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Chimpanzee Intercommunity Conflict: Fitness Outcomes, Power Imbalances, and Multilevel Selection

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1 Introduction

This chapter is the first of five comprising Part III. Though, as in Chap. 6, we have previously allowed some lexical analyses to interpolate Part II's historical-empirical thrust, Part III is predominately statistical-empirical, even as it continues to review relevant literature and history. Although, consistent with the mandate of this monograph, we aim ultimately to establish the reality of human group selection, this initial chapter alone treats the subject of intergroup conflict in chimpanzees. To thoroughgoing evolutionists, the relevance will be self-evident; we only add that establishing evidence of multilevel selection in such a highly related species foundationally supports the empirical argument for human multilevel selection, as presented in the four subsequent chapters constituting Part III of this volume (for behavioral differences between these taxa see Chap. 9 in this volume, as well as Glowacki, Wilson, & Wrangham, 2017).

Contrary to some theoretical perspectives claiming that lethal violence between groups is a phenomenon restricted to contemporary nation-states, current literature indicates that aggressive intergroup competition

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is quite common across nonhuman clades (Kitchen & Beehner, 2007). In the last four decades, researchers have reported several instances of intergroup killings in gray wolves, cheetahs, hyenas, spider monkeys, and lions (Wrangham, 1999). Presumably due to the implications for understanding the evolutionary origins of warfare, these reports have generated heated debates concerning the nature of lethal intergroup aggression in nonhuman species. This is especially the case for publications addressing the various socioecological correlates of lethal intercommunity interactions in common chimpanzees (*Pan troglodytes*).[1] Although comparative data indicate that between-group killings emerged as an evolutionary adaptation, little agreement exists regarding the potential benefits obtained by attackers (for example, territorial expansion, recruitment of females, and elimination of sexual competitors). Similarly, some researchers have hypothesized that the social organization of chimpanzee communities enables attackers to raid and eliminate rivals without facing onerous costs. Despite disagreements, explanatory models reliably neglect multilevel selection, describing chimpanzee intercommunity aggression as an adaptation in terms of traditional, individual selectionism. This restrictive theoretical assumption, however, has limited the possibility of examining the persistence of chimpanzee intergroup competition due to multilevel selective pressures. Hence, in addition to providing the reader with an overview on this subject, the present chapter offers empirical evidence of multilevel selection operating on the number of male chimpanzee patrols.

2 Chimpanzee Intercommunity Conflict from an Adaptationist Perspective

During the early 1970s, the Kasekela community at Gombe, Tanzania, underwent a demographic fission (Feldblum, Manfredi, Gilby, & Pusey, 2018). While the original group remained in the north, the newly formed community of Kahama, comprising six mature males, one adolescent male, and three females, occupied the southern valley (Goodall, 1986; Williams et al., 2008). Intercommunity tolerance was short-lived. In 1974, Kasekela initiated a series of attacks against Kahama, reducing the southern group from a range of 10 km^2 to 1.8 km^2 (Goodall, 1986).

During this time, Kahama also suffered from the incursions of Kalande, another chimpanzee community in the south (Goodall, 1986). Three years after the first attack of Kasekela, Kahama finally collapsed. Kasekela immediately seized the abandoned regions, expanding its range to 17 km^2. Though this could have been the beginning of a period of further territorial expansion for Kasekela, this trend eventually reversed its course. Kahama served as a buffer between Kasekela and the southern communities (Goodall, 1986). Even though the identity of the aggressors is not known (perhaps chimpanzees from the Kalande community), Kasekela became the target of several attacks leading to multiple casualties (Goodall, 1986). The southern conflict led to a considerable reduction in Kasekela's territory, decreasing it to 9.6 km^2 in 1981 (Goodall, 1986). Kasekela and Kahama's territorial fluctuations evidenced the impact of intercommunity conflict on population stability. Detailed examinations of Kasekela's mortality patterns across forty-seven years concluded that out of eighty-six deaths with known causes, seventeen were the product of intraspecific aggression, with eight of these resulting from lethal intergroup interactions (Williams et al., 2008; Wilson, 2013). Moreover, half of the twelve Kahama and Kasekela males (aged between twenty and thirty) who died during the observation period were known or suspected to have been killed during intercommunity attacks (Williams et al., 2008). Albeit it is presumed that some of the females who disappeared during this time could have also been the target of foreign chimpanzees raiding the territory, only two such attacks were directly observed (Williams et al., 2008).[2]

Although intergroup killings were thought at first to be exclusive of the chimpanzees at Gombe, independent observations conducted at Kibale National Park, Uganda (Watts et al., 2006), provided yet another detailed account of intercommunity aggression and territorial expansion. Between the years of 1999 and 2008, chimpanzees at the Ngogo community eliminated eighteen foreign rivals (Mitani, Watts, & Amsler, 2010). Most of these attacks (n = 13) occurred during patrols close to the northeastern border of the Ngogo community. Even though Mitani et al. (2010) did not have an exact count of the number of individuals in the Northeastern community, assuming the targeted group was equivalent in size to other chimpanzee unit-groups (e.g., 47 individuals), the Northeastern faction experienced a death rate of 2790 per 100,000 per year, according to their calculations. Presuming Ngogo and Northeastern communities had similar group sizes (~150 chimpanzees), this number still implies a rate of 867 per 100,000 per year, an estimate that exceeds the killing rate experienced by some small-scale human societies (Mitani et al., 2010). Echoing Gombe's intergroup killings, the confrontations at Ngogo also generated significant territorial changes. By 2009, Ngogo chimpanzees acquired 6.4 km^2 from their Northeastern rivals, representing a 22% territorial expansion.[3]

