to this context, but the researchers did not try to follow them when they departed. Observations were made on 38 groups at

TABLE I. Details of Study Sites and Methods Used (Bai vs. Habituation, Length of Study)*

Subspecies	Western gorillas	Western gorillas	Western gorillas	Western gorillas	Grauer's gorillas ^a	Mountain gorillas ^{b,c}
Study site	Bai Hokou, Dzanga-Sanga Reserve, Central African Republic	Lossi, Odzala National Park, Republic of Congo	Maya Nord, Odzala National Park, Republic of Congo	Mbeli Bai, Nouabalé-Ndoki National Park, Republic of Congo	Kahuzi-Biega National Park, Democratic Republic of Congo	Parc National des Volcans, Rwanda
Type of study	Habituation	Habituation	Bai	Bai	Habituation	Habituation
Length of study	5 years	6 years	11 months	6.5 years	26 years	33 years
No. of groups monitored	1	5	36 in 1996–1997 16 in 1998	20	4	9–17
Group years	5	17	36	62.6	73	200

*Group years per study site equals the number of groups observed multiplied by the time each was observed; in the bai studies the observers made ad lib observations of visits to the bai by the gorillas during routine monitoring of the bai.

^aYamagiwa & Kahekwa [2001].

^bKalpers et al. [2003].

^cRobbins [1995, 2001].

Maya Nord, near Odzala National Park, Republic of Congo, from October 1996 to June 1997 (105 days) [Magliocca et al., 1999] and August–September 1998 (27 days). Data from 20 groups that were monitored from February 1995 to July 2001 at Mbeli Bai, Nouabalé-Ndoki National Park, Republic of Congo, are included in this study. We present only data or analyses that are not found in Magliocca et al. [1999], Parnell [2002a], or Stokes et al. [2003].

A drawback to bai studies is that groups spend only about 1% of their daily time in the bai [Magliocca & Gautier-Hion, 2002; Parnell, 2002b]. Therefore, certain demographic events that occur between visits to the bai are missed (e.g., death vs. emigration beyond the observed population, infants that are born and die before the group revisits the bai, etc.). However, this is also a problem in groups that are not well habituated or monitored on a nearly daily basis. Bai studies are advantageous in that researchers can collect information on changes in composition for many groups.

The age categories we employed mainly followed Watts [1990b]: infants (0–3 years), juveniles (3–6 years), subadults (6–8 years), adult females (>8 years), and blackback males (8–12 years). At Mbeli Bai, silverbacks were split into two categories: “young silverbacks” (12–15 years old) and “silverbacks” (>15 years old) [Watts & Pusey, 1993]. At Lossi, blackback males were those estimated to be 11–13 years old, and silverbacks were those estimated as >14 years old. The ages of all animals born prior to the onset of the studies are estimates, and for immature gorillas these are probably accurate to within 1 year (for more details see Magliocca et al. [1999] and Parnell [2002a]).

We measured both the intervals between surviving births and between births when the previous infants died. We also obtained infant mortality and annual birth rates, which were calculated as the total number of births divided by the total adult female-years per study site. This differs from the method of Stokes et al. [2003], who estimated a birth rate for each group and then averaged those values.

Immigration, emigration, and transfers (primary/natal and secondary) were defined according to Pusey and Packer [1987] and Sicotte [2001]. However, we distinguished between voluntary and involuntary transfers. A voluntary transfer is when a female disperses from an intact group. An involuntary transfer is when a female joins a new male after her previous group has disintegrated because its only silverback died [Stokes et al., 2003]. In most cases, we assumed that the animals that were first observed as immatures were still in their natal group. A group fission occurred when more than one individual, including a silverback, emigrated together. Group disintegration occurred when, upon the death of a silverback, all remaining members of the group transferred to another group or to a lone male. A group was considered multimale if it contained more than one silverback male. A nonreproductive group was a social unit with no adult females, regardless of how it was formed. This differs slightly from Parnell’s [2002a] functional definition of an all-male group as one formed by solitary adult males who join one another.

RESULTS

Birth and Mortality Parameters

The birth rate was 0.180 at Lossi (12 births in 68 adult female years in Apollo’s group), and 0.198 at Mbeli Bai (32 births in 162 adult female years). These values did not significantly differ from each other (Chi-squared test (X^2) = 0.10, $df = 1$, $P = 0.711$), nor did they differ significantly from those obtained at

TABLE II. Reproductive Parameters and Summary of Dispersal Patterns and Transitions of Group Structure Observed in Western Gorillas, Grauer's Gorillas, and Mountain Gorillas

