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Variation in the social organization of gorillas: Life history and socioecological perspectives

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Abstract

A focus of socioecological research is to understand how ecological, social, and life history factors influence the variability of social organization within and between species. The genus *Gorilla* exhibits variability in social organization with western gorilla groups being almost exclusively one-male, yet approximately 40% of mountain gorilla groups are multimale. We review five ultimate causes for the variability in social organization within and among gorilla populations: human disturbance, ecological constraints on group size, risk of infanticide, life history patterns, and population density. We find the most evidence for the ecological constraints and life history hypotheses, but an over-riding explanation remains elusive. The variability may hinge on variation in female dispersal patterns, as females seek a group of optimal size and with a good protector male. Our review illustrates the challenges of understanding why the social organization of closely related species may deviate from predictions based on socioecological and life history theory.

KEYWORDS

dispersal, infanticide, male, male philopatry, multimale groups, relatedness

1 | INTRODUCTION

Some of the earliest comparative analyses seeking to understand variability in primate social organization focused on the occurrence of the most common grouping patterns, particularly one-male groups versus multimale groups.[1,4] Socioecological theory posits that ecological conditions influence how primate females distribute themselves, which then influences the distribution of males.[3,5–8] The distribution and abundance of food resources, predation risk, the temporal distribution of estrus females, as well as risk of sexual coercion by males (e.g., infanticide) all may contribute to female grouping patterns.[2] Furthermore, male–male competition for access to females, both within and between groups, may limit or favor the formation of multimale groups.[9] In addition to interspecies differences in social organization, socioecological theory has also been used to explain variation within species.[10–13] In particular, there are species in all primate taxa that vary in the proportion of social groups that are one-male and multimale (e.g., Verreaux's sifaka,[14] Phayre's leaf monkeys,[15] hamadryas baboons,[16] ursine colobus monkeys,[17] hanuman langurs,[18] black howler monkeys,[19] and mountain gorillas[20]). In a critical review of primate socioecology, Clutton-Brock and Janson[21] recommend that to understand variability in within-species and between-species grouping patterns researchers should consider how feeding competition and predation interact with variation in reproductive strategies and life history parameters of both sexes.

Gorillas are interesting species to consider variation in social organization because dispersal by both sexes appears to be universal in western gorillas, but both philopatry and dispersal are observed in male and female mountain gorillas.[22] Gorillas, along with other extant great apes, also provide a valuable model for understanding dispersal patterns of *Homo*, so studies of their social organization may be valuable for research into human evolution.[23–25] There is debate concerning whether the last common ancestor of African apes and humans had a social organization similar to that of chimpanzees, gorillas, or neither, as the last common ancestor shared certain life history, sexual morphology, sociosexual, and socioecological, characteristics with both.[24]

Prior to 2001, the genus *Gorilla* was considered only one species, but currently two species of gorillas are recognized, with each having two subspecies (Table 1).[26] The two species are separated by about 1,000 km, with western gorillas (*Gorilla gorilla*) occurring in seven central African countries, and eastern gorillas (*Gorilla beringei*) living in

TABLE 1 Subspecies of gorillas, the countries where they occur, the estimated area of habitat, and the estimated population size

Species/subspecies	Countries found	Area of habitat	Estimated population size (census estimates)
Eastern gorilla (*Gorilla beringei*)			
Mountain gorilla[85,86] (*G. b. beringei*)	Rwanda, Uganda, Democratic Republic of Congo	700 km^2	~1,000
Grauer's gorilla[165] (*G. b. graueri*)	Democratic Republic of Congo	21,000 km^2	3,800
Western gorilla (*Gorilla gorilla*)			
Cross River gorilla[178] (*G. g. diehli*)	Nigeria, Cameroon	600 km^2	<300
Western lowland gorilla[184] (*G. g. gorilla*)	Gabon, Cameroon, Equatorial Guinea, Central African Republic, Angola, Democratic Republic of Congo	445,000 km^2	~361,900

three (Figure 1). The two species split roughly 1.2 to 3 MYA, but some gene flow continued until as recently as 80,000 to 200,000 years ago.[27] The subspecies of Cross River gorillas diverged from western lowland gorillas roughly 17,800 year ago, with gene flow as recently as ~420 years ago.[28] The subspecies of Grauer's gorillas and mountain gorillas separated approximately 10,000 years ago, and the two populations of mountain gorillas (Virungas and Bwindi) split about 5,000 years ago.[29]

Studies at field sites across Africa have enabled us to make comparisons of different populations living in variable ecological conditions, but most research has focused on mountain gorillas. A brief history of research on gorillas can be found in Box 1. Ecological conditions vary considerably among gorilla populations (Table 2).[30–36] For example, the mean daily maximum temperature for the Virunga Massif is 8 °C less than the mean daily minimum for western gorillas. The amount of fruit in the diet ranges from <1% to about 30% annually, and the density of herbaceous species in their habitat varies substantially. All gorilla populations occur within a few degrees of the equator (Figure 1), so ecological differences arise mainly from altitude, with gorillas occupying areas from sea level to over 3,500 m.[32,34–36]

Gorillas live in cohesive social groups consisting of one or more adult males, adult females, and immature offspring.[22,37–39] Most multimale groups, defined as groups containing more than one adult silverback male and at least one breeding female, contain only two adult males (silverbacks), but on rare occasions they may contain up to six adult males.[40] Gorilla groups are not territorial, but have overlapping home ranges,[41–44] and their social organization is based on female defense polygyny rather than resource defense polygyny.[45] Male–female associations are believed to exist because females seek protection against predators and/or infanticide by other males.[22,39] Feeding competition is thought to be too weak to maintain nepotistic alliances among females and they may transfer between groups several times in their lives.[46–48] Approximately 50% of female mountain gorillas disperse from their putative natal group before reproducing,[49] but no cases of females remaining philopatric in their natal group have been reported for western gorillas.[48,50]

Gorilla groups form when females join solitary males (Figure 2). Such a group will have a one-male organization until a male offspring