In contrast to Ngogo, another community at Kibale, Kanyawara, underwent a 46.8% range contraction, falling from 29.5 km^2 to 13.8 km^2 in 8 years (Wilson, Kahlenberg, Wells, & Wrangham, 2012). Except for the suspected death of three adult males[4] (Wilson et al., 2014; Wrangham, Wilson, & Muller, 2006), over 80% of the 120 intercommunity contacts between 1992 and 2006 were limited to acoustic displays (Wilson et al., 2014). These events often occurred at the borders of Kanyawara's territory, within a range of 288 to 4406 meters away from the community's center (Wilson et al., 2012). Despite the low death rate, the threat of between-group conflict eventually forced Kanyawara chimpanzees to avoid regions where they tended to encounter the opposing parties (Wilson & Glowacki, 2017).

Within the fields of primatology and physical anthropology, reports of lethal aggression in chimpanzees, such as the cases of Kahama, Kasekela, Ngogo, and Kanyawara, generated an array of responses ranging from scientific curiosity to skepticism (Power, 1991; Sussman, 2013). Although their arguments varied, the views of skeptics can be classed under the general umbrella of *human impact hypotheses* (HIH), an array of perspectives denying the adaptive function of lethal aggression, and instead explaining these killings as a product of human activities, such as food provisioning or habitat degradation. According to Wilson et al. (2014), the premises of HIH can be summarized by the following predictions:

1. The killing rates should not significantly differ between chimpanzees and bonobos, with the severity of ecological impact superseding any cladistic effect.
2. Due to the increasing rate of environmental disturbance over time, killings should also exhibit a positive temporal trend.

3. There should be no significant difference in the frequency of lethal attacks perpetrated by males or females.
4. Both males and females should be equally represented as the victims of the attacks.
5. There should be no noticeable difference regarding the age of the victims.
6. Genetic relatedness between the attackers and the victims should not have any influence on the rate of killings.
7. There should be no numerical asymmetries between the attackers and the victims during the attack.

Other researchers, remaining unconvinced that chimpanzee intercommunity aggression was the product of human disturbance, suggested that this behavior instead evolved as an adaptation to natural conditions. Following Wilson et al. (2014), the predictions of the *adaptive strategies hypotheses* (ASH) can be summarized as follows:

1. Chimpanzees should display higher killing rates relative to bonobos.
2. Even if human ecological encroachment increases over time, killing rates should not be affected by these temporal changes.
3. Males should be the perpetrators of the attacks more often than females.
4. Males should be the victims of attacks more often than females.
5. Relative to adults, younglings are predicted to be at higher risk of being killed.
6. Attackers are expected to preferentially kill individuals more distantly related to them, such as members of other communities.
7. Perpetrators are expected to outnumber the victims during attacks.

Despite the preponderance of evidence tending to disconfirm the HIH, researchers supporting this alternative hypothesis remained unconvinced. Due to persistence of the HIH in the literature, Wilson et al. (2014) collected data on intergroup killings from eighteen chimpanzee and four bonobo communities from various online databases and publications.[5] Their study also gathered information on the dimensions of the protected area, the presence of ecological disturbance, the number of adult males in the community, the number of animals per km^2 (not associated with human environmental disturbance), the location of the community in Eastern or Western Africa, and whether or not the researchers artificially provisioned the apes. The authors reported 152 killings, including inferred and suspected fatal attacks, in 15 of the 18 chimpanzee communities. Model comparisons determined that those including community density and number of males as predictors best fitted the data. More detailed examinations concluded that even though females occasionally killed other individuals, males were more often the perpetrators of lethal attacks. Similarly, a generalized linear mixed model estimated that infants and adult males had a higher probability of being victims of these attacks. With respect to intercommunity conflict, over 60% of the 99 victims were killed by members of a different community, suggesting an inclination toward targeting either unrelated or distantly related individuals. Hence, the data favors ASH over HIH across a variety of sites.

