9

Lethal Intergroup Competition in Non-State Societies: From Small-Scale Raids to Large-Scale Battles

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1 Introduction

This chapter will provide a synthesis of the current evolutionary literature concerning lethal coalitional aggression in small-scale societies. Attacks, raids, skirmishes, ambushes, and other forms of intergroup aggression present significant risk of injury or death, irrespective of group size, though the means of differentiation among groups, like the mechanisms of ensuring coordination within groups, change as a function of group size. Human coalitional violence is often explained via *kin selection* and *reciprocal altruism*, such that an individual's assumption of risk is compensated by fitness-enhancing benefits to relatives and allies. These explanations become increasingly inapplicable in progressing from bands and tribes to chiefdoms and states. The growth of larger social aggregations compelled the emergence of institutions enforcing intragroup cooperation above and beyond the effects of underlying social networks based on kinship and direct reciprocity. Perspectives reviewed herein, such as *cultural group selection*, consider the cultural evolution of such institutions in generating between-group variance and facilitating lethal intergroup

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competition. According to these theories, cultural transmission, group differentiation, symbolic ornamentation, punishment of defectors, and ethnocentrism are integral components of intergroup competition, with lethal coalitional aggression being an extreme manifestation of between-group rivalry. Furthermore, due to the significant fitness costs imposed upon defeated factions, the study of lethal coalitional aggression in small-scale societies provides fertile ground for examining the interaction between group-level and individual-level selective pressures.

2 Intergroup Violence in Warlike Societies

To this day, cross-cultural studies on human violence have provided a powerful framework for examining how socioecological and cultural factors may influence the persistence of human intragroup and intergroup aggression. Fabbro (1978), for example, reviewed seminal ethnographic papers describing peaceful societies. The author identified seven social organizations allegedly lacking physical interpersonal violence: (1) the Siriono of Bolivia, (2) the !Kung of the Kalahari Desert, (3) the Semai of Malaya, (4) the Mbuti of Equatorial Africa, (5) the Hutterites of North America, (6) the inhabitants of Tristan da Cunha in the South Pacific, and (7) Canada's Copper Eskimo. However, contrary to Fabbro's predictions, Knauft (1987) and Kelly (2000) established the reality of lethal intragroup violence among the Semai, the !Kung, the Mbuti, and the Copper Eskimo, groups respectively experiencing homicide rates of 30.3, 41.9, 39.7, and 419[1] per 100,000 annually. Margaret Mead's *Coming of Age in Samoa* exemplifies the studied mischaracterizations of the prevailing Boasian anthropological paradigm. These inaccuracies extend equally to intragroup and intergroup violence, such that small-scale societies are imagined to be at peace among themselves and with their neighbors. This, too, is fantastical. As extensively reviewed by Ellingson (2001), Pinker (2000, 2012), and our chapter on Lawrence Keeley's anthropological legacy (Hertler, Figueredo, Peñaherrera-Aguirre, Fernandes, & Woodley of Menie, 2018), lethal intergroup violence has been associated with high civilization, at least since Rousseau imagined "noble savages" subsequently corrupted by cultural institutions.[2] The absence of war among these purportedly peaceful primitives, perforce, suggested that lethal violence was a byproduct of complex civilization. As we will see, the ethnographic data says otherwise.

The archaeological and ethnographic record suggests that non-state societies frequently experience raids, ambushes, and massacres (Beckerman et al., 2009; Gat, 2008, 2015; Guilaine & Zammit, 2008; Keeley, 1997; Lahr et al., 2016, LeBlanc & Register, 2003; Pinker, 2012; Soltis, Boyd, & Richerson, 1995; Wrangham & Glowacki, 2012). Examining the frequency of warfare across 50 hunter-gatherer societies, Ember (1978) calculated that 64% of social systems waged war at least once every two years, in contrast to the previously presumed general absence of small-scale intergroup conflict (Lee & Devore, 1968). While 26% experienced war *occasionally*, only 10% *rarely* or *never* exercised any form of intergroup conflict.[3] Adopting a similar methodology, Boehm (2013) collected ethnographic information on 49 bands of foragers from Africa, the Arctic, Asia, Australia, and the Americas. These societies were characterized by their nomadic and egalitarian lifestyle, as well as by their economic autonomy, meaning that they are not dependent on economic exchanges with neighboring horticulturalists, fur traders, sedentary foragers, or equestrian cultures. Boehm referred to them as *Late Pleistocene Appropriate* (LPA), due to their hypothesized resemblance with behaviorally modern prehistoric cultures (45,000 years ago). Boehm's database on LPA foragers allowed him to reconstruct the approximate frequency, in terms of central tendencies, of inter-band conflict in the past. Boehm's analyses revealed that 59% of LPA bands experienced at least one form of intergroup conflict, such as revenge killings, raids, or intense warfare (Boehm, 2013). Although far from suggesting the universality of lethal intergroup aggression, this estimate provides additional evidence against the prevalence of peace among foragers. In terms of conflict resolution, Boehm determined that bands employ various mechanisms to temporarily or permanently finalize confrontations. Even though highly mobile, only 35% of LPA foragers used avoidance as an avenue to resolve conflicts (Boehm, 2013). Moreover, bands attempted to negotiate conflicts in some way (59%) or reach a temporary truce (27%). In only 16% of the cases, combatants attended formal peace meetings.