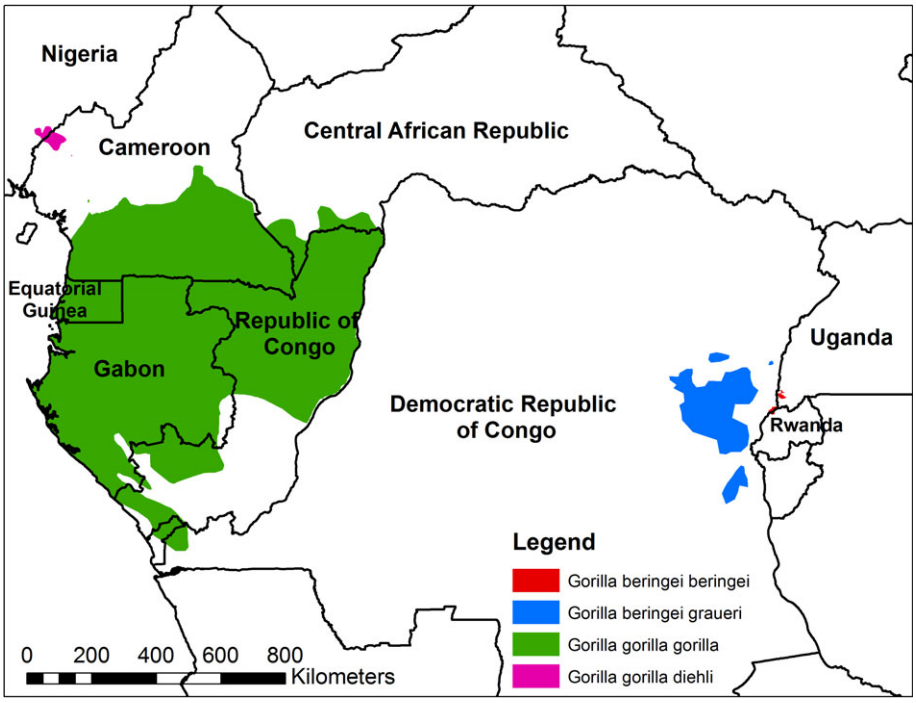

FIGURE 1 Distribution of the two species and four subspecies of gorillas across Africa [Color figure can be viewed at wileyonlinelibrary.com]

BOX 1 BRIEF HISTORY OF GORILLA RESEARCH

Western gorillas were first described in the wild in the late 1850s during the explorations of Paul Du Chaillu in Gabon. This roughly coincided with the publication of Darwin's *On the Origin of Species* and fueled the controversy of whether humans had descended from apes.[132] The amount of research conducted on the four subspecies of gorillas has not been equal, resulting in most of our knowledge being about mountain gorillas and much less about the other three subspecies. This box provides a general overview and not a fully comprehensive discussion of all research done on wild gorillas. In the past half a century or so, scientists have used a variety of methods to study wild gorillas, including habituating groups, observing unhabituated gorillas in forest clearings ("bais"), and using indirect signs of unhabituated gorillas.

The first major scientific study on gorillas was conducted by George Schaller in the late 1950s, which provided us with a remarkable summary of gorilla ecology, social organization, and behavior based on less than 2 years of research on mountain gorillas.[38] Dian Fossey's pioneering work began in 1967, as she was the first to fully habituate gorillas for research.[37] Fossey's work described many aspects of gorilla social behavior and ecology, as well as brought worldwide attention to the dire situation of these critically endangered animals.[37,43,133] Following in Fossey's footsteps came more detailed studies at Karisoke Research Center on social behavior[22,39,46,63,64,134–136] and feeding ecology.[34,137,138] Political conflict broke out in Rwanda in 1990, leading to a decade of civil unrest that restricted the ability for foreign researchers to work at Karisoke, but routine monitoring of the Karisoke study groups continued by Rwandan field staff.[139] Since 2000, studies have been conducted on a variety of topics including, but not limited to, male relationships,[40,120,140,141] social ontogeny and personality,[142,143] feeding ecology and ranging patterns,[42,144] feeding competition,[145] behavioral endocrinology,[146–148] body size and growth patterns,[149] and reproductive success.[55,71,90,150] Fossey's legacy lives on with 2017 marking 50 years of research at the Karisoke Research Center.

In addition to Karisoke, many mountain gorilla groups in the Virunga Volcanoes have been habituated since the 1980s for tourism in Rwanda, Uganda, and DRC.[151] These groups have provided useful demographic data for understanding population dynamics.[57,72] Furthermore, routine censuses of the entire Virunga population have been carried out since the early 1970s, allowing us to make a detailed assessment of the population growth.[82,86]

About 30 km away from the Virungas, the only other population of mountain gorillas lives in the ecologically distinctive habitat of Bwindi Impenetrable National Park, Uganda. Bwindi started receiving international attention in the late 1980s, with initial research on the Bwindi Mountain gorillas focused on aspects of their feeding ecology and morphology.[152] Since the late 1990s, various projects have focused on social behavior,[105,153,154] feeding ecology,[31,44,122,155–159] and population genetics.[70,80] Similar to the Virunga population, demographic data has been obtained from groups habituated for tourism and intensive park-wide censuses also have been conducted, contributing to studies of population dynamics.[47,85,160]

Grauer's gorillas in Kahuzi-Biega National Park, DRC were habituated in the early 1970s.[161] Research on their feeding ecology and social organization began in the 1980s.[35] Niche partitioning with chimpanzees has also been a focus of research.[162,163] Political instability in eastern DRC has made it difficult to work in the region.[164] Survey work to obtain estimates of population size for this subspecies has occurred through large areas of eastern DRC.[165]

Western gorillas are much more difficult to habituate than mountain gorillas because the forests where western gorillas live have less herbaceous vegetation in the understory and more closed canopy that reduces visibility, which makes it much more difficult to find and follow them. The first intensive research on western gorillas was in Lopé National Park, Gabon in the 1980s, showing that western gorilla ecology and diet is dramatically different from mountain gorillas.[62,166] Unfortunately, western gorillas were never well habituated at Lopé. In the late 1980s and 1990s efforts to habituate and study western gorillas occurred at Bai Hokou, in Central African Republic. This work further increased our knowledge of the ranging patterns and feeding ecology of western gorillas.[167,168] By the late 1990s, one group of western gorillas was habituated at Bai Hokou, which eventually led to additional studies on their feeding ecology and aspects of their social behavior.[95,96,169] Additionally, in the mid-1990s, Diane Doran began the Mondika study site, about 50 km away from Bai Hokou, where research on two groups of habituated gorillas provided more information on their social behavior.[30,98,104,170,171] Groups have also been habituated in Odzala National Park, Republic of Congo.[59] Western gorillas recently have been habituated at two sites in Gabon.[32,172]

In many locations, western gorillas routinely feed in open clearings, referred to as "'bais," which provides a unique opportunity to collect data on group organization of many groups without habituating the gorillas. Such studies have occurred in Maya Bai,[61] Lokoué Bai,[60] and Mbeli Bai.[56] Ebola decimated the population at Lokoué Bai, killing approximately 90% of the gorillas in the area and resulted in studies of how the population has recovered from such an extreme demographic event.[173,174] Mbeli Bai, with data collection spanning 20 years, has yielded studies on infant development,[175] female social relationships and transfer patterns,[48,176] sexual coercion,[177] and male reproductive success.[45,66]