3 Intercommunity Conflict and Individual Fitness Outcomes

Even though cross-regional examinations indicate that intercommunity killings are not a product of anthropogenic factors, there is little agreement among researchers endorsing ASH on the fitness benefits attained from intercommunity incursions. According to Wilson (2013), some of the hypothesized benefits include restricting foreign males from copulating with resident females, accessing feeding grounds, defending themselves or others from an attack, and encouraging the migration of foreign females into the community. Evaluating the *female acquisition hypothesis*, lethal and nonlethal intercommunity aggression seems to encourage females to abandon their group and migrate into the attacker's community. The case of the K-group community at Mahale Mountains in Tanzania offers compelling evidence. In seventeen years, the K-group community went from being demographically stable to experiencing the systematic disappearance of its males (Nishida, Hiraiwa-Hasegawa, Hasegawa, & Takahata, 1985). This demographic change encouraged all cycling females to associate with males from a rival community (M-group; Nishida et al., 1985). Eventually, at least by 1983, the K-group was reduced to three females and one adolescent male. Although M-group males were not observed killing K-group males (Mitani et al, 2010; Nishida et al., 1985), demographic estimations for the 1966–1999 period indicate that 3.8% of the total number of deaths could have been the product of intergroup conflict (Nishida et al., 2003; Wilson, 2013). In addition to offering a unique glimpse into female dispersal patterns after male disappearance, K-group's fate provides evidence of community extinction occurring without the complete elimination of the chimpanzee population (Nishida et al., 1985). Besides the latter case, support for the female recruitment hypotheses emerges from the observed differential treatment of foreign females. Researchers have reported that females exhibiting signs of sexual receptivity, such as anogenital swellings, are less vulnerable to intergroup aggression (Nishida et al., 1985; Williams, Oehlert, Carlis, & Pusey, 2004). In contrast, non-swollen females were more likely to suffer from intercommunity attacks.[6] Furthermore, individual differences, such as the female's age as well as her offspring number, increased the risk of experiencing an aggressive encounter (Williams et al., 2004). It is worth noting that socioecological factors could mediate these dynamics. For instance, mathematical modeling has predicted that males inhabiting groups with low reproductive skew should be more inclined to attack foreign females (Pradhan, Pandit, & Van Schaik, 2014).

Communities could also benefit from territorial expansion by accessing coveted feeding grounds (Wilson, 2013). Resource acquisition could impact the life history of females and the group's social dynamics. Researchers at Gombe analyzed data collected over eighteen years of observation to determine the association between community range size and several demographic indicators (Williams et al., 2004). Although community range size did not have any influence on the total number of adult males nor on the number of adult females (for a more recent take on the association between territory size, group size, and number of males, see Lemoine et al., 2020a; likewise, see Lemoine et al., 2020b, for a study on the variation in female reproductive success due to between-group differences in number of males), it did predict the time that males interacted in mixed-sex parties, as well as the size of mixed-sex groups (Williams et al., 2004). Furthermore, these analyses concluded that a larger home range decreased the females' interbirth intervals (Williams et al., 2004). A more recent perspective, the *group augmentation hypothesis*, also argued in favor of indirect as well as direct benefits obtained by individuals. According to Langergraber, Watts, Vigilant, and Mitani (2017), males could be more inclined to patrol, depending on the influence of several sociodemographic factors. Although no immediate benefits are obtained if group size increases, such augmentation could provide a positive effect on the males' future reproduction (Langergraber et al., 2017). Relying on a generalized linear mixed model, the authors examined the effects of paternity success, dominance rank, age, maternal relatedness, and male group size, on the total number of male patrols. The model detected that only paternity success and the males' rank positively predicted patrol participation (Langergraber et al., 2017). In terms of long-term reproductive success, Langergraber et al. (2017) identified that most males who did not have any offspring when they joined patrol parties would eventually sire offspring. These results further support the hypothesis that males could obtain delayed fitness benefits by providing immediate service to the community.

4 Intergroup Killings and Power Imbalances in Chimpanzees

Concentrating exclusively on the benefits of intercommunity killings provides a partial perspective of the adaptive nature associated with this behavior. Some authors have argued that the accrued toll associated with attacking another group will also influence the prevalence of this behavioral phenotype. According to the imbalance of power hypothesis, raiding a rival community imposes several costs to attackers, including those entailed from spending time and energy patrolling the territory to the risk of suffering injury and death during the incursion (Manson & Wrangham, 1991; Wilson, 2013; Wrangham, 1999). Raiding parties, however, decrease exposure to lesions and death by targeting individuals who are either foraging or traveling alone (Manson & Wrangham, 1991; Pandit et al., 2016; Wilson, 2013). Furthermore, animal species living in societies governed by fission-fusion dynamics are expected to be vulnerable to lethal intergroup conflict (Wrangham, 1999). The outcome of the raid depends on the numerical asymmetry between the number of attackers and the number of defenders (Wilson, 2013; Wilson et al., 2014). The hypothesis, however, does not imply that a numerical asymmetry will decrease the cost to zero, as raiders will still spend a portion of their bioenergetic budget reaching the target (Amsler, 2010; Wilson, 2013); instead, it offers a framework for studying the likelihood that the raiding party will physically engage a target once they encounter it.

Empirical evidence agrees with the imbalance of power hypothesis. A field experiment conducted with three chimpanzee communities in the Taï National Park in Cote d'Ivoire detected significant variation in vocal and locomotor behavior in response to a recording simulating the presence of a nearby chimpanzee (Herbinger, Papworth, Boesch, & Zuberbühler, 2009). Researchers played three simulated *pant-hoots*, the first recorded from one of the males in the focal community; a second recorded in a neighboring community; and a third recorded in a community 70 km away. Focal chimpanzees in the *member* condition had a higher frequency of pant-hoot vocalization relative to both the *neighbor* and the *stranger* conditions. Herbinger et al. (2009) determined that the number of males present influenced the likelihood of responding to the recordings. The chimpanzees' reactions extended to other behavioral dimensions; for instance, patrolling increased during the playback of strangers and neighbors (Herbinger et al., 2009).