In a similar vein, Otterbein (1989) classified 100 societies according to their frequency of warfare (*continuous*, *frequent*, *rare/never*) and their level of political organization (states, chiefdoms, tribes, and bands). Otterbein detected a curvilinear trend between the percentages of societies experiencing continuous warfare and the level of sociopolitical complexity: bands 33.3%, tribes 80%, chiefdoms 50%, and states 40%. This pattern also replicated the associations between different types of subsistence economy and continuous warfare: foraging 20%, animal husbandry 88.9%, shifting cultivation 85.7%, and intensive agriculture 47.1%. Hence, although intergroup conflict exists in bands of hunter-gatherers, it intensifies in tribal societies dependent on the practices of animal husbandry or horticulture. Subsequent analyses by Wrangham, Wilson, and Muller (2006) also concluded that killing rates in farmers (595 per 100,000 per year) far exceed those of hunter-gatherers (164 per 100,000 per year).

Additional cross-cultural comparisons further supported the hypothesis that small-scale societies were subject to intense lethal intergroup interactions. Keeley (1997) reviewed the historical, archaeological, and ethnographic literature, generating a detailed database on deaths due to warfare. In contrast to the percentage of US and European males killed in combat during the twentieth century (less than 1%), tribal societies, such as the Jivaro in lowland Amazonia, were subject to considerably more intense competition (59% of male deaths being due to warfare). Keeley concluded that this pattern extended to prehistoric societies.[4] Expanding on Keeley's dataset, Pinker (2012) calculated that, across 21 prehistoric archaeological sites (14,000 BC to AD 1770), 15% of deaths were due to warfare, with estimates ranging from 0% (Gobero, Niger, 14,000–6200 BC) to 60% (Crow Creek archaeological site, South Dakota, AD 1325). The sample included a variety of hunter-gatherers and horticulturalists endemic to Asia, Africa, the Americas, and Europe, suggesting that lethal intergroup violence was not limited to any geographical region or type of subsistence economy. Furthermore, these metrics were within the ranges displayed by contemporary small-scale societies, indicating a degree of consistency across past and present non-state societies. According to Pinker's (2012) database, extant hunter-gatherers (n = 8) reached an average of 14% of war deaths, with values ranging from 4% (the Anbara in Australia) to 30% (the Ache in Paraguay).

The average for contemporary Amazonian, New Guinean, and European tribal societies (n = 10) was close to 25%. Pinker (2012)[5] estimated that 0.7% of individuals died in battles during the twentieth century. Although critics could argue that war deaths are not limited to direct combat casualties, Pinker's (2012) evidence suggests that, even after adding deaths due to wartime famines, epidemics, or genocides, the percentages of war-related deaths remain considerably lower (3%) relative to that of small-scale societies.

Similarly, Walker and Bailey (2013) analyzed the degree of lethal conflict across a sample of 44 lowland Amazonian societies. The authors estimated that violence accounted for 30% of all adult deaths, with the majority corresponding to male victims (69%). Cross-cultural comparisons also revealed considerable variation in mortality estimates, from 6% in the Tsimane to 56% in the Waorani. Walker and Bailey thereafter delineated cumulative violent deaths into three categories: (1) *within-village homicides*; (2) *internal warfare*, in which rival factions are part of the same ethnolinguistic group; and (3) *external warfare*, in which rival factions differ in their ethnolinguistic group of origin. Internal warfare occurred more frequently (55% of events in the database), though subsequent analyses demonstrated that external warfare killed more people (Walker & Bailey, 2013). This difference has been attributed to the lack of significant social connections between groups, such as affinal or consanguineal kinship (Ellsworth & Walker, 2014). Despite the lethality of these confrontations, attackers died in only 2% of the incursions.[6]