The least amount of research effort has focused on the Cross River gorillas of Cameroon and Nigeria. No efforts have been made to habituate Cross River gorillas because of the threat of poaching. Most of the research since the 1990s has focused on determining their abundance and distribution.[36,178] Indirect studies of their feeding ecology have shown that they live in the most seasonally extreme habitat of any gorillas, with a prolonged dry season.[36] Research on a landscape scale has shown that there are many areas of suitable habitat that the Cross River gorillas could expand into, assuming that human disturbance and poaching can be controlled.[179]

The past 50 years of research on gorillas has shown that they can occupy a wider range of habitats than initially thought and they are flexible in their diet, social interactions, and grouping behavior. Gorillas have and will continue to serve as a useful species for testing predictions of socioecological models to understand how ecology influences social organization of primates. Studies that link disciplines, such as cognitive ecology, would be fruitful avenues of future research. To best understand the behavioral and ecological diversity that gorillas exhibit, we need continued long-term field sites as well as research at additional locations. Research on gorillas at a variety of sites can help us understand human evolution and contribute to their conservation.

becomes a silverback, at which point the group will become multimale.[51–54] If the male offspring disperse or the dominant male dies, the group returns to a one-male organization. Multimale mountain groups can include father-son dyads as well as half-brothers, cousins, or unrelated males.[20,40,47,55] Multimale groups may fission, resulting in either one-male or multimale groups depending on the number of silverbacks in each new group. Takeovers by outsider males rarely occur and adult males almost never immigrate into breeding groups. The lack of immigration means that male philopatry is the primary proximate reason for the occurrence of multimale groups. In other words, multimale groups are rare among western gorillas because all of the subordinate males disperse as they reach adulthood.[56,57]

Approximately 40% of mountain gorillas groups in both the Virunga and Bwindi populations are multimale.[20,47,58] In contrast, multimale groups of western gorillas have only rarely been observed in the wild.[50,56,59–62] Approximately 5% of western gorilla groups and 5% of Grauer's gorilla groups are multimale (Table 2).[35,57] Initially, multimale groups were thought to be only a temporary phase prior to the emigration of maturing males, creating what has also been referred to as "age-graded groups."[1,51] This appears to be what occurs in western gorillas.[56,57,60] However multimale groups in mountain gorillas are not simply a short, transient stage as males reach maturity and then eventually emigrate, but rather are more common and long-lasting than initially expected with mature silverback males sometimes coresiding for a decade or longer.[20,40,47]

The occurrence of multimale groups in gorillas is unexpected because they have several morphological and physiological features that are predicted to occur in one-male breeding systems. There is large sexual dimorphism in body size and canine size, and males have small testes.[22] In addition, females have relatively short periods of receptivity and very small sexual swellings. Male–male competition influences the social organization of gorillas, including the number of males per group.[53,63,64] However, female choice, particularly in terms of choice of male/social group, also plays a role.[22] It is still not entirely clear what influences female choice of males,[65] but it is hypothesized to be influenced by males' protective ability, size, and/or strength.[66,67]

Here, we discuss five nonmutually exclusive, ultimate causes that may explain the variability in occurrence of one-male versus multimale groups in gorillas: human disturbance, ecological constraints on group size, risk of infanticide, life history patterns, and population density. First, we will consider the fitness consequences of male dispersal from the perspective of both dominant and subordinate males, which is the proximate mechanism that shapes the social organization of each gorilla population.

TABLE 2 Ecological, demographic, and life history variables of gorillas

	Virunga Mountain gorillas (*Gorilla beringei beringei*)	Bwindi Mountain gorillas (*Gorilla beringei beringei*)	Grauer's gorillas (*Gorilla beringei graueri*)	Western gorillas (*Gorilla gorilla gorilla*)
Group size (mean ± SD)	12.5 ± 9.1[86]	9.6 ± 6.4[85]	10.0 ± 6.3[35]	8.4 ± 4.3[56]
Multimale groups	40%[57]	45%[47]	5%[35]	5%[57]
Interbirth interval (months)	47.8 ± 9.0[110]	56.6 ± 14.4[47]	55.2[35]	62.0 ± 10.0[118]
Age of male emigration	15.3[57]	Unknown	Unknown	Unknown
Male tenure length (years)	15.7[72,193]	Unknown	14.6[35]	Unknown
Disintegrations per group year	0.05[193]	Unknown	0.03[35]	0.08–0.11[192,194]
Natal female dispersal	50%[49]	Unknown	Unknown	100%[48]
Temperature (mean minimum and maximum)	4–15 °C[34]	13–25 °C[31]	13–27 °C[35]	23–27 °C[32]
% fruit in diet	<1%[34]	10–15%[153]	Unknown	~30%[30]
Herbaceous vegetation (stems per m^2)	8.8[34]	4.4–10.6[31]	Unknown	0.3–2.3[32,33]

Variables concerning the social organization of mountain gorillas are reported from censuses of their entire populations and the other demographic data comes from habituated groups. Data on Grauer's gorillas comes from habituated groups and censusing of one section of Kahuzi-Beiga National Park, DRC. Data sets on demographic and life history variables for western gorillas generally come from an observations made at a forest clearing, with the exception of the rate of group disintegration that is estimated from long term genetic analysis of unhabituated gorillas. Dietary data for all populations come from habituated groups and their surrounding habitat.

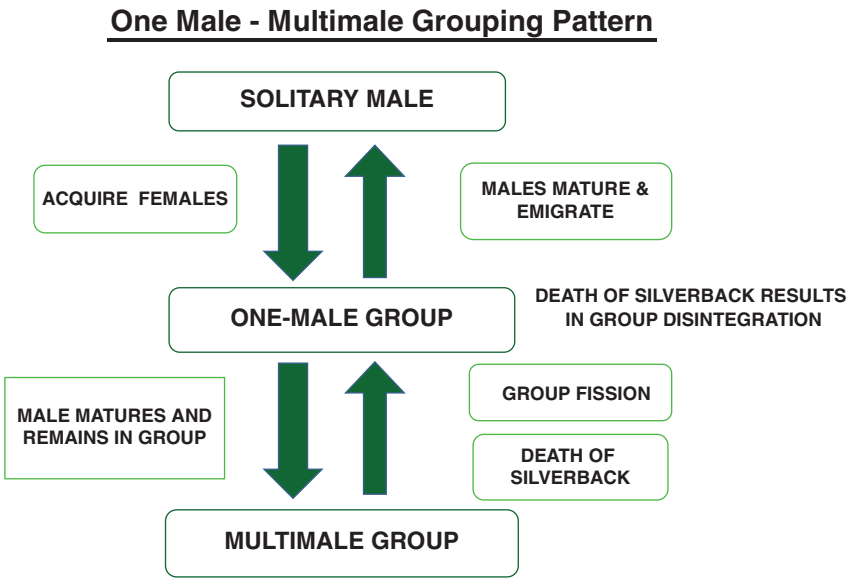

FIGURE 2 Group transitions from solitary males to one male groups to multimale groups [Color figure can be viewed at wileyonlinelibrary.com]

2 | FITNESS CONSEQUENCES OF MALE DISPERSAL

2.1 | Dominant males: Tolerate or evict subordinates?