In a similar experiment at Kanyawara, the probability of vocalizing in response to a recording increased with the number of males in the party (Wilson, Hauser, & Wrangham, 2001). The number of males present also increased the probability of approaching the speaker. No significant relation existed between the male's agonistic rank and the mean approach rank to the speaker. Although further examinations should consider the role of individual differences in counter-calling and patrolling, current evidence indicates that both high-ranking and low-ranking males are more likely to respond to the presence of a foreign rival depending on the number of males in the party (Wilson et al., 2001). Inspired by Lanchester's theory of conflict (1916),[7] researchers examined the relevance of chimpanzee numerical assessment during intercommunity conflict (Wilson et al., 2002). By adding the data collected during the playback experiments into derived equations, these researchers estimated that a party of adult male chimpanzees (A) would engage a rival group (B) if A is 1.5 times larger than B (Wilson et al., 2002).

Observational data at Kanyawara provides further evidence. Several logistic regression models analyzed the effect of the number of adult males, the number of females in estrus, number of infants, the distance from the range center, and the food value of the disputed resource (as indicated by the proportion of forage time spent in the location where the encounter occurred) on the probability of counter-calling, as well as on the probability of approaching rivals (Wilson et al., 2012). Male chimpanzees at Kanyawara were more likely to vocalize toward foreign rivals, depending on the number of adult males in the group (Wilson et al., 2012). Model-averaged parameter estimates identified that the number of males present had a significant positive effect on the probability of approaching foreign rivals. The number of infants in the group did not have a significant effect. Neither the distance from the center nor the food value had any significant effect on the probability of approaching the intruders. The local conditions of the encounter area also seemed to be unrelated to engaging rivals. Instead, the numerical asymmetry has a significant influence on the direction and escalation of the conflict. Moreover, the number of estrous females had a negative effect on engaging rivals. According to Wilson et al. (2012), adult males face a trade-off: either defend the range or mate-guard females with sexual swellings. Mate guarding not only reduces the likelihood that the female will copulate with males from the neighboring groups, but also limits the risk of copulations between the female and interloping males from her own group (Wilson et al., 2012). This pattern, however, does not generalize across chimpanzee communities. Mitani and Watts (2005) scrutinized the influence of various socioecological indicators on patrolling through a series of logistic regressions. The analyses included the size of the male party, the presence of estrous females, the availability of fruit, reports of chimpanzee hunting behavior during the patrol, and if they made vocal or visual contact with competing factions. While male party size and fruit availability positively predicted male patrols, the presence of estrous females did not have a significant effect.

5 Chimpanzee Intercommunity Conflict and Multilevel Selection

Before we proceed with our examination of multilevel selection in chimpanzee intercommunity conflict, it is essential to provide the reader with a review of key concepts and methodologies associated with multilevel selection theory (MLS), only alluded to previously. Damuth and Heisler (1988) distinguished between two types of multilevel selection: MLS1 and MLS2. According to these authors, MLS1 can be said to occur when:

1. Group selection is operationalized as the effects of group membership on individual-level fitness;
2. Fitness is defined as limited to individuals;
3. Characters or traits are defined as restricted to individuals;
4. Populations are comprised of individuals, and are classified into groups;
5. Explicit evolutionary inferences are limited to the observed variations in frequency among different types of individuals in the population.

Alternatively, MLS2 is characterized by:

1. Group selection is operationalized as the variations in frequency among different types of groups;
2. Groups exhibit differential fitness;
3. Groups feature variations in characters or traits;
4. Populations contain groups, which in turn are comprised of individuals;
5. Explicit evolutionary inferences referring to changes in the frequencies of different types of groups within a population.

More recently, authors such as Okasha (2006) further explored the distinction between MLS1 and MLS2 by reconsidering how fitness is defined. For Okasha, the group's fitness is calculated in MLS1 as the average individual fitness across all individuals within the group. Alternatively, MLS2 operationalizes the collective's fitness as the number of offspring *groups* sired by each group. Even though, at first glance, the MLS1/MLS2 distinction seems to mirror the difference between aggregate and emergent properties, this is not always the case. In MLS1, for example, it is feasible that in addition to a group's *aggregate trait*, which is computed as an average based on the individual-level data, a group's *emergent property*, which denotes a trait that is irreducible to individual characteristics, could significantly predict the individuals' fitness (Okasha, 2006). Similarly, according to Okasha (2006), MLS2 is not limited to the covariation between emergent group-level traits and the number of offspring groups. Aggregate traits may also have a significant effect on the probability of group reproduction.

Distinguishing between types of MLS is just the first step before conducting an examination based on MLS theory. To explore MLS hypotheses, it is necessary to employ an analytic procedure design to detect both individual- and group-level effects. Developed in 1987 by Heisler and Damuth, *contextual analysis* emerged as an extension of regression models wherein individual- and group-level traits are viewed as predictors of individual-level outcomes. Group traits, also known as contextual characters, may differ depending on the estimation procedure. While an aggregate character is often calculated from the individual data (e.g., as an average), a global character refers to a unique property of the collective irreducible to the characteristics of individuals within the group. Hence, according to these authors, MLS1 assumes that selection operates not only upon the individual but also on contextual characters. Contextual analysis is best represented by the following regression equation (Eq. 8.1):

$$w_{ij} - w_{..} = \beta_I \left(z_{ij} - z_{..}\right) + \beta_C \left(z_{i.} - z_{..}\right) + \varepsilon_{ij} \tag{8.1}$$