Unique among researchers reviewed in this section, Walker and Bailey relate observed mortality estimates in small-scale Amazonian societies explicitly to multilevel selection. As per Walker and Bailey, in contrast with other populations around the globe, Amazonian organizations exhibit considerable levels of genetic variation between groups, as indicated by their high autosomal *Fst* values[7] and low heterozygosities (Wang et al., 2007). The level of genetic differentiation observed in eastern South America is attributable to genetic drift and *assortative fissioning*, in which the daughter groups produced by a split become more homogeneous by recruiting subsets of similar individuals. If individuals marry between allied communities, and if these groups then cooperate against a common rival, selection can operate along the boundary between the marriage-trade cluster and the rival outgroup faction without unduly eroding between group genetic heterogeneity. Walker and Bailey (2013) also suspected that reproductive leveling, such as the absence of land and livestock inheritance, the restriction of polygyny, and an increase in shared paternity, could also promote multilevel selection in Amazonia.

3 Revenge and Residence Patterns

As mentioned in the previous chapter, lethal killings are not a uniquely human phenomenon. Evidence indicates that chimpanzee intercommunity raids and human deadly intergroup aggression feature numerous similarities, including (1) groups practicing collective territoriality, (2) males establishing coalitions and alliances, (3) attackers experiencing low risk of injury or death, and (4) raiders systematically weakening the rival group's cohesion (Manson et al., 1991; Wilson, 2013). Nevertheless, noticeable differences also exist. For instance, although revenge and treachery feature predominantly in lethal confrontations across small-scale human societies (Beckerman et al., 2009; Kelly, 2005; Valentine & Beckerman, 2008; Walker & Bailey, 2013), there is no evidence these behaviors facilitate chimpanzee intercommunity competition. This section then focuses on revenge, residence patterns, and their relation to lethal intergroup conflict.

In small-scale human societies, revenge killings often operate differently depending on the identity of the killer. Rather than interpreting a within-village homicide as a collective affair, the group typically views the attack as a personal loss (Kelly, 2005). This distinction avoids dragging other members of the community into the conflict, circumscribing the dispute between the murderer on the one hand and the victim's immediate kin and allies on the other (Kelly, 2005). Moreover, grievers have at their disposal an array of alternatives destined for dealing with the killer and settling disputes (Boehm, 1999). Mourners, for example, could ask for *weregild*, *éraic*, *galanas*, or any related form of blood money compensation (Dunbar, Clark, & Hurst, 1995) or demand the murderer's expulsion from the group (Boehm, 1999); these terms are commonly accepted by the murderer's kin and allies. However, if these solutions are deemed unacceptable, the only recourse is to kill the murderer (Boehm, 1999). Although grievers could eliminate the killer without first consulting other members of the community, such an action could bring escalating revenge cycles. To circumvent these risks, it is not uncommon for executioners to meet with influential people in the community (so-called big men) as well as with the killers' relatives and friends (Boehm, 1999). Hence, revenge takes the form of capital punishment, in which only the murderer is considered liable (Kelly, 2005).

In contrast to these within-village revenge homicides, where a victim's allies, or kin, precisely dispense lethal aggression toward the murderer, the attackers in *intergroup retaliatory raids* instead direct lethal aggression against *any* member of the rival group, a style of vengeance termed *social substitutability* (Kelly, 2005). Hence, social substitutability can generate additional grievances, rather than settling the dispute. In turn, retaliatory incursions can thereafter create new grievances, leading to future killings (Gat, 2010). The underlying political structure can also create the necessary conditions for a continuing state of intergroup violence. Without a dispassionate Hobbesian *Leviathan* to justly mediate conflict, families, lineages, and clans can be dragged into chronic clashes by retaliating disproportionately, injudiciously, or unjustly (Gat, 2017). In consequence, small-scale societies organized as multilevel systems are more prone to revenge cycles.