	Western gorilla	Grauer's gorilla ^a	Mountain gorilla
Birth rate (births/adult female/year)	0.18 (Lossi) 0.198 (Mbeli)	Not calculated	0.226 ^b
Interbirth interval (surviving births only)	4–6 years (n = 6)	4.6 years (n = 9, range 3.4–6.6 years)	3.9 years (n = 62) ^b
Infant mortality (to age one year)	8.3% (Lossi) 42.9% (Mbeli)	19.6%	24% ^b
Infant mortality (to age three years)	22.0% (Lossi) 65% (Mbeli)	26.1%	34% ^b
Infanticide	Suspected cases	Not observed	Observed (n = 6) ^g
Adult male emigration	Common	Common	< 50% ^{d,e}
Female natal/primary transfer	Common	Common	Common ^c
Female secondary transfer	Common	Common	Common ^c
Multimale groups	Rare	Rare	Common ^{d,f}
Nonreproductive groups	Observed	Not observed	Observed ^{d,h}
Group formation by solitary male	Observed (n = 2)	Observed (n = 6)	Observed (n = 2) ^d
Group formation by group fissioning	Not observed	Observed (n = 2)	Observed (n = 5) ^f
Group disintegration	Observed (n = 6)	Observed (n = 3; due to poaching)	Observed (n = 5) ^f
Group takeover by outsider male	Not observed	Not observed	Not observed

^aYamagiwa & Kahewka [2001].^bGerald [1995].^cSicotte [2001].^dRobbins [1995, 2001].^eWatts [2000].^fKalpers et al. [2003].^gWatts [1989].^hYamagiwa [1987a,b].

Karisoke (97 in 430 adult female years [Gerald, 1995]; Mbeli: $X^2 = 0.50$, $df = 1$, $P = 0.461$; Lossi: $X^2 = 0.80$, $df = 1$, $P = 0.363$; Table II).

We have only preliminary data on interbirth intervals, and cannot yet do statistical comparisons with data on Grauer's and mountain gorillas (Table II). At Mbeli Bai, the mean interbirth interval was 62.3 months (n = 3); however, this value should be viewed cautiously because of the lack of continuous monitoring of the groups. At Bai Hokou, one female who had a small infant at the start of the study did not produce another during the 5 years of the study. At Lossi, from 1995 to 2002, there were three interbirth intervals of 4, 5, and 6 years (birth dates were estimated to only the nearest year) for females that had surviving offspring. At Lossi, females whose infants died before age 3 all had another infant within the next year (n = 3), which implies that they conceived within months of the infant's death.

The age at first reproduction has not yet been measured at any western gorilla site. At Lossi, all females that reached maturity in Apollo's group (n = 5) emigrated or disappeared before they had their first offspring.

Preliminary data on infant mortality are available from Lossi and Mbeli Bai. Of the 12 infants born at Lossi, one died before 1 year of age, which gives an 8.3% first-year mortality. Of the nine infants that could have attained age 3 by the end of data collection, two died, and thus the infant mortality rate was 22%. No causes of infant death at Lossi are known. At Mbeli Bai, the first-year infant mortality was 42.9% ($n = 28$), and infant mortality to age 3 was 65% ($n = 20$). However, one group had 100% ($n = 5$) infant mortality in a 2-year period (causes unknown). If this group is removed from the analysis, the rates are 28.6% for first-year mortality and 50% for infant mortality.

There were no new cases of observed or suspected infanticide in any of the study sites, but this may be due to the low numbers of group disintegrations observed. Two of nine (22%) infant deaths were suspected infanticides at Mbeli Bai [Stokes et al., 2003]. During a group fusion (see below) at Maya Nord, eight females with young infants joined an unknown silverback, and all mothers and infants survived.

Leopard predation was strongly suspected in three deaths (although scavenging cannot be ruled out): a silverback in very poor physical condition at Mbeli Bai, a silverback at Bai Hokou, and a blackback at Lossi. No estimates of the frequency of leopard encounters or the density of leopards were available. No cases of male mortality resulting from intraspecific aggression are known, but scars and wounds assumed to be from fights between silverbacks are common at Mbeli. Overall, six silverback deaths have occurred in 67 silverback-years of observation at Mbeli, which is not significantly higher than the nine observed deaths in 135 silverback-years at Karisoke (males in social groups only [Robbins, 1995]; $X^2 = 0.341$, $df = 1$, $P = 0.559$).

Dispersal Patterns

At Mbeli Bai, seven of eight males (88%) emigrated while they were blackbacks or young silverbacks. This proportion is significantly higher than male emigration at Karisoke (four of 11 males in heterosexual groups [Robbins, 1995]; $X^2 = 5.0$, $df = 1$, $P = 0.026$). No data are yet available for Bai Hokou, Lossi, or Maya Nord.