It has been assumed that the dominant male controls whether subordinate males remain in his group, because he could evict them before they reach full maturity.[68,69] Such evictions are not reported from field studies, however, and computer simulations suggest that the reproductive success of dominant male mountain gorillas is relatively insensitive to whether their subordinate males emigrate or remain philopatric.[69] The potential consequences of retaining subordinates may be minimized when they do not reach emigration age until late in the tenure of the dominant male, and because the costs are offset by benefits to the dominant male.[69]

There are several potential costs for the dominant male to tolerate subordinates. First, the dominant male may lose some share of reproduction to the subordinates. Paternity analyses initially indicated that dominant males sire up to 85% of the offspring born in multimale groups, but subsequent studies have shown lower skew in groups with more subordinate males.[55,70,71] Second, a dominant male may lose females if the group fissions.[40,52] Third, up to 24% of dominance tenures end due to usurpation by subordinates, so the dominant male may lose future reproductive opportunities.[49,72]

The main benefits for the dominant male to tolerating subordinates are a reduced risk of infanticide for his offspring (see section 4.3 below), as well as an increased ability to retain females.[69] A lower risk of infanticide may help to explain why females are significantly less likely to transfer out of multimale groups than one-male groups.[49,72] Females transfer during intergroup encounters so silverbacks in multimale groups also benefit from increased herding of adult females away from rival males during intergroup encounters.[73]

2.2 | Subordinate males: Stay or go?

The main benefits for subordinate males to remain philopatric are the opportunity to sire offspring within their natal group, as well as the chance to obtain a dominant role through usurpation, group fission or the death of the higher ranking male(s). Those benefits need to be weighed against the opportunities to form their own breeding group after emigration.[53,69] Computer simulations suggest that subordinate male mountain gorillas will typically have higher reproductive success if they remain philopatric rather than emigrating.[53,69] Nonetheless, field studies show that approximately 45% of mountain gorilla males disperse.[40] The probability of emigration has not been consistently correlated with the number of potential mates in the group, the number of potential competitors, or the age of dominant male.[40,53] The dispersal decisions were apparently voluntary and not due to an increase of aggression from the dominant male.

If staying/queuing appears to be a better strategy than emigrating for mountain gorillas in these computer models, then why do some male mountain gorillas emigrate and why aren't all mountain gorilla groups multimale? One potential explanation is that the computer models do not account for variability in male quality (e.g., ability to outcompete other males; physical size and strength), which is generally considered an important source of variance in reproductive success.[66,67] Emigrant males have fewer copulations in their natal group prior to their emigration than philopatric males,[74] which may suggest that they have lower quality than philopatric males or are in groups with fewer unrelated females. If emigrants are merely "making the best of a bad job," then their lower reproductive success does not necessarily indicate whether dispersal is the best strategy for any particular individual.[75]

A second explanation is that the computer models used to assess fitness benefits for philopatric versus dispersing males do not account for inclusive fitness,[53,69] which is a major consideration in most reproductive skew models and in the underlying theory that reducing kin competition is an ultimate cause for natal dispersal.[68,76] Emigration by subordinate males appears to have little impact on the reproductive

success of the dominant male, so inclusive fitness within that dyad may be unimportant.[69] When groups start to contain many males, however, inclusive fitness may be a more important issue for determining the optimal level of competition (and queuing) among subordinates. Such broader influences of inclusive fitness when more than two males are in a group are difficult to incorporate into theoretical models of dispersal and other reproductive strategies.[77,78]

A third potential explanation is that the computer models do not account for inbreeding avoidance.[53,69] Relatedness between males and females is significantly higher within groups than among groups in the Virungas, which reflects the potential for inbreeding within groups.[79] Approximately 50% of females remained in their natal group, but almost all natal nulliparous females were with at least one sexually active male who was not old enough to be their father, so the presence or absence of such mating alternatives also did not determine whether they left.[49] Father-daughter inbreeding avoidance was observed within multimale groups, but approximately 10% of infants had parents who were either mother-son pairs or half-siblings.[71] The risk of inbreeding can be reduced through sex-biased differences in dispersal distances, and male mountain gorillas disperse farther than females.[79,80] Nonetheless, the influences of inbreeding and familiarity among adults on the dispersal patterns of both sexes warrant additional research.[40,49]

Further study of the potential variability in fitness consequences of male dispersal versus philopatry within mountain gorilla populations could improve our understanding of the differences between mountain gorillas versus other subspecies: why do all males of the other three subspecies consistently emigrate? Such differences in dispersal patterns provide the proximate mechanism that leads to a higher proportion of multimale groups among mountain gorillas than western gorillas. Few studies have addressed this topic in other species with both one-male and multimale groups. In both hamadryas and gelada baboons, the presence of follower males led to longer tenures, more females per group, and increased reproductive success for the dominant male and also provided benefits for the followers.[16,81] In contrast, Port et al.[14] found no benefits for dominant male Verreaux's sifakas to have followers, but those followers have higher fitness than males that do not join groups (floaters).

3 | HYPOTHESES FOR VARIATION IN SOCIAL ORGANIZATION

3.1 | Human disturbances

Harcourt and Stewart[22] proposed that the occurrence of multimale groups in mountain gorillas is a response to human disturbance, because multimale groups occur almost exclusively in the two mountain gorilla populations living in very small habitats (Virunga Massif, 450 km^2; Bwindi, 330 km^2) that have suffered from high levels of encroachment.[82] To test this prediction, a comparison of western and mountain gorilla populations suffering from the same level of human disturbance would be needed, but such scenarios are not available. Nonetheless, other evidence refutes this hypothesis.

Human disturbances could affect the dispersal patterns and social organization of gorillas in several ways. First, poachers can directly reduce the proportion of multimale groups by reducing the number of adult males. A disproportionate number of silverbacks were killed in Virungas during the 1970s, and in Kahuzi-Biega during the 1990s and 2000s,[83,84] but in contrast, western gorilla populations living in areas known to have low levels of poaching do not have multimale groups.[56,57] Second, poaching could indirectly increase male philopatry and multimale groups, if males remain in groups to reduce their risk of such predation.[7,22] This second hypothesis would not explain why Bwindi and the Virungas have similar proportions of multimale groups, despite fewer human disturbances at Bwindi in recent decades.[47,85] Third, human habituation could increase male philopatry and multimale groups, if males remain in "safe havens" that receive greater protection by park staff.[22] There was heavy human encroachment due to war and political instability in the Virungas during the 1990s and 2000s.[82,86] However, the third hypothesis would not explain why multimale mountain gorilla groups were observed as early as the late 1950s,[38] nor why many unhabituated mountain gorilla groups are multimale. Furthermore, no western gorilla groups that have undergone habituation have become multimale.