Further still, there is covariation between warfare and sociodemographic factors such as residency patterns (patrilocality vs. matrilocality). At first glance, it would be expected that relative to patrilocal societies, matrilocal organizations would rarely wage war due to their absence of consanguineous bonds between males. This, however, is not the case. Matrilocal societies, such as the Waorani, also engage in lethal intergroup competition (Erickson, 2008). With both patrilocal and matrilocal societies displaying between-group killing, researchers have concentrated instead on the influence of residence patterns and migration on internal and external warfare.[8] Divale, for example, suggested (1974) that patrilocal communities can transition to matrilocality after migrating into a territory already occupied by another society. Matrilocality, Divale hypothesized, could disrupt fraternal interest groups, limiting the frequency of internal warfare among the immigrant communities. Greater cooperation between migrant groups reorients the war effort toward defeating native rivals. As per analyses of Divale's sample of 43 societies, groups that migrated within 500 years were more likely to be matrilocal. In terms of warfare, matrilocal organizations tended to wage only external warfare, rather than either internal warfare alone or any combination of internal and external warfare (Divale, 1974). These associations remained significant after statistically controlling for the degree of sociopolitical complexity. Divale also suspected that the coevolution of matrilocality with external warfare was the product of communities losing their young males at an accelerating rate.[9] These circumstances forced the heads of the households to establish coalitions and alliances with men outside of their communities (Divale, 1974; Otterbein, 2004). Otterbein (2004) further expanded on the association between war, kinship, and fraternal interest groups. Tribal warfare, unlike intergroup conflicts between bands of hunter-gatherers, relied on the "recruitment" of males from nearby villages based on their respective kinship lineages. Since patrilineages contain fraternal interest groups, the risk of internal conflicts pervades tribal organizations (Otterbein, 1968, 2004). The threat of external warfare generally forces internal disputes to be suspended or resolved until rival groups are defeated. Regarding mobilization in matrilineal/matrilocal societies, Otterbein (2004) concurs with Divale (1974). During wartime, matrilineal villages featuring recurrent peaceful interactions with each other often dispatched their warriors as part of their contribution to the war effort (Otterbein, 2004).

4 Parochial Altruism and Group Differentiation

Having considered some relevant ethnographic and archaeological evidence, it is now crucial to review explicitly evolutionary explanations of non-state warfare, which emphasize the interplay between ingroup altruism and outgroup antagonism.

Bowles and Gintis (2013) generated a mathematical model for the evolution of altruism under multilevel selection dependent on five assumptions: (1) individuals inhabiting partially isolated groups can either be altruists or non-altruists; (2) altruists incur a cost when they generate a benefit collected by other group members; (3) a member of a group comprised exclusively of altruists attains greater gains relative to an individual living in a group of non-altruists; (4) within mixed groups, altruists fare worse compared with non-altruists; and (5) the expected fitness of the individual is equal to (a) the effects of variation in the frequency of the altruistic allele in the group, plus (b) the existence of the altruistic allele in the individual, and (c) the baseline replication rate (Bowles & Gintis, 2013). Using an adapted version of Price's equation[10,11] for this model, these considerations allow for the separate estimation of within-group and between-group selection. Bowles and Gintis assumed that the change in the frequency of altruists will be zero, if the absolute magnitude of between-group selection and within-group selection remains equal. Alternatively, the enlargement of groups containing altruists and the reduction in the size of groups with fewer altruists counterbalance the natural decline in the number of altruists (Bowles & Gintis, 2013). As an additional step, Bowles and Gintis also adapted Wright's inbreeding coefficient (F_{ST}; 1935), referring to

> The ratio of the between-group variance in the fraction of altruists to the total population variance, which is the within-group plus the between-group variance of the fraction of altruists. (p. 55)

Altering this equation in terms of payoffs, Bowles and Gintis suggested that, if F_{ST} is larger than the ratio between the cost and the benefit, the proportion of altruists will rise, while if F_{ST} is lower, their proportions will decline. Given the costs associated with ingroup altruism and parochialism, it follows that selective pressures should act against the persistence of lethal intergroup conflict. Yet, as evidenced in the previous section, warfare remains a pervasive state among small-scale societies. Choi and Bowles (2007) simulated the potential interactions between four behavioral types: (1) tolerant altruists, (2) tolerant non-altruists, (3) parochial non-altruists, and (4) parochial altruists. Since combat requires hostility toward outsiders and the agent's willingness to accrue a cost, the authors limited this behavior to parochial altruists. In terms of individual gains, Choi and Bowles' model (2007) allowed parochial altruists to attain a direct benefit from warfare, assuming this gain would remain lower than the costs. In contrast, altruists accrued a cost to themselves by providing a public good whose value was to be distributed equally among adult members of the group.