where w_{ij} is the individual level of fitness, $w_{..}$ is the average fitness across all individuals, z_{ij} corresponds to the individual-level trait, $z_{..}$ is the average trait value across all individuals, z_i is the average trait value for each group, and ε_{ij} is the equation's error term. Hence, β_I is the partial regression coefficient between the individual-level trait and the individual-level fitness, after controlling for the average phenotype at the level of the group. Alternatively, β_C is the partial regression coefficient between the mean phenotype at the level of the group and the individual-level fitness, after controlling for individual-level effects. Heisler and Damuth argued that any evidence of group selection requires β_C to be significantly different from zero. The flexibility of contextual analyses allows the inclusion of multiple predictors into the equation. For example, a model with two traits z_1 and z_2 generates the following equation (Eq. 8.2):

$$\begin{aligned} w_{ij} - w.. = \beta_{I1}\left(z_{1ij} - z_1..\right) + \beta_{I2}\left(z_{2ij} - z_2..\right) \\ + \beta_{C1}\left(z_{1i.} - z_1..\right) + \beta_{C2}\left(z_{2i.} - z_2..\right) + \varepsilon_{ij} \end{aligned} \tag{8.2}$$

It is worth noting, however, that analogous to other statistical procedures employed to examine multilevel selection, contextual analyses operate under a set of specifiable conditions. Okasha (2004) summarizes these elements as follows:

1. Group selection does not require fitness variation between groups, meaning that *soft selection* can occur as long as β_C is nonzero;
2. Group selection depends on global trait variation between groups;
3. Group selection does not rely on the nonrandom formation of groups;
4. Group selection does not require individual fitness to be group-dependent;
5. Individual-level selection depends on within-group fitness variation.

Critics have argued that the lack of group reproductive isolation and the occurrence of migration between groups violate the conditions that are presumably necessary for group selection to occur (Wrangham & Glowacki, 2012). Though this assumption was indeed one of the tenets of naïve group selection theory, researchers favoring a more contemporary multilevel selection view of evolution argue that the *trait-group* rather than the *deme* is the operative level of group selection, such that demographic isolation is no longer considered a necessity for group selection to operate (Sober & Wilson, 1998). Similarly, MLS1 describes fitness as a feature of individuals rather than groups (Okasha, 2006). Moreover, even when fitness is estimated at the level of the group, it is equal to the average fitness of all individuals within that collective. The distinction between MSL1 and MLS2 has not only theoretical but methodological implications. For example, the multilevel selection hypotheses generated for this chapter were developed under the premise that chimpanzee groups provide a context for individuals to replicate their genes (MLS1). Having provided this theoretical and methodological overview, we can proceed to describe the contextual analyses conducted on male chimpanzee patrolling behavior. For an illustration in this chapter, we used Langergraber et al.'s (2017, 2018) Ngogo database of chimpanzee territorial behavior to assess whether the aggregate frequency of patrolling in male chimpanzees predicted the observed variation in the reproductive success of male chimpanzees (providing evidence of MLS1). This online resource contains data on the participation of males above 13 years of age across 284 patrols observed between the years of 1996 and 2015. The dataset also includes information on (1) the male's age (estimate computed as a quadratic term); (2) his dominance rank, calculated from the outcome of agonistic interactions; (3) his maternal relatedness, estimated from the number of genetic relatives alive at the time of the patrol; and (4) his paternity success, computed as the sum of the male's genetic relatedness to his offspring that were alive at the time of the patrol.[8]

Prior to conducting the analyses, the participation dataset was reshaped into a transposed matrix[9] with males as columns and patrols as rows.[10] In turn, this array was transformed into a polychoric correlation matrix to be subsequently examined with a principal axis factor analysis. The factor analysis identified thirteen main factors. Horn's parallel analysis supported this number of dimensions. After classifying each male chimpanzee into one of these groups, we proceeded to compute the various variance component terms defined in (Eq. 8.1) (see Table 8.1 for a list of the equations estimated along with the corresponding description).

A general linear model (using Type II sums of squares) revealed that the aggregate number of male participations in patrols ($Patrols_C$) significantly predicted the individual relative fitness ($\beta = 0.456$, $p = 0.012$). In contrast, the number of patrols conducted by each individual ($Patrols_I$) had no significant effect on the individual relative fitness ($Relative\ w_I$; $\beta = 0.176$, $p = 0.318$). The overall model explained 36% of the variance ($p < 0.000$). A Linear Mixed Model (LMM) with REML, variance components, and Group as a random factor reached similar conclusions ($Patrols_I$: $\beta = 0.176$, $p = .306$; $Patrols_C$: $\beta = 0.447$, $p = 0.018$). A model comparison recommended the inclusion of both individual and

