

Intergroup Aggression in Chimpanzees and War in Nomadic Hunter-Gatherers

Evaluating the Chimpanzee Model

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Abstract Chimpanzee and hunter-gatherer intergroup aggression differ in important ways, including humans having the ability to form peaceful relationships and alliances among groups. This paper nevertheless evaluates the hypothesis that intergroup aggression evolved according to the same functional principles in the two species—selection favoring a tendency to kill members of neighboring groups when killing could be carried out safely. According to this idea chimpanzees and humans are equally risk-averse when fighting. When self-sacrificial war practices are found in humans, therefore, they result from cultural systems of reward, punishment, and coercion rather than evolved adaptations to greater risk-taking. To test this “chimpanzee model,” we review intergroup fighting in chimpanzees and nomadic hunter-gatherers living with other nomadic hunter-gatherers as neighbors. Whether humans have evolved specific psychological adaptations for war is unknown, but current evidence suggests that the chimpanzee model is an appropriate starting point for analyzing the biological and cultural evolution of warfare.

Keywords Lethal raiding · Peace · Imbalance-of-power · Cultural war-risk hypothesis · Parochial altruism

Introduction

Since the 1971 discovery that wild chimpanzees (*Pan troglodytes*) sometimes kill members of neighboring groups (Goodall et al. 1979), similarities between chimpanzee intergroup aggression and human warfare have prompted a “chimpanzee model”

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of war proposing intergroup killing as strategic and adaptive (Goodall 1986; Manson and Wrangham 1991; Roscoe 2007; Trudeau et al. 1981; van der Dennen 2002; Wilson and Wrangham 2003; Wrangham 1999, 2006; Wrangham and Peterson 1996). The model proposes that chimpanzee groups (also known as communities) compete with each other over land, food, and females (Williams et al. 2004). Males benefit their groups by severely attacking members of neighboring groups, but they do so only in carefully selected contexts (local “imbalances of power”) that impose little risk of harm on the aggressors. Success in killing shifts the long-term balance of power toward the aggressors by increasing their numerical superiority and hence their ability to win future contests over resources. It therefore tends to lead to a long-term rise in survival and reproductive success for members of the group. Selection has accordingly favored male tendencies to search for and take advantage of safe circumstances to cooperate in killing members of neighboring rival groups.

Given that nonlethal intergroup hostility is widespread (Crofoot and Wrangham 2009), why does this pattern of killing occur only in particular species such as chimpanzees and humans? According to the imbalance-of-power hypothesis (Wrangham 1999), a combination of two features favors an evolved tendency of lethal intergroup killing. They are group territoriality and a fission-fusion grouping system with sufficient variance in power between groups that aggressors can easily kill victims without being harmed themselves. Group territoriality constrains access to resources and therefore favors success in dominating neighboring groups. A fission-fusion system allows individuals to attack only when they assess that a cheap victory is likely. Since hunter-gatherers are routinely territorial and also forage in subgroups of varying size, the chimpanzee model should be applicable to humans (Manson and Wrangham 1991; Wrangham and Peterson 1996).

The chimpanzee model has been criticized for supposedly expecting patterns of warfare to be insensitive to cultural and environmental influences (e.g., “an unchanging universal for all human societies”; McCall and Shields 2008:8). In fact, however, it allows for the incorporation of environmental and cultural influences on behavior in the same way as other explanations of aggression (e.g., Anderson and Bushman 2002). For example the perceived safety of the aggressors, which is a critical variable determining the probability of aggression, is determined by numerous influences, such as the nature of weapons, complexity of the habitat, and cultural norms concerning homicide. We expect a particularly strong influence to come from the degree of political control within societies, which can affect whether individuals fight voluntarily or under coercion. Political relationships among societies should have similarly strong effects: for example, power asymmetries intensifying the perceived dangers of intergroup aggression or alliances promoting peace.

The human societies in which war is expected to most closely resemble the chimpanzee pattern are those that, as in chimpanzees, are most acephalous (lacking in political control) and independent (not subordinate to or bound by obligations to other societies) and have the simplest weaponry. One example of such societies is urban gangs, whose intergroup behavior has important similarities to that of chimpanzees (Wrangham and Wilson 2004). A second is that of nomadic hunter-gatherers neighboring other nomadic hunter-gatherer societies. In this paper we review accounts of warfare among nomadic hunter-gatherers to test whether they conform

to three expectations of the chimpanzee model: exhibiting continual hostility to other groups, attacking outgroup members only when safe, and benefiting from the attacks.