The model also assumed the action of two types of selection: (1) *selective extinction*, the product of intergroup antagonism favoring parochial altruism; and (2) *within-group selection*, promoting tolerant non-altruists and selecting against parochial altruists (Choi & Bowles, 2007). The payoffs received by each adaptive strategy are dependent on the presence or absence of war. Under peaceful circumstances, tolerant individuals in each group attain a net benefit. Since parochial altruists cannot obtain any gains from these conditions, tolerance prevails (Bowles & Gintis, 2013; Choi & Bowles, 2007). The number of parochial altruists in each group predicts the likelihood of intergroup hostility. Intergroup antagonism can turn into warfare if one of the groups contains a higher number of warriors. Hence, group survival depends on the number of warriors per group. The conquering group randomly draws a set of individuals from its ranks and proceeds to replace the proportion of members "killed" in the other group. Reproduction occurs when individuals are randomly paired, with the number of resultant offspring being proportional to the breeding pair's percentage of the group's benefits. The simulation predicted an increase in the frequency of wars when parochial altruists comprised most of the population (Bowles & Gintis, 2013; Choi & Bowles, 2007). The analyses predicted two cutoff points in the frequency of parochial altruists leading to the outbreak of intergroup conflict. Simulations with fewer than 30% parochial altruists generated lower war frequencies due to the limited opportunities for hostile intergroup interactions. In contrast, settings with more than 80% fighters often predicted martial impasses where warriors refused to attack due to the balanced fighting ability between groups. Similarly, the simulated frequency of war and parochial altruism was dependent on population parameters such as migration rates and group sizes. An increase in these parameters decreased the simulated magnitude of between-group variation (Choi & Bowles, 2007).

As mentioned before, a critical assumption of this model rests on partial isolation between groups. According to Bowles (2006), most empirical estimates of genetic F_{ST} are higher than 0.02, a threshold indicating F_{ST} is at equilibrium[12] and interdemic selection unfeasible. In subsequent years, for example, Bowles and Gintis (2013) assembled a list of F_{ST} values in a sample of extant hunter-gatherer populations. The authors classified the data based on three indices. Hence, while F_{DG} provided information on the genetic differentiation between demes within the same ethnolinguistic cluster, F_{GT} and F_{DT} referred to the magnitude of between-group and between-deme variance within the same metapopulation. Across all indices, the mean differentiation value was 0.080. Removing F_{DG} from the analyses slightly increased this estimate (0.087; Bowles & Gintis, 2013). These metrics are inconsistent with traditional descriptions of isolated bands of hunter-gatherers displaying group-level cooperation due to reciprocal altruism, or kin selection.

The work of Bowles and Gintis cited above represents one interpretation, though the degree of genetic differentiation in small-scale societies remains inconclusive. For example, Langergraber et al. (2011) computed F_{ST} scores based on autosomal microsatellite genotypes collected from hunter-gatherers and food-producing organizations. The authors generated pair-wise comparisons between food producers (FP-FP), between hunter-gatherers and food producers (HG-FP), and between hunter-gatherers (HG-HG). The average F_{ST} for FP-FP (0.015), HG-FP (0.011), and HG-HG (0.005) were below 0.02. These inconsistencies led some researchers to consider cultural evolutionary dynamics as the driver of human intergroup variation (Richerson et al., 2016).[13] For instance, Zefferman and Mathew (2015) reviewed the literature collecting information on the *genetic* and *cultural* F_{ST} values of small- and large-scale human societies. The authors then proceeded to compare these estimates with the genetic F_{ST} of chimpanzee communities and Argentine ant supercolonies. Though differing from the average genetic F_{ST} estimate *between* different Argentine ant supercolonies, F_{ST} estimates between human societies were relatively similar to the values *within* Argentine ant supercolonies, which are generally composed of multiple related nests within about one hectare, and also similar to F_{ST} estimates between chimpanzee communities. Alternatively, the human cultural F_{ST} between-groups estimates for both small-scale and state societies were considerably higher than the genetic F_{ST} values in human societies, chimpanzee communities, and Argentine ant supercolonies. As per Zefferman and Mathew, these results suggest that cultural F_{ST} values are more likely to be of sufficient magnitude than genetic F_{ST} estimates to allow for the evolution of large-scale lethal intergroup conflict in humans.