Table 8.1 Glossary of variables names and equations employed in these analyses

Term	Equation	Description
Relative w_I	*Z(wij-w..)*	Standardized *individual's* relative fitness
$\mathit{Patrols}_I$	*Z(zijpatrols-z..patrols)*	Standardized number of patrols at the *individual* level[a]
$\mathit{RPatrols}_I$	*Z(zijRpatrols-z..Rpatrols)*	Standardized number of patrols at the *individual* level[a] relative to the total number of opportunities
$\mathit{Age}^2{}_I$	$\mathit{Z(zijAge^2\text{-}z..Age^2)}$	Standardized quadratic transformation of age at the *individual* level[a]
$\mathit{Dominance}_I$	*Z(zijav_rank -z..av_rank)*	Standardized dominance rank at the *individual* level[a]
Maternal r_I	*Z(zijMtrnl_Rlt -z..Mtrnl_Rlt)*	Standardized value for the males' coefficient of maternal relatedness at the *individual* level[a]
$\mathit{Patrols}_C$	*Z(zi patrols -z..patrols)*	Standardized number of patrols at the *aggregate* level[b]
$\mathit{RPatrols}_C$	*Z(zi Rpatrols -z..Rpatrols)*	Standardized number of patrols at the *aggregate* level[b] relative to the total number of opportunities
$\mathit{Age}^2{}_C$	$\mathit{Z(ziAge^2\text{- }z..Age^2)}$	Standardized quadratic age at the *aggregate* level[b]
$\mathit{Dominance}_C$	*Z(ziav_rank -z..av_rank)*	Standardized dominance rank at the *aggregate* level[b]
Maternal r_C	*Z(ziMtrnl_Rlt -z..Mtrnl_Rlt)*	Standardized coefficient of maternal relatedness at the *aggregate* level[b]

[a] The *individual* level is defined as the difference between the individual score and the grand mean of each trait, as in a general linear model

[b] The *aggregate* level is defined as the difference between group mean and the grand mean of each trait, as in a general linear model

contextual information, (Only $Patrols_I$: $\Delta\ BIC = 4.140$, $weight = 0.112$; $Patrols_I$ and $Patrols_C$: $\Delta\ BIC = 0.000$, $weight = 0.888$). It was pertinent to further explore the latter results based on males' relative patrol participation ($RPatrols_I$), which are the number of times a male joined a patrol party divided by the total number of patrol opportunities available. The results remained unaltered. The aggregate estimate of relative patrolling ($RPatrols_C$) significantly predicted the individual-level relative fitness ($Relative\ w_I$; $\beta = 0.582$, $p = 0.004$). In contrast, the relative individual-level values of patrolling ($RPatrols_I$) had no significant effect on the relative fitness ($Relative\ w_I$; $\beta = -0.056$, $p = 0.769$). The overall model accounted for 29% of the variance ($p = 0.000$). The LMM detected the same pattern ($RPatrols_I$: $\beta = -0.056$, $p = 0.755$; $RPatrols_C$: $\beta = 0.570$, $p = 0.007$). Fit comparison favored the full model (Only $RPatrols_I$: $\Delta\ BIC = 5.987$; $weight = 0.048$, $RPatrols_I$ and $RPatrols_C$: $\Delta\ BIC = 0.000$, $weight = 0.952$). To determine whether these results were a statistical artifact of the method, the same procedure was employed to examine the association between the individual ($Dominance_I$) and the aggregate ($Dominance_C$) values for the male's dominance rank. In contrast to the results of the previous analyses, the individual level of dominance rank significantly predicted the individual-level relative fitness ($Relative\ w_I$; $\beta = 0.716$, $p = 0.000$), whereas the aggregate value of male dominance ($Dominance_C$) did not have any significant effect ($Relative\ w_I$; $\beta = 0.033$, $p = 0.853$). The model explained 55% of the variance ($p < 0.000$). Multicollinearity diagnostics were computed for each GLM ($Patrols_I$ and $Patrols_C$: $VIF = 2.327$; Condition Index for min Eigenvalue = 2.677; Variance proportion = 0.88; $RPatrols_I$ and $RPatrols_C$: $VIF = 2.511$; Condition Index for min Eigenvalue = 2.814; Variance proportion = 0.89; $Dominance_I$ and $Dominance_C$: $VIF = 3.411$; Condition Index for min Eigenvalue = 3.399; Variance proportion = 0.92).

A sequential canonical analysis (SEQCA), the results of which are displayed in Table 8.2, examined a cascade model of the association between age,[11] dominance rank, maternal relatedness, and the number of patrols at both the *individual* and *aggregate* levels. The model accounted for 72% of the variance ($p = 0.0001$). $Patrols_C$ was positively and significantly predicted by Age^2_I and $Dominance_I$; similarly, Age^2_C and $Dominance_C$ positively predicted the *aggregate*-level number of patrols. In the next step of the cascade,

Table 8.2 Sequential Canonical Analysis of individual level number of patrols ($Patrols_I$), aggregate level number of patrols ($Patrols_C$), and individual level relative fitness ($Relative\ w_I$)