In addition to the potential influences of poaching and habituation, humans may have altered the dispersal patterns and social organization of mountain gorillas by reducing the suitable habitat in which to move. Although some emigrating western gorillas and mountain gorillas remain near their natal area, genetic studies have shown long dispersal distances for others.[41,79,80,87,88] Options to disperse long distances have declined for mountain gorillas in recent decades, as many mountain gorillas now live along a park boundary.[85,86] In contrast, most western gorillas live in large, contiguous tracks of rainforest, where male dispersal is not constrained by such barriers. Thus, limited dispersal destinations could help to explain why male emigration and one-male groups are less common among mountain gorillas than western gorillas. However, in cases where male dispersal could be constrained by natural barriers, (i.e., western lowland gorillas with boundaries created by water in Loango National Park, Gabon,[89]) or human barriers (i.e., Grauer's gorillas in the highland sector of Kahuzi-Beiga is only ~100 km^2), multimale groups rarely occur.[35]

The possibility that human disturbance has had an influence on grouping patterns in mountain gorillas cannot be ruled out, but there is also no practical way to test the hypothesis. However, human disturbance would be expected to have detrimental effects on behavior or reproductive success, although it could also have neutral or positive effects via the removal of predators or improved food availability. In fact, over four decades, the habituated groups in the Virunga Massif that have been monitored on a nearly daily basis experienced a higher growth rate than the unhabituated groups, which is believed to be due to better protection including veterinary interventions that may have reduced mortality.[82] Furthermore, no negative effects on female reproductive success have been in observed in multimale groups compared to one-male groups.[72,90]

3.2 | Ecological conditions influencing social organization

An initial model of ecological influences on primate social organization proposed that females form groups to defend resources, particularly clumped patches of food.[8] A subsequent model proposed that groups form primarily to reduce predation risks, and that the benefits of resource defense are generally outweighed by feeding competition within groups.[7] Socioecological models have undergone further refinements (discussed below), but the primary ecological influences on female group size are still considered to be predation risk and food availability.[2,21] Several studies have shown that males will distribute themselves according to female group size.[5,91] Thus, the proportion of one-male versus multimale groups in a gorilla population may depend on how the number of females per group is influenced by predation risk and/or feeding competition.

3.2.1 | Predation

Leopards are the only known predator of gorillas aside from humans.[92–94] Leopards are found in most areas where western gorillas occur, yet they have not been observed in either the Virungas or Bwindi for decades.[38] Due to body size dimorphism, silverbacks may provide better protection against predators than other group members, so the number of silverbacks might be more important than overall group size. If predation risk drives the occurrence of multimale groups, then multimale groups and larger groups should be more common for western gorillas than mountain gorillas. Thus, the risk of predation does not seem to explain the differences in social organization between western gorillas and mountain gorillas.

3.2.2 | Feeding competition

Mountain gorillas live in habitats with higher densities of terrestrial herbaceous vegetation and lower fruit availability than western gorilla habitat (Table 2).[31–34] The diet of western gorillas includes significant quantities of fruit, which tends to be more spatially and temporally clumped than herbaceous vegetation (Table 2).[30,32,35,95] Western gorillas have longer daily travel distances and are less spatially cohesive (i.e., larger average interindividual distance) than mountain gorillas, suggesting that their food resources are less abundant and more clumped.[96–98] Therefore, both scramble competition and contest competition are predicted to be higher within groups of western gorillas than mountain gorillas, which could lead to more constraints on their group size.[99]

The intensity of scramble competition is typically assessed by examining the relationships between group size versus daily travel distances, activity budgets, and/or reproductive success.[100] We do not have such data for western gorillas, and little evidence of scramble competition has been observed in mountain gorillas. No negative effects of group size on female reproductive success were observed among Virunga mountain gorillas, even when groups were five times larger than the average size.[90] Group size did not have a significant influence on day journey length in Bwindi mountain gorillas.[101] and showed only a weak effect for Virunga mountain gorillas.[102] However, there was a positive relationship between group size and monthly home range size, and the rate of revisits to areas declined as group size increased in Bwindi, suggestive of scramble competition.[101]

The intensity of contest competition within groups has been assessed by examining the relationship between dominance rank versus energy intake and/or reproductive success.[103] The relationship between dominance rank versus energy intake was not significant for female western gorillas.[104] In contrast, dominance rank was positively correlated with energy intake within one group of Bwindi mountain gorillas.[105] Further evidence of contest competition has been observed among Virunga mountain gorillas, as high dominance rank gives females better access to food resources, higher energy intake rates, and higher reproductive success suggesting that feeding competition has more of an impact than previously thought.[90,145]

A comparison of group size between the two species may shed light on ecological constraints from feeding competition. Approximately 5%–15% of mountain gorilla groups have contained more than 20 individuals in the past decade.[85,86] In contrast, such large groups have rarely been observed in lowland gorillas, and they have almost always been one-male groups.[35,59,83] Despite such differences in the proportion of large groups, however, Yamagiwa et al.[35] found no difference in median group size of western, Grauer's, and mountain gorillas. However, when comparing the number of adult females (not total group size), a more recent analysis found that mountain gorilla groups contained an average 5.1 $\pm$ 2.7 adult females, which was significantly greater than 3.6 $\pm$ 1.5 for western gorillas.[57] Collectively, these results provide modest support for the hypothesis that feeding competition is limiting the group sizes of western gorillas more than mountain gorillas.

3.2.3 | Distribution of males versus females

Multimale groups are more common among mountain gorillas than western gorillas, so according to the prediction that the distribution of males is ultimately determined by the distribution of females, we should expect multimale groups to contain more adult females than one-male groups.[5,91] From a proximate perspective, however, the distribution of male gorillas is determined primarily by whether they emigrate or remain philopatric. Thus, when comparing the influence of the distributions of females on the distribution of males in groups in each gorilla species, it may be insightful to consider only the groups that contain potential male emigrants (i.e., multimale groups), rather than all groups. When considering only multimale groups (and excluding all-male groups), the number of adult females in multimale groups was 5.3 $\pm$ 3.2 for mountain gorillas versus 1.6 $\pm$ 0.67 for western gorillas, which is greater than the difference for all groups (previous paragraph).[57] Thus, when focusing on groups with potential male emigrants (multimale groups), the comparison between gorilla species provides greater support for the hypothesis that the distribution of males is ultimately determined by the distribution of females.[57]