Recent examinations have also compared the difference in magnitude between genetic and cultural F_{ST}. Bell, Richerson, and McElreath (2009), for example, collected data from the *World Values Survey*, an online database describing various beliefs and values. The authors limited their analyses to geographically adjacent polities, assuming neighboring societies would compete more frequently. Cultural F_{ST} scores were contrasted to genetic F_{ST} estimates previously published in *The History and Geography of Human Genes* (Cavalli-Sforza, Menozzi, & Piazza, 1994). Average cultural F_{ST} scores (0.080) differed from average genetic F_{ST} (0.005). Employing the left component of Equation 9.1,[14] Bell et al. calculated the genetic and cultural group benefits of altruistic traits, with results suggesting that genetic benefits (mean = 437) considerably exceeded the cultural benefits (mean = 16) of altruism. According to the authors, this difference provides evidence that selection can promote the persistence of cultural traits associated with group-oriented behaviors.

While considering the relative magnitudes of genetic and cultural F_{ST} values in multilevel selection, it is important to keep in mind that trait-group selection theory, as covered in previous chapters of this volume, does not require the more stringent assumptions of naïve group selection theory, such as reproductive isolation or an absence of migration between groups. Dispensing with these unnecessarily restrictive requirements renders these models more tractable. Additionally, individually selected selfishness does not undermine mean group altruism due to altruistic punishment, as discussed in previous chapters. Evidence of altruistic punishment is provided by Mathew and Boyd (2011), who collected information on 88 raids conducted among Turkana communities, a pastoralist culture located in East Africa. Warriors accrued severe costs, suffering from injuries or death during these confrontations. Due to the acephalic political structure of Turkana's communities, men are not directly instructed to participate in a raid. However, refusal to join a raiding party must be adequately justified. Since an incursion often involves multiple participants, it is not uncommon for some individuals to defect at any point in time. Desertions occurred in 43% of the attacks. Men also defected by staying behind, refusing to engage the enemy, and fleeing the area. Acts of cowardice occurred in 45% of raids. Even though defections are a pervasive phenomenon, free riders rarely go unpunished. Indeed, Mathew and Boyd estimated that other group members punished at least one deserter in 47% of the cases of desertion. Individuals also punished at least one defector in 67% of cases of cowardice. In both instances, sanctions ranged from public recriminations and financial penalties to corporal punishment.

5 Ultrasociality and the Evolution of Large-Scale Warfare

In contrast to small-scale societies such as bands or tribes, large-scale societies, such as chiefdoms and states, feature considerable levels of *ultrasociality*, in which genetically unrelated (or only distantly related) individuals cooperate regularly (Richerson & Boyd, 1998; Turchin, 2010, 2013; Turchin, Currie, Turner, & Gavrilets, 2013). Ultrasocial norms and institutions[15] allowed some small-scale societies to defeat rival neighbors (Turchin, 2016). In modeling the impact of intergroup warfare and the diffusion of military technology, Turchin et al. (2013) predicted that the outcome of an attack during warfare rested on the attackers' average level of ultrasociality.[16] Social systems displaying a higher capacity for collective endeavors were more likely to defeat their competitors. Employing an agent-based simulation, Turchin's mathematical model matched historical data quite closely, predicting over 65% of the variance, paralleling the spread of large-scale societies in Africa and Eurasia (1500 BC to AD 1500).

Geopolitical factors also have a significant effect on the severity of warfare. Turchin (2010), for example, examined the lethality of warfare in steppe societies, comparing culturally similar groups to that of rival factions differing in their meta-ethnic affiliation.[17] As per Turchin, atrocities frequently occurred as part of external confrontations occurring close to steppe borders. For example, the likelihood of genocide was 1.4% during internal conflicts, whereas it reached 63% on steppe frontiers. In addition to the presence of meta-ethnic frontiers, as per Turchin, some biogeographical regions exhibited the necessary conditions for the evolution of *mega empires*, which are defined as social organizations comprising a population of at least 10 million inhabitants and occupying an area of at least 1 million Km^2 (Turchin, 2013). Besides the influence of specific biomes, the presence of draft animals (such as *perissodactyl* or *artiodactyl* ungulates) enabled the rise and spread of these complex conglomerates. Turchin gathered information on large-scale polities from various published databases.[18] As predicted, mega-empires emerge more frequently in arid and transitional zones featuring domesticates, such as horses or camelids. Analyses revealed that over 90% of mega-empires appeared on steppe frontiers.