Some immature males have transferred between heterosexual groups at Mbeli Bai and Lossi. At Lossi, a subadult male transferred from Apollo's group along with two nulliparous females into a group that was not regularly monitored. At Mbeli, 11 immature male individuals (eight juveniles, two subadults, and one blackback) dispersed without their mothers. Four of these males immigrated into the population from unknown groups, six transferred between known groups, and one emigrated out of the population. Four of the seven emigrations were involuntary transfers (after the silverback died and the group disintegrated), and the remaining three (all juveniles whose mothers were no longer in their groups) were voluntary. Of the three voluntary emigrations, one emigrated out of the population (however, the possibility of death cannot be ruled out), one emigrated to a reproductive group, and the third emigrated to a nonreproductive group.

Female voluntary transfer has been observed at all study sites except Maya Nord, where observations lasted for only about 1 year. At Lossi, the estimated ages of females at presumed natal transfers were 8–9 years ($n = 3$). Two other females disappeared at age 10.

Group Composition and Transitions

Group sizes were within previously reported ranges (range = 2–29 [Parnell, 2002a]). At one extreme is the Munye group at Bai Hokou, where from 1998 until June 2003 the group diminished from eight to two (a silverback and juvenile male). Groups at Lossi were at the other extreme—for example, Apollo's group increased from 17 to 23 members from 1995 to 2002.

At all study sites the groups were predominantly one-male. At Mbeli Bai, two of the 20 groups were multimale for brief periods (<2 years) prior to the dispersal of young silverbacks. One group monitored for 2 years at Lossi also contained two silverbacks. It is not possible to perform a statistical comparison of the prevalence of multimale groups between sites, but it is clear that they occur less frequently in western gorillas than the range of values (8–42% of groups [Kalpers et al., 2003]) observed in censuses of the Virunga Volcanoes over the past three decades.

Nonreproductive groups were observed at three sites. At Bai Hokou, the group became nonreproductive (one silverback and one juvenile male) after all of the females emigrated. At Maya Nord, two groups contained only one silverback and several immature members. At Mbeli Bai, four groups had a nonreproductive structure for 13 months to 3 years, but all of these groups were observed as breeding groups at some time as well. These groups resulted when all females emigrated out of the group; however, in two cases females later immigrated into these groups, so they became reproductive again. No adult male was ever observed to immigrate into these nonreproductive units.

Two cases of group formation were observed at Mbeli Bai, the only site where repeated observations of solitary males were made. Of the nine solitary males, one acquired two females who have subsequently bred, but the other eventually lost all of his females. His body was later found with signs of leopard predation. There is a probable third case of a male who was not seen as a solitary, but first appeared only with females known from other groups. In 2002 he had the biggest group observed in the study population ($n = 16$), with eight adult females. The success of solitary males at Mbeli Bai seems comparable to the case in the Virungas (two of 10 [Robbins, 1995]); however, the latter data should be viewed with caution because solitary male mountain gorillas have not been regularly monitored. Group fissioning still has not been observed at any western gorilla study sites.

Our ability to measure the tenure of silverbacks as group leaders is limited by the length of the study periods. At each study site the tenure of a silverback for at least one group containing adult females lasted through the entire study period (Bai Hokou: 4.8 yr; Lossi: 6 yr; Mbeli Bai: 6.5 yr). However, other silverback tenures are known to be short. Males have been observed to be solitary for as long as 6 yr at Mbeli Bai.

Group disintegrations have been observed at Mbeli Bai ($n = 5$ in 63 group years). This value is approximately three times higher than that observed in mountain gorillas ($n = 5$ in 200 group years [Kalpers et al., 2003; Robbins, 1995]), suggesting that there is a higher rate of group disintegrations per observed group years at Mbeli Bai. No cases of group takeovers have been observed at any sites. However, at Maya Nord a group containing a younger silverback and four adult females integrated/fused with a larger group containing eight adult females. It is unknown whether the older silverback of the large group died or was chased away by the younger male.

DISCUSSION

Birth and Mortality Parameters

The preliminary data did not reveal any significant differences in the reproductive parameters of female western and mountain gorillas (Table II). Nonetheless, birth rates at Mbeli and Lossi were both lower than at Karisoke, and the few observed interbirth intervals were generally longer. More information is needed before we can ascertain whether this finding holds true, and understand how the variable nutritional, ecological, and social conditions of each species interact to lead to the observed reproductive patterns [Altmann & Alberts, 2003; Bentley, 1999; Borries et al., 2001; Tutin, 1994].

Obtaining sufficient data for analyses of mortality patterns is probably one of the greatest challenges for researchers of long-lived species [Galliard et al., 1998]. Given the difficulty of observing predation events, and the slow life histories of gorillas, the discovery of three cases of probable leopard predation suggests that it is an important cause of mortality in certain populations. Additional data are also needed before we can understand the impact that infanticide, male–male competition, predation, and disease have on the mortality rates of all age/sex classes, and growth rates of populations (e.g., in chimpanzees [Boesch & Boesch-Achermann, 2000; Hill et al., 2001; Nishida et al., 2003]).