We present this idea with the aim of distinguishing among alternative concepts of the evolutionary basis of war. The chimpanzee model contrasts with two other broad kinds of hypotheses. First, humans may have been subject to selection for human-specific psychological traits adapted to war. This type of proposal (a human-specific model) resembles the chimpanzee model in suggesting that humans participate in war because of psychological tendencies that have been selectively favored through the success of dominant groups. However it differs in predicting that the patterns of war in humans will be distinguished from intergroup aggression among chimpanzees partly by the presence of novel psychological traits not found in chimpanzees. One such trait is parochial altruism. According to the “parochial altruism” model, humans evolved to take self-sacrificing risks in warfare (Alexander 1990; Bowles 2009; Choi and Bowles 2007; Darwin 1871). This idea conforms to evidence of self-sacrificial behavior and is supported by some genetic modeling (Bowles 2009), though challenged by some data (Langergraber et al. 2011). Other candidate psychological traits include tendencies for strong reciprocity (Gintis 2000), or revenge-seeking (Boehm 2011).

Second are “nonadaptive models,” which argue that humans have no evolutionarily shaped predispositions for intergroup aggression, leaving patterns of war to be determined entirely culturally (Goldschmidt 1988; Keeley 1996; Kimball 1974; Malinowski 1941; Mead 1940). These ideas conform to the fact that societies are often peaceful, that warriors are often reluctant to kill, and that the act of killing can provoke psychological trauma in the killers (Collins 2008; Grossman 1995; Fry 2006, 2007; Roscoe 2007; Smith 2007).

An important implication of the chimpanzee model is that if both chimpanzees and humans evolved a tendency to kill members of other groups in safe contexts, the evolutionary psychology of both species should be the same with respect to risk-taking in intergroup aggression. Therefore if humans take more self-sacrificial risks in intergroup aggression than chimpanzees do, the difference is cultural rather than biological. We call this inference the “cultural war-risk hypothesis.” The cultural war-risk hypothesis conforms to well-established conclusions that cultural norms can promote individual military prowess (Alexander 1990; Fisher 1930; Mead 1940; Soltis et al. 1995), and also that cultural group selection can explain how such norms arise and are maintained (Soltis et al. 1995). It complements those ideas by proposing that in societies where cultural institutions promoting military prowess are relatively few or weak, human warfare is expected to closely follow the chimpanzee model.

Because this paper focuses on adaptive significance it could in theory be based on data from any species that kills members of neighboring groups in a manner conforming to the imbalance-of-power hypothesis, such as wolves (*Canis lupus*) appear to do (Mech et al. 1998). In practice, however, chimpanzees offer an especially valuable heuristic system not only because their pattern of killing has prompted an explanatory model but also because, like humans but unlike wolves, their groups contain many breeding males. Note that the focus on adaptation rather than phylogeny means that the question of whether the last common ancestor of humans and living apes behaved more like chimpanzees (Wrangham and Pilbeam 2001) or bonobos (*Pan paniscus*: de Waal 1998) is irrelevant to this paper. Bonobos resemble

chimpanzees in having aggressive territorial interactions between groups (Kano 1992), but because they show no evidence of lethal intergroup aggression they do not provide a behavioral model for understanding intergroup killing.

In sum, our aim is to compare chimpanzee intergroup aggression and hunter-gatherer warfare so as to evaluate the merits of the chimpanzee model compared with human-specific and nonadaptive models. In light of claims that chimpanzee intergroup killings are too rare to justify functional analysis (Sussman 1998; Sussman and Marshack 2010), we begin by reviewing recent data from wild chimpanzees.

Definitions

Following Bowles (2009) we use “war” to mean relationships in which coalitions of members of a group seek to inflict bodily harm on one or more members of another group; “groups” are independent political units. This definition is broader than many because it includes all kinds of fighting, whether in a surprise attack (raid or ambush), chance meeting, or planned battle. We distinguish “simple” from “complex” war (cf. Kelly 2005; Otterbein 2004; van der Dennen 2007). Simple (or “primitive”) warfare is a style found in small-scale hunter-gatherer and farmer societies whose communities are not integrated with each other by any political officials. It is dominated by raiding and feuding, is often motivated by revenge, and has few lethal battles, where battles are escalated conflicts between prepared opponents. Complex warfare, by contrast, also sometimes called “real warfare,” “true warfare,” or “warfare above the military horizon” (Turney-High 1949), occurs in larger societies containing political hierarchies. It includes lethal battles fought by soldiers under orders from leaders, and its goals are typically conquest and/or subjugation. It has no known analogues in chimpanzees or other nonhumans.

We use “society” to refer to a group of people sharing the same cultural systems and language or dialect. Within societies of nomadic hunter-gatherers (typically numbering a few hundred or thousand) are smaller residential groups (often 25–40 individuals) we call bands. “Nomadic” means that instead of living in permanent villages, bands occupy temporary camps, albeit normally within a fixed territory.

Chimpanzee Intergroup Violence

To assess the status of the chimpanzee model we first review recent data from the five longest-term research sites of chimpanzees where study groups have neighbors (Budongo and Kibale, Uganda; Gombe and Mahale, Tanzania; and Tai, Ivory Coast). This section summarizes work by Boesch et al. (2008), Mitani et al. (2010), Sherrow and Amsler (2007), Watts et al. (2006), Williams et al. (2004), Wilson and Wrangham (2003), Wilson et al. (2004), Wrangham et al. (2006), and Wrangham (2010). We organize the material according to six important issues for the chimpanzee model: (1) How predictable is intergroup hostility? (2) Under what conditions do lethal attacks occur? (3) What is the death rate from intergroup aggression? (4) How dangerous is aggression for the aggressors? (5) Do communities of successful killers tend to benefit? (6) Are aggressors influenced by rewards or punishments?