In contrast to the comparison between gorilla species, the comparisons within species do not support the hypothesis that that the distribution of males is primarily determined by the distribution of females. Among mountain gorillas, the number of adult females in multimale groups was not significantly different from one-male groups (5.3 $\pm$ 3.2 vs. 4.9 $\pm$ 2.6). Among western gorillas, the number of adult

females in multimale groups was significantly lower than one-male groups (1.6 ± 0.67 vs. 3.8 ± 1.5), which is in the opposite direction of expectations.[57] If the group sizes of multimale western gorilla groups were constrained by ecology, then those groups would not have been larger when they were one-male. Instead, females were leaving multimale groups containing aging dominant males, and variation in social organization within populations were attributed to the typical life cycle of a group.[56] Thus the most relevant variable, the number of adult females when groups contain potential male emigrants (are multimale), may be determined by the mate choices by adult females rather than ecological constraints.[57]

3.3 | Risk of infanticide

Refinements to the initial socioecological models have considered infanticide as an important influence on social organization.[3,106] Infanticide can be an adaptive strategy for males who were unlikely to have sired the infant, if the death of the infant shortens the interval until the mother becomes fertile again, and if the male is likely to sire her next offspring.[107] Multimale grouping patterns are considered to be a key counterstrategy against infanticide.[106,108]

Gorillas have some of the longest interbirth intervals among primates, and those intervals are significantly shorter after an infant dies, so infanticide may be considered an adaptive strategy for male gorillas to reduce the reproductive success of other males.[109,110] Known or suspected cases of infanticide have been reported in nearly all populations studied for a notable length of time.[48,83,84] Strong evidence of infanticide by mountain gorillas has been based on direct observations of an attack, as well as bite wounds on a dead infant following an encounter with outside males.[84] Infanticide has been especially common after the silverback dies in a one-male group and the females join an outsider male, who had little chance of siring their unweaned offspring, and had a high probability of siring their next offspring.[84] In contrast, infanticide rarely occurs when the dominant silverback dies in a multimale group, perhaps because the other resident silverbacks could be the father or a close relative of the infant.[84,111] Infanticide has not been directly observed in western gorillas, but has been inferred from a significant increase in infant mortality following the disappearance/death of the silverback.[45,48] Disappearances of infant western gorillas could also be due to predation.[45]

As stated in section 3.1, adult female gorillas and dominant males may both prefer multimale groups due to the lower risk of infanticide when the dominant male dies. If a primary benefit of multimale groups is to reduce the risk of infanticide, then such groups may be less common if the risk is reduced for other reasons. Two potential reasons are dispersed male networks and variance in male strength.

3.3.1 | Dispersed male networks

Bradley et al.[41] found a high degree of relatedness among neighboring male western gorillas, suggesting that males do not disperse far from their natal group. The researchers proposed that closely related males would not exhibit aggression against each other, nor commit infanticide against the offspring of their kin, hence precluding the value of multimale groups. The dispersed male network hypothesis may be supported by the seemingly low levels of aggression reported during some intergroup encounters among western gorillas, but some encounters involve intense aggression[59]; and rates of infanticide have not been reported for encounters between groups when the dominant male is alive. However, other genetic studies did not find evidence that dispersing males remain in their natal areas, but rather showed that the gene flow is more geographically limited for females than for males.[87,88] Additional empirical support for the dispersed network hypothesis could be obtained by replicating the genetic evidence of their existence elsewhere, and by examining how behavior during intergroup encounters is influenced by the relatedness between males, number of silverbacks and potential migrant females in each group, familiarity between groups (e.g., frequency of encounters), competition for food resources, and if the presence of researchers influences the behavior of unhabituated gorillas.

3.3.2 | Variability in male strength

The "Pradham model" predicts that females will generally prefer to reproduce in multimale groups to minimize the risk of infanticide.[78] One potential exception to the prediction may arise if dominant males are much stronger in one-male groups than multimale groups.[17,72,78] The mathematical model defined "strength" to coincide with longer dominance tenures, which can partially offset the risk of infanticide when those tenures end.[78] Dominant male mountain gorillas have lower replacement rates (i.e., longer tenures) in one-male groups than multimale groups,[72] so the male strength model may help to explain why some females remain in one-male groups, even though those groups have a higher rate of infanticide when the dominant male dies.

The Pradham study also suggested that females could accept one-male groups when dominant males were much stronger than subordinates and solitary males, especially if multimale groups imposed any extra costs that were not incorporated into the model.[78] If so, then the higher proportion of one-male groups among western gorillas would support the model if they have greater variance in male strength than mountain gorillas (i.e., western gorillas would have a greater difference in strength between dominant males versus other silverbacks in the population). The body size of dominant male western gorillas has been positively correlated with number of adult females per group and infant survival, which suggests that social organization depends on male traits, albeit not precisely the trait that was defined in the Pradham model.[45,66,67]

3.3.3 | Rates of infanticide

Even if western gorillas have dispersed male networks and greater variability in male strength than mountain gorillas, they do not seem to have lower risk of infanticide when the dominant male dies. Such suspected cases of infanticide have represented 12% of all observed births at the Mbeli study site (although some may have died from predation or other causes), which is significantly higher than 1.7% in the same context for Virunga mountain gorillas.[72] Thus, despite the possibility of dispersed male networks and variability in male strength among western gorillas, their overall rate of death from infanticide has not been lower than mountain gorillas. Consequently, the relative risks of infanticide do not seem to explain why western gorillas have fewer multimale groups than mountain gorillas.

3.4 | Life history theory

The life history of an organism is defined by its stages of maturation and reproduction, such as the gestation length, interbirth intervals, age of weaning, age of first reproduction, and life span.[112,113] The presence of parents and other relatives can influence the dispersal patterns of their offspring, which may contribute to variation in social organization, such as the occurrence one-male groups versus multimale groups.[20,114] Differences in the rate of maturation and other life history parameters can affect the probability that individuals will reach adulthood in a group that still contains their mother, their putative father, and/or other familiar males.[21,115]

Western gorillas are considered to have a slower life history than mountain gorillas, as expected for a species with a more frugivorous diet.[47,116–118] Western gorillas are weaned at a later age and have longer interbirth intervals than Virunga mountain gorillas (Table 2).[35,47,110,118,119] Infant mortality is higher in western gorillas than mountain gorillas.[45] Male western gorillas also become silver and fully mature at later ages than the Virunga mountain gorillas: 14–18 years versus 12–14 years.[116] The later age of maturation for western gorillas may reduce the probability that males will reach adulthood in the same group as their parents, which could reduce their probability of creating and maintaining multimale groups, if longevity is the same in both species.

3.4.1 | Male maturation versus dominance tenure length

Gorillas form one-male groups when females join a solitary male, and males rarely immigrate into breeding groups, so the groups typically do not become multimale until their offspring become silverbacks.[20] If the dominant male dies while the group is still one-male, then the group disintegrates and his male offspring become solitary or join nonbreeding groups. Thus the probability for creating multimale breeding groups may depend upon the age when males reach adulthood, relative to the length of male dominance tenures.