The coevolution of large-scale warfare within sociopolitically complex systems extends beyond monarchical mega-empires in Afroeurasia. Truly, warfare is exclusive to neither antiquity nor monarchy. In fact, contrary to the *democratic peace theory*, self-governing peoples are sometimes aggressors and can act belligerently in their own interest, as per the predictions of multilevel selection theory. Though not pacific, democracies are exceptional in terms of martial success. Reiter and Stam (2002), for example, gathered historical information on interstate wars (from AD 1819 to 1990) involving more than a thousand casualties. After classifying each faction as a *dictatorship*, an *oligarchy*, or a *democracy*, Reiter and Stam determined that, when democracies initiated the attack, they won in 93% of the cases, as compared to success rates for oligarchies and dictatorships, which were, respectively, 58% and 60%. Similarly, when a polity was the target of aggression, democracies defeated invaders 63% of the time, relative to dictatorships and oligarchies, which, respectively, defeated invaders in 34% and 40% of instances. In attempting to explain these results, Reiter and Stam (2002) surmised that democratic leaders more judiciously decided when to initiate war, perhaps suggesting that democracies are less often pressed unwisely into war. More than this, public opinion and political accountability also had a significant effect, with democratic leaders facing continuous scrutiny during war. Hence, rather than pinnacles of pacifism, democratic regimes successfully play the part of both passive and active belligerents (Reiter & Stam, 2002), perhaps because group interests are more carefully considered when deciding whether to wage war and because group solidarity is increased when individuals perceive themselves as citizens rather than subjects.

6 Conclusions

Although researchers have examined instances of human intergroup competition in an array of economic and religious contexts, warfare remains the best-documented facet of collective human behavior emerging in competitive settings. Rather than being limited to nation-states, lethal intergroup aggression occurs across non-state societies, as we have seen in this chapter, and has precedents in comparative primatology, as we have seen in the previous chapter. We have furthermore observed how local raids between small-scale societies became large-scale battles requiring the collective action of myriads of relatively unrelated individuals against rivals having different cultures, institutions, and languages. Showing multiple ways in which human warfare was elaborated alongside the growth of groups, *cultural group selection theory* emphasizes the evolution of symbolic markers, allowing groups to cooperate with neighbors and compete against factions lacking these identifiers. In addition to the transmission and persistence of symbolic markers within groups, residence patterns also influenced intergroup aggression. The theories reviewed herein, inclusive of their methods and findings, are relevant to multilevel selection for their ability to reconstruct group formation and fractionalization. As we have also noted, the *theory of parochial altruism* (Bowles & Gintis, 2013) and the *meta-ethnic frontier theory* (Turchin, 2003, 2007) are pointed elaborations of multilevel selection theory, which view the evolution of warfare as the product of ingroup prosociality and outgroup hostility. Part III's first chapter used review and analysis to establish intergroup conflict's biological precursors, while this second chapter used ethnography and modeling to explain the cultural elaboration of those precursors with respect to lethal intergroup conflict in small-scale societies. Hence, we are positioned to apply multilevel selection theory to Ancient Rome and Modern Europe, presenting analyses of representative large-scale societies of antiquity and modernity.

Notes

1. Kelly (2000) considers the homicide rate of Copper Inuit to be of the same order of magnitude to the one reported for the Gebusi (419 per 100,000).
2. Possibly from a mixture of industrialized warfare, high absolute death tolls, and ideological motivations, Modern Western nations are assumed especially bellicose. These attributions are doubly incorrect, as violence decreases with civilization and is restricted in the Modern West.
3. Removing cultures dependent on equestrian or fishing economies from the analysis did not alter the overall results, with 12% of societies living peacefully with other groups (Ember, 1978).
4. For example, attackers killed close to 50% of males at the Nubian site of Djebel Sahaba (12,000–10,000 BC; Keeley, 1997; Wendorf, 1968).
5. In addition to the percentage of deaths, other metrics such as standardized rates provide additional information by taking into consideration the number of living individuals in the population. Pinker calculated that the average rate for 27 non-state societies, including hunter-gatherers and horticulturalists, was of 524 war deaths per 100,000 individuals per year. Alternatively, twentieth-century states such as Germany and the United States suffered lower annual death rates (144 and 3.7 per 100,000, respectively; Pinker, 2012). Adding all deaths due to genocides, purges, battles, and war-related famines during the twentieth century generated a rate of 60 per 100,000 per year, close to 9 times lower than the average of non-state societies (Pinker, 2012).
6. Several factors have been attributed to the raiders' relative low rate of injury or death. First, although attackers can use shock weapons to inflict blunt trauma during hand-to-hand combat, projectiles, such as spears, arrows, and darts, enable raiders to injure or kill their rivals from a safe distance (Keeley, 1997). Second, raiders tend to choose solitary victims or smaller groups that are unlikely to successfully fend off an attack (Glowacki, Wilson, & Wrangham, 2017). Third, if competing groups

share an ethnolinguistic background and maintain a minimum level of open communication (as in lowland Amazonian societies, in which the frequency of treachery tactics was 9.5 times higher during internal conflicts relative to external clashes), the killing party could host a meeting or feast with the sole intention of eliminating their rivals (Walker & Bailey, 2013).