Dispersal and Reproductive Strategies

The optimum strategy for female gorillas to maximize reproductive success should be to reduce both intragroup feeding competition and risk of infanticide [Sterck et al., 1997; Stokes et al., 2003; Watts, 2000]. A preference for smaller groups seems consistent with higher intragroup feeding competition in western gorillas, whereas a preference for multimale groups may be in response to infanticide risks in mountain gorillas. If there are few or no multimale groups in western gorilla populations, females may then preferentially transfer out of groups with older silverbacks, and into groups containing younger silverbacks to minimize the risk of infanticide (as in Thomas langurs [Steenbeek et al., 2000]). Additional information is needed to elucidate how female transfer patterns are influenced by several factors, including ecological conditions, group size constraints, the rate of intergroup encounters, the rate of group disintegrations, and population density.

Compared to eastern gorillas, western gorillas have a higher proportion of males that emigrate, and multimale groups are less common (Table II). These comparisons suggest that male eastern gorillas may typically attain higher reproductive success by dispersing and trying to form groups than by queuing for dominant positions in multimale groups, as is the case for mountain gorillas [Robbins, 1995; Watts, 2000]. Our data show that male eastern and western gorillas both have low success rates in acquiring females after emigration; however, the comparison is very preliminary.

Given the low success rate of emigrating males, and the biased adult sex ratio in groups, it is clear that male–male competition should be very high in both western gorillas and eastern gorillas. However, the observed differences between the species lead to intriguing questions about differences in the degree of reproductive skew found among the males, and the genetic structuring of social groups in the two species [Bradley et al., 2004; Bradley et al., 2001]. We need more information on within- and between-group social interactions, relatedness among individuals, and reproductive success of males to better understand the variability in both female and male strategies, and grouping patterns in gorilla species.

Group Composition and Transitions

If female western gorillas prefer smaller groups, and male western gorillas have higher emigration rates, it is somewhat surprising that the average group size is similar to that observed in eastern gorillas. On a proximate level, the dispersal patterns of both females and males would tend to reduce group size. However, such a reduction may be offset by the higher rates of group disintegration, because whenever a group disintegrates and its females join an existing group, the number of groups declines and the average group size increases. Further studies are needed to examine the relationships between individual dispersal, group transitions, and group size, and to explore the ultimate causes of the observed social structure (Robbins and Robbins, 2004).

All of the nonreproductive groups observed at these western gorilla study sites formed by default when females deserted bisexual groups. The same process has been documented in Virunga mountain gorillas; however, a merger of immature males and a solitary silverback, and immigration of immature males into nonreproductive groups, as previously reported in the Virungas [Robbins, 1995, 1996; Yamagiwa, 1987a,b], has only recently been observed in western gorillas in a new bai study in Odzala National Park [Gatti et al., 2003]. There have been reports of immature western gorilla males involuntarily and voluntarily immigrating into heterosexual groups. This is surprising not only because these males are dispersing at a young age, but also because one would expect these males to be viewed as future competitors to adult silverbacks and therefore unlikely to be tolerated. However, such males may not pose a threat to the dominant silverback if there is nearly universal male dispersal.

Future Directions

Long-term research at multiple sites has started to answer some questions about western gorilla social structure, demography, and life histories, to document variation within and across populations, and to raise questions about differences in eastern gorillas. Only continued long-term observations of multiple groups at multiple sites will reveal the extent of the variation and eastern-western differences. Studies at bays, in particular, can yield remarkable information on the social structure and demography of several groups simultaneously. Two recently initiated bai studies have also shown variability in bai usage and/or the density of gorillas in different forests [Gatti et al., 2003; Latour, 2003]. Following habituated groups yields fewer demographic data, but contributes to our understanding of how individual behavior leads to group-level phenomena and the social system of western gorillas. Since several groups are now becoming habituated [Cipolletta, 2003; Doran et al., 2002], we should soon have data on foraging behavior and within-group social interactions, including feeding competition and reproductive strategies. From the broader perspectives of socioecological theory and conservation management, we need accurate estimates of gorilla densities, food availability, parasite and disease prevalence, interspecific competition, and human disturbance before we can understand the interaction of these variables with population dynamics, grouping patterns, and individual behavior [Barton et al., 1996; Dunbar, 1985; Kappeler & van Schaik, 2002; Korstjens & Schippers, 2003; Ostro et al., 2001; Sterck, 1999; Strier, 1997; Yamagiwa, 1999].

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