The average tenure length is 12–15 years for the Virunga mountain gorillas, but comparable data has not been reported for western gorillas.[45,72] Regardless, male mountain gorillas did not have a significantly higher probability than western gorillas of reaching adulthood in a group where their putative father (defined as the silverback who was dominant when the subordinate male was an infant) was still the dominant male.[57] The results suggest that male mountain gorillas might have shorter dominance tenures than western gorillas, which would be consistent with their faster life history. Male mountain gorillas might also have shorter dominant tenures due to greater mating competition, especially in multimale groups where those tenures end at a faster rate than in one-male groups.[72] Thus, a more precise comparison of this pathway for creating multimale groups would be to focus specifically on the tenure length of males who became dominant when a female joined a solitary male, while excluding males who became dominant through other mechanisms.

3.4.2 | Mothers matter

Gorilla groups remain multimale when the subordinate silverbacks are philopatric, and multimale groups can become one-male when silverbacks die or disperse. Among subordinate male mountain gorillas, the probability of philopatry (versus dispersal) is significantly higher if their mother is still in the group.[40] Proximity to their mother could help those males to develop relationships with other adult females and with the dominant silverback.[40,51,120] The later age of maturation for western gorillas may reduce the probability that males will reach adulthood in the same group as their mother, which could reduce their probability of creating and maintaining multimale groups. The probability for males to reach adulthood with their mother was 50% for mountain gorillas, which is significantly higher than 18% for western gorillas.[57] Thus, the presence of the mother may help to explain the higher proportions of male philopatry and multimale groups among mountain gorillas versus western gorillas. The presence of the mother was higher for all ages of maturing male mountain gorillas, so it may arise primarily from lower dispersal rates of female mountain gorillas, rather than the earlier age of maturation for male mountain gorillas.[57] Unfortunately comparable rates of female transfers from different sites are not yet available.

3.5 | Population density

Intraspecific variation in one male groups and multimale groups has been attributed to population density and intruder pressure in some species.[14,121] Moore[121] also showed that the influence of density on the occurrence of multimale groups in Hanuman langurs was not linear but exhibited a quadratic effect, such that multimale groups were more likely at low densities, possibly due to the high costs of search time for dispersing males to establish new groups, and were more common at high densities due to high intruder pressure. Mountain gorillas occur at densities of about 1 gorilla per km^2,[85,86] which is intermediate in the range of densities (0.1–5.4 gorilla per km^2) observed in western gorilla populations.[33] Thus, in contrast with Hanuman langurs, the higher proportions of multimale gorilla groups do not seem to occur in populations with the lowest or highest population densities.

4 | DISCUSSION

The observed variation in grouping patterns of gorillas is likely a result of a complex interplay of socioecological and life history factors. Our review of the literature supports the suggestion that explanations for variation in primate social organization should look beyond the role of ecology and include the life history patterns and reproductive strategies of both sexes.[21] Recent research has provided insight into how variation in ecological conditions may lead to variation in life history characteristics, including interbirth intervals and age of male maturation.[47,116,118,122] This study also lends support to the concept of variability selection, in which behavioral adaptations to environmental variability may reflect more generalist than specialist strategies that may result in some degree of mismatch between ecology and behavior in the short term, but lead to long term adaptive flexibility.[123,124]

Gorillas live in a wide range of ecological conditions (Table 2), so their dietary and behavioral patterns may reflect a more generalist strategy, enabling them to survive through climatic changes over many millions of years. Male gorillas may be generalists in their dispersal patterns (philopatry or dispersal), with the current environmental conditions for western gorillas resulting in exclusive male dispersal whereas those for mountain gorillas resulting in the mixed strategy of philopatry and dispersal.

Our summary supports Harcourt and Stewart's[22] review, which stresses how the social organization of gorillas is a result of competing interests of males and females. In sum, a multimale organization may result in benefits for females, alpha males, and subordinate males, with alpha males suffering few costs. The occurrence of one-male and multimale groups, largely due to variation in male dispersal patterns, may hinge primarily on variation in female dispersal patterns, as females seek to reside in a group of optimal size and with a good protector male. Such patterns are likely to vary depending on ecological conditions. Variation in gorilla grouping patterns may further exemplify how difficult it is to unify female and male strategies, as well as the relative influence of food resources, infanticide, and predators, into one socio-ecological model.[2,21,125] Other factors, including feedback loops and phylogenetic lag, may also be at play.

4.1 | Feedback loops and phylogenetic lag

Certain demographic parameters may be causing a positive feedback loop that leads to multimale groups in both mountain gorilla populations.[20,22,57] If female dispersal rates decline, there is an increased probability that sons will reach maturity with their mothers in the group, which may reduce the likelihood of male dispersal because males are less likely to emigrate when their mothers are present (Figure 3).[40] In other words, a reduction in female dispersal could lead to a decline in male emigration, because sons are less likely to emigrate if their mother has also stayed in the group. Female mountain gorillas have lower dispersal rates from multimale groups than from one-male groups, which may be due to lower risks of infanticide in multimale groups. Multimale groups also have a lower rate of disintegrating than one-male groups, which would favor their existence. The positive feedback loop may not lead to an exclusively multimale social organization, however, because a male's mother might die before his decision to migrate. Thus, no matter how philopatric the females are, there is a likelihood that some sons would leave. If so, then demographic stochasticity in female mortality may prevent the expression of "pure" strategies for male emigration, thereby maintaining a proportion of one-male groups in the population.

It is also possible that the current patterns of male dispersal reflect an evolutionary disequilibrium, with some male mountain gorillas emigrating voluntarily even though the current fitness consequences are unfavorable.[126] In support of this possibility, Lindenfors et al.[91] suggested that there is an evolutionary lag in the way that males respond to the distribution of females in primates. Male emigration is typically a once-in-a-lifetime decision for gorillas, and the consequences of the decision unfold gradually throughout the subsequent lifetime of a male (and beyond, through infanticide risks to his offspring). Many emigrants fare just as well as many philopatric males and there is notable variance for both strategies of philopatry and emigration. If a silverback cannot reliably assess the optimal strategy, then behavioral plasticity within each individual lifetime may be limited, and social queuing may evolve more slowly than other behaviors. Nonetheless, natural selection leads to near-fixation rather rapidly (e.g., <50 generations), even if the fitness differential is only a few percent, so any evolutionary disequilibrium could be a recent phenomenon. An evolutionary disequilibrium might be the latest cycle in a longer-term pattern of fluctuating selection, or it could represent the first time that the mountain gorillas are diverging from the one-male organization of western gorillas.