7. Wang et al. (2007) examined autosomal microsatellite data collected from 24 Amerindian populations. The analyses concluded that the F_{ST} values for Amerindian samples located in eastern South America ($F_{ST} \times 100 = 14.7$) were considerably higher relative to the worldwide estimate ($F_{ST} \times x100 = 7.1$).
8. See Turchin and Korotayev (2006) for a mathematical examination of population pressure and internal warfare in non-state societies.
9. For a complementary take, see Ember and Ember (1971).
10. In 1970, George Price developed a mathematical expression describing the change in the frequency of an allele A nested within a group (Δp). Price (1970, 1972) proposed that Δp was equal to the covariance between the individual gene frequency and the number of offspring sired by each partner (assuming each offspring is the product of half of each parent's contributions).
11. This adaptation, however, made no distinction between MLS1 and MLS2. Okasha (2009), for example, demonstrated that Price's equation differs depending on the type of multilevel selection. The author derived the following formula for MLS1:

$$cov(w_i, z_i) = cov(W_k, Z_k) + E_k\left(cov_k\left(w_{jk}, z_{jk}\right)\right)$$

wherein the overall covariance between trait and fitness is equal to the group-level covariance (mean fitness and mean trait) and the average of intragroup covariance (individual trait and individual fitness; Okasha, 2009). This formulation, however, assumes that the group's fitness is equal to the average individual fitness, and the group trait equals the average individual character (Okasha, 2009). In this case:

$$\bar{w}\Delta\bar{z} = cov(w_i, z_i)$$

Concerning MLS2, the focal units are the individuals and the groups (Okasha, 2009). Extending Price's equations to MLS2, Okasha proposed the following:

$$\bar{Y}\Delta\bar{Z} = cov\left(Y_K, Z_k\right) + E\left(Y_k \Delta Z_k\right)$$

The change in average group trait is equal to the covariance between the trait of the group and group's absolute fitness (number of offspring groups) and the average of the total fitness multiplied by the groups' transmission fidelity.

12. According to Bowles and Gintis (2013), the equilibrium level of genetic differentiation is represented by the following formula:

$$F^{*}_{ST} = \frac{1}{1 + 4m_e + N_e}$$

where m_e is the rate of migration between groups and N_e is the group size.

13. Some critics of the parochial altruism hypothesis claim that self-sacrificial behavior rose due to the cultural effects of warfare rather than as the outcome of its evolutionary selective forces (Wrangham, 2019).
14. In Equation 9.1, the numerator represents an increase in the average group's fitness based on an increase in the number of altruists in the group.

$$\frac{\beta\left(w_g, p_s\right)}{\beta\left(w_{ig}, p_{ig}\right)} > \frac{1 - F_{ST}}{F_{ST}}$$

Alternatively, the denominator indicates a decline in fitness in an individual featuring an altruist allele (Bell et al., 2009).

15. Institutions involved in maintaining cooperation in large-scale societies; these social subsystems attain collective or higher-order benefits by imposing a cost on individuals or other lower-level components (Turchin, 2013).
16. The authors employed the following formula to model the association between ultrasociality and the outcome of a confrontation between polities:

$$\bar{U}_{att} = \frac{\sum_j \sum_i U_{ij}}{S_{att}}$$

In this equation the term $\bar{U}_{att}$ represents the success of the attack, where S_{att} is equal to the polity's size, and U_{ij} corresponds to an ultrasocial trait, ranging from 0 to 1, and present in the *i*th particle within the *j*th group.

17. The author assigned the outcome of each confrontation a value ranging from 0 to 10, where 0 represented a non-violent takeover and 10 indicated that over 50% of the defeated population was killed or enslaved. The study examined events from AD 1 to 1700.
18. For example, Chase-Dunn, Hall, & Turchin, 2007; Taagepera, 1997; Turchin, Adams, & Hall, 2006

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