Variables	Effect size	C.I. (LB)	C.I. (UB)	*F*-ratio	df1/df2	*p-value*
Overall ($V = 1.553$)	$E = 0.72$	0.00	1.00	8.05	18/135	<0.0001
Y variable: $Patrols_C$						
Age^2_I	$sR = 0.60$	0.38	0.75	87.51	1/45	<0.0001
$Dominance_I$	$sR = 0.47$	0.22	0.67	55.07	1/45	<0.0001
$Maternal\ r_I$	$sR = -0.14$	−0.41	0.14	5.08	1/45	0.03
Age^2_C	$sR = 0.37$	0.10	0.59	33.88	1/45	<0.0001
$Dominance_C$	$sR = 0.28$	0.00	0.52	18.85	1/45	<0.0001
$Maternal\ r_C$	$sR = 0.01$	−0.27	0.29	0.04	1/45	0.84
Multiple	$R = 0.90$	0.81	1.00	33.40	6/45	<0.0001
Residual: Mean = 0.00; SD = 0.43; Skew/Kurtosis = 0.40/−1.31; Range = −0.65–0.65						
Y variable: $Patrols_I$						
Prior Y variables						
$Patrols_C$	$sR = 0.76$	0.60	0.85	167.22	1/44	<0.0001
X variables						
Age^2_I	$sR = 0.03$	−0.25	0.31	0.30	1/44	0.58
$Dominance_I$	$sR = 0.33$	0.06	0.56	32.42	1/44	<0.0001
$Maternal\ r_I$	$sR = 0.25$	−0.03	0.50	18.40	1/44	0.00
Age^2_C	$sR = -0.18$	−0.44	0.10	9.58	1/44	0.00
$Dominance_C$	$sR = -0.26$	−0.51	0.02	20.23	1/44	<0.0001
$Maternal\ r_C$	$sR = -0.06$	−0.34	0.22	1.10	1/44	0.30
Multiple (Xs only)	$R = 0.53$	0.46	0.60	13.67	6/44	<0.0001
Residual: Mean = 0.00; SD = 0.64; Skew/Kurtosis = 0.73/0.34; Range = −1.38–1.50						
Y variable: $Relative\ w_I$						
Prior Y variables						
$Patrols_I$	$sR = 0.52$	0.28	0.70	63.42	1/43	<0.0001
$Patrols_C$	$sR = 0.30$	0.02	0.53	20.94	1/43	<0.0001
X variables						
Age^2_I	$sR = 0.56$	0.33	0.73	73.03	1/43	<0.0001
$Dominance_I$	$sR = -0.10$	−0.37	0.18	2.55	1/43	0.12
$Maternal\ r_I$	$sR = 0.03$	−0.25	0.31	0.25	1/43	0.62
Age^2_C	$sR = -0.29$	−0.53	−0.01	20.25	1/43	<0.0001
$Dominance_C$	$sR = -0.18$	−0.44	0.10	7.66	1/43	0.01
$Maternal\ r_C$	$sR = 0.12$	−0.17	0.38	3.19	1/43	0.08
Multiple (Xs only)	$R = 0.68$	0.60	0.78	17.82	6/43	<0.0001
Residual Mean = 0.00; SD = 0.54; Skew/Kurtosis = 0.47/0.83; Range = −1.20–1.52						

Notes: $N = 52$. As measures of effect size, the symbol *sR* represents the semi-partial correlation coefficient (statistically controlled for all prior “X” predictor and “Y” criterion variables) and upper-case *R* represents the combined multiple correlation for all predictor (“X”) variables within each equation, while *E* is the multivariate eta (η) or “trace” correlation. For the 90% confidence intervals (C.I.), *LB* lower bound, *UB* upper bound

$Patrols_C$ positively and significantly predicted $Patrols_I$. $Dominance_I$ and $Maternal\ r_I$ also positively predicted the *individual*-level number of patrols. Moreover, $Age^2{}_C$ and $Dominance_C$ were negatively associated with $Patrols_I$. Finally, in the last step of the cascade, $Patrols_I$ and $Patrols_C$ positively predicted the individual-level relative fitness; $Age^2{}_I$ and $Age^2{}_C$ also significantly predicted the relative w_I, featuring a positive and negative effect respectively.

6 Conclusions

Evidence collected by Jane Goodall convinced primatologists and evolutionists that neither Westernization nor Modernization could capably explain lethal intergroup conflict. Thereafter, data gathered from multiple African sites now suggests that lethal intergroup conflict in chimpanzees is a natural adaptation. Some unyielding critics continued investing in, and insisting on, anthropogenic explanations. Most primatologists and evolutionists, now satisfied with the adaptive function of lethal intergroup conflict, instead debated whether its direct and indirect fitness benefits were derived from the recruitment of females from targeted communities, territorial expansion, the elimination of sexual rivals, or shortened interbirth intervals.[12] Multilevel selection theory provides an overarching framework within which to consider lethal intergroup competition's potential adaptive advantages. Some researchers remained skeptical, preferring simpler explanations, such as selfish gene theory over multilevel selection theory. Overemphasizing the principle of parsimony in relation to that of explanatory power, however, ignores the basic scientific principle that the rejection of a hypothesis should not be conducted prior to its empirical examination.[13] From this present exploration, we gain evidence for multilevel selection theory. The contextual analysis and subsequent statistical tests (GLMs and SEQCA) supported the claim that in addition to individual-level attributes, aggregate-level traits have significant effects on the relative fitness of individuals. The results of this chapter complement, rather than contradict, the information collected in the last four decades on chimpanzee intercommunity competition. As per the results of the SEQCA, both at the individual and aggregate levels, the number of patrols independently predicted the individuals' relative fitness. These data offer foundational evidence that multilevel selection is operative in a closely related animal model, allowing us to better contextualize human lethal intergroup competition within multilevel selection theory in the next chapter.