4.2 | Priorities for research

To further understand the factors maintaining the variable social organization in gorillas, future research should focus on how female dispersal patterns under differing ecological conditions influences male dispersal patterns. This could include research on within and between population levels of scramble and contest feeding

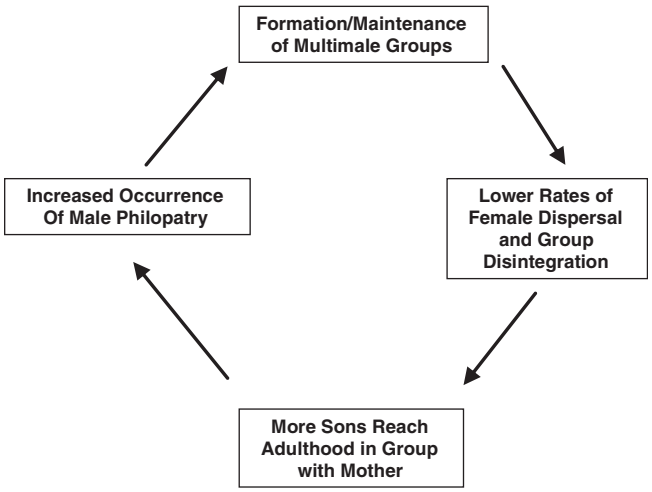

FIGURE 3 Feedback loop of demographic events that could lead to the maintenance of a multimale organization in mountain gorillas

BOX 2 GORILLA CONSERVATION

Currently all four subspecies of gorillas are classified as critically endangered.[180] On a broad scale, habitat loss, poaching, and disease are the major threats to gorillas everywhere, but the intensity of each threat is variable and location-specific. While the number of mountain gorillas remaining is exponentially smaller than western gorillas (<1,000 vs. >200,000), they have received exponentially more financial resources and conservation efforts per gorilla.[82,151,181,182]

The rapid decline of Grauer's gorillas in the past two decades, from roughly 18,000 to only 3,700 individuals, is of foremost concern.[165] Such a large decline has been due to civil war, leading to increased insecurity, artisanal mining, bushmeat hunting, and deforestation, and the inability of law enforcement to operate effectively.

In contrast to Grauer's gorillas, the number of mountain gorillas in the Virunga Massif has more than doubled in size from approximately 250 to just over 600 gorillas during the same time period, largely due to extreme conservation efforts including tourism, veterinary interventions on habituated gorillas, and intensive monitoring even during times of civil unrest.[82,151] Furthermore, people living near mountain gorillas do not eat them, which has likely prevented higher mortality due to hunting. Transmission of respiratory disease from humans to mountain gorillas is a main threat, particularly since as many as 50,000 tourists visit them annually.[183] Mountain gorillas' habitat is restricted to less than 1,000 km^2, which is unlikely to change given the surrounding areas have an extremely high density of subsistence farmers, stressing that conservation efforts must be maintained for these two populations.[85,86]

Western gorillas are much more abundant and occupy a larger range than eastern gorillas (approximately 656,000 km^2), but their numbers are expected to decline rapidly.[181,184] Ebola has decimated some populations of western gorillas and poses a large risk for a rapid decline of western gorillas.[174,185] While only a few hundred tourists view habituated western gorillas each year, the risk of disease transmission is still present.[186] On a larger scale, commercial logging, industrial agriculture, and resource extraction (petroleum and minerals) are increasing threats for western gorillas across the Congo Basin because they lead to habitat destruction and fragmentation that opens up areas further to poaching and risk of disease transmission.[181,187,188] Based on a modeling exercise of survey data from across Central Africa, 18 priority conservation landscapes were determined in 2014 that encompass approximately half of the range for western gorillas.[181]

Cross River gorillas live in an extremely fragmented habitat; approximately 300 gorillas are found in 14 subpopulations in an area of only 600 km^2 across a landscape of about 12,000 km^2.[178,179] Their distribution appears to be primarily limited by human disturbance, and to a lesser extent food availability.[179,189] Dispersal among these subpopulations may be limited by the distance between them, as well as the type and level of human activity occurring in those areas.[179] Modeling showed that conservation management strategies that focused on both law enforcement and behavior change of local human populations are needed to ensure future growth of this subspecies.[190]

Conservation efforts should focus on law enforcement, land-use planning, and engagement with the private sector.[181,187] Research, both long term studies and large scale surveys, makes a valuable contribution to conservation efforts by providing information on ecological needs and population dynamics of gorillas. Monitoring ape populations is crucial for understanding changes in population numbers and for measuring the effectiveness of conservation strategies; innovative methods such as camera traps and genetic analysis of noninvasively collected samples are being applied.[191] Support for protected areas and their staff in range countries as well as efforts outside of protected areas on local, national, and international levels are part of the enormous resources needed to conserve gorillas.

competition, which may put limits on group size. Such research could be done in conjunction with studies on how the lifetime reproductive success of males is influenced by dispersal patterns of males and females, routes to attaining alpha status, group transitions (group formations, disintegrations, and transitions between one-male and multimale organization via usurpation or inheritance), male lifespan, body size, and causes of mortality. Determining the fate of males that disperse to become solitary is challenging, because of the difficulties of following single individuals, but studies conducted at open clearings, such as Mbeli Bai as well as genetic tracking studies that cover several years provide a means for monitoring solitary individuals.[85,86,89,192] Genetic studies also enable us to examine group transitions, individual trajectories, and reproductive success of males on a larger spatial scale than what is typically possible with habituated groups. Modeling can also be a fruitful approach to understanding the relationships between life history characteristics and reproductive success in social species that have long life spans.[14,69] Needless to say, we can only study gorillas if healthy populations in a variety of habitats are properly protected (see Box 2).

4.3 | Gorillas and human evolution

Studying extant great apes can help us to understanding the origins of human societies. According to a phylogenetic reconstruction of Hominidae, gorillas are the least derived among the Hominidae, making them a useful model for reconstructing traits of our ancestors and understanding the origins of human societies.[24] Additionally, there is disagreement whether the socioecology and social organization of recent human ancestors were more a gorilla-like, chimpanzee-like, or neither.[23,127] Flexible male and female dispersal or philopatry are shared among gorillas and *Homo*,[128] suggesting that strict male philopatry and female dispersal in chimpanzees and bonobos are derived traits. Maternal support of sons may have promoted male philopatry in both *Pan* species, and to a lesser extent in early humans.[57] Plasticity

in life history strategies is observed in *Homo* and it may have played a role in the evolution of various unique human life history traits.[129] Similarly, there is flexibility in social organization and behavior in orangutans, chimpanzees, and bonobos.[130,131] Consequently, models examining the evolution of hominins would benefit from considering within and between species variation in ecology, life history, and dispersal patterns for all the extant apes.

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