Notes

1. Chimpanzees inhabit multimale-multifemale communities characterized for their fission-fusion dynamics, within which individuals decrease the intensity of intragroup competition by foraging or exploring in subgroups (Aureli et al., 2008; Lehmann & Boesch, 2004; Lehmann, Korstjens, & Dunbar, 2007). Chimpanzees are polygynandrous, with males and females copulating with multiple individuals (Van Schaik, 2016). Although male reproductive skewness has been reported, males also employ an array of alternative mating tactics such as sperm competition (Dixson, 2012; Muller & Pilbeam, 2017) and collective mate guarding (Watts, 1998). In contrast to other primates living in polygynous societies, where a single male has a reproductive monopoly, chimpanzees display an attenuation in their sexual dimorphism (e.g., in canine size; Plavcan, 2001, 2012; Plavcan, Van Schaik, & Kappeler, 1995). Chimpanzees exhibit sex-biased dispersal, with females abandoning their natal group after reaching sexual maturity (Langergraber, Mitani, & Vigilant, 2009; Mitani, Watts, & Muller, 2002; Pusey, 1980). Male philopatry has considerable social *sequelae* such as the development of intracommunity coalitions and alliances (Chapais, 2009; Gilby et al., 2013; Wilson & Glowacki, 2017).
2. While Madame Bee fell during a Kasekela attack to Kahama in 1975 (Goodall, 1986; Williams et al., 2008; Wilson et al., 2014), Patti died during a conflict between the Mitumba and Kasekela in 2005 (Williams et al., 2008; Wilson et al., 2014).
3. The annexation of this area generated several behavioral changes. For example, Ngogo chimpanzees spent over 30% of the observation time foraging and socializing in the captured region, a pattern that lasted for at least five months (Mitani et al., 2010).
4. Julian, Badfoot, and Light Brown, in 1991, 1998, and 2001

5. A similar approach was adopted in previous publications. For example, Wrangham et al. (2006) generated a comprehensive cross-site database describing instances of intracommunity and intercommunity lethal aggression from five sites and nine communities. Following traditional epidemiological procedures, the authors estimated the sites had a median mortality rate of 69 per 100,000 per year, based on observed and inferred cases, and 287 per 100,000 per year, including suspected cases (Wrangham et al., 2006). Communities also exhibited noticeable differences in killing rates. Even though the total rate across communities ranged from 125 to 306 per 100,000 per year, some communities experienced higher rates than others (Wrangham et al., 2006). Kahama, for example, reached a value of 12,000 per 100,000 per year, while Sonso did not experience any attack (Wrangham et al., 2006). Across communities, adult and adolescent males were often the victims of these attacks, with a rate of 355 per 100,000 per year, followed by infants and juveniles with 92, and adult and adolescent females with 28. This value stands in contrast to the frequency of intracommunity lethal aggression, with infants and juveniles displaying a median rate of 429 per 100,000 per year, as compared to adult and adolescent males with 254 per 100,000 per year (Wrangham et al., 2006).
6. Though this pattern generalizes to other chimpanzee communities, regional differences exist between Eastern and Western communities. In contrast to chimpanzees from Gombe, female chimpanzees at the Taï National Park experience less severe, life-threatening attacks (Boesch et al., 2008). Moreover, the frequency of sexual interactions between neighboring communities at Taï is five times greater than that of Eastern communities (Boesch et al., 2008). These behavioral differences could be attributed to socioecological variations. Taï chimpanzees forage in larger parties and exhibit more social cohesion (Boesch, 1991; Boesch et al., 2008). Higher levels of gregariousness allow vulnerable individuals to be rescued by nearby supporters during intercommunity encounters, a phenomenon uncommon in Eastern communities (Boesch et al., 2008). Taï's larger group size could also be attributed to higher predation rates (Boesch, 1991). It is worth noting, however, that even under circumstances of greater social cohesion, intercommunity killings do occur (Boesch et al., 2007, 2008).
7. Lanchester's "linear law" predicts that the largest group will not deploy all its units in a battle. Victory will depend on the relative difference in fighting force between the factions (Wilson, Britton, & Franks, 2002).

According to the "square law," if one of the groups outnumbers the other, the largest group should allocate all its units in a concentrated attack. The numerical advantage will influence the outcome of the conflict (Wilson et al., 2002).

8. Given that previous publications have used reproductive success as a proxy for fitness in chimpanzees (Gilby et al., 2013), the present study employed a similar approach by using the males' paternity success as a surrogate for the individual's fitness.
9. We would like to thank Robyn Stea for help in coding these data and JohnMichael Jurgensen for his feedback on this chapter.
10. Even though traditional factor analyses rely on the extraction of latent variables from observable indicators across individuals (an R-type matrix), it is also statistically feasible to determine underlying groups by examining the correlations between individuals across occasions (an S-type matrix; Gorsuch, 2015).
11. Langergraber et al. (2017) squared this variable. The present chapter retained this transformation.
12. Researchers have also argued that the persistence of lethal intercommunity competition arises from the low costs accrued by raiding males when targeting vulnerable or solitary individuals in the rival group. Even though the experimental and observational evidence endorses perspectives concentrating on examining the low fitness costs of ambushes and incursions, such as the imbalance of power hypothesis, these results should not discourage researchers from further examining the fitness benefits obtained by raiding males. Similarly, future studies should consider the role of multilevel selection in the evolution of chimpanzee intercommunity competition.
13. See Sober and Wilson (1998), for a detailed overview of the logic inconsistencies associated with the parsimony argument.

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