1. Peaceful intergroup association involving calm or affiliative interactions are theoretically possible in chimpanzees since they have been seen in a closely related primate (bonobos; Idani 1991). However they have not yet been reported for chimpanzees. Nevertheless most interactions between chimpanzee communities involve no physical contact between opposing individuals (Goodall 1986). Instead, a party (subgroup) from one community hears (or, less often, sees) another party, leading to mutual calls or to one immediately avoiding the other. On rare occasions two parties come into mutual view at close quarters (e.g., 15 m away), either by accident or because one approached the other quietly. When both parties contain several adult males those on each side are likely to give loud calls and may display with aggressive postures and fast charges in a series of rushes toward the opposition and equally rapid retreats to safety. Two or more males typically charge at the same time and in close proximity. Such “battles” can be prolonged (at least 45 min, based on personal observation) and are emotionally tense, to judge from near-continuous screaming, barking, and hooting. But even then individuals contact each other only occasionally, such as when a male comes close enough to slap a rival during a charge, or when a small coalition from one group succeeds in temporarily isolating an individual from the other group. The interaction ends with one or both parties moving away. Sometimes both retreat toward the center of their own territories. At other times one party may advance at the other’s expense (“win”): larger parties are thought to win more often, but there are no published data on this point. Thus in most intergroup interactions it appears that power is sufficiently balanced that individuals avoid the risk of attempting physical contact with opponents.
2. Lethal attacks have been reported only where there is a strong asymmetry of power between subgroups, typically when several males encounter either a lone male from the neighboring community or a lone mother with her dependent offspring. Occasionally an individual has been left isolated by the flight of companions. Lethal encounters are rare because lone adults tend to avoid the border zone between two communities. However, since avoidance of the border zone probably leads to its food resources being underexploited, individuals in a community territory that has a temporary food shortage may be willing to risk the chance of encountering neighbors. Asymmetric encounters can also occur when a large party penetrates deep into the range of its neighbor, appearing to look for opportunities to attack vulnerable opponents.

In a potential challenge to the model’s predicted importance of power asymmetry, Boesch et al. (2008) suggested that chimpanzees might attack others even when they do not have a large imbalance of power in their favor. However, they reported no specific observations in support of this idea.

3. The rate of death from intergroup attacks varies widely, but the overall pattern supports the chimpanzee model by showing that there is a significant risk of being attacked, especially for males. In a survey of nine study communities in the five longest-studied populations of chimpanzees with more than one community, Wrangham et al. (2006) reported that the median risk of violent death for chimpanzees from intercommunity killing was 69–287 per 100,000 per year. Victims were principally adult males (42.4%) and infants (51.5%) ($n=33$ deaths, excluding suspected cases). Data in Wrangham et al.’s (2006) review came from

up to 2004. At that time coalitionary killing had not been seen in intercommunity contexts in Budongo or Tai. In Budongo intercommunity interactions (and even the location of intercommunity boundaries) remain poorly understood, but seven infant corpses have been found in contexts suggestive of intergroup killing (Reynolds 2005). In Tai two cases of coalitionary killing have now been recorded (Boesch et al. 2008). Evidence of coalitionary killing has also come from a 6-month study of unhabituated chimpanzees in Gabon (Boesch et al. 2007), from Kalinzu Forest in Uganda (Hashimoto and Furuichi 2005), and in the Republic of the Congo, where Goossens et al. (2005) described the results of 8 years of monitoring of 37 wild-born captive chimpanzees released into the Conkouati-Douli National Park. Goossens et al. (2005:461) reported that “encounters with wild chimpanzees were a major cause of mortality in released males, and 40–50% of released males would have died without veterinary intervention.” They concluded: “males should not be released where wild chimpanzees occur, as they are likely to be attacked and killed.” Such data lead to two general conclusions, summarized by Boesch et al. (2007:1033): “(1) wild chimpanzees may be very aggressive even in the absence of human observers, which can lead to conspecific killings, in contradiction to the suggestion of Clark (2002) and Power (1991); and 2) wild chimpanzees resort to intercommunity killing through most of their natural range, from groups in rather open habitat to ones in the dense forest, as well as groups that are artificially provisioned, ones under regular human observation, and ones not habituated to human presence.”

4. Killers have not been seen to be badly injured: their worst wounds have been scratches (Watts et al. 2006). By contrast, killers impose severe wounds often covering much of the exposed surfaces of the bodies of victims, including broken bones, castration, and torn thorax, despite intense resistance by healthy victims fighting for their own lives or the lives of their infants (e.g., Muller 2002). The difference is explained by aggressors confining their attacks to occasions when they have a large imbalance of power in their favor, a result of superior numbers. Some aggressors then immobilize the victim while others beat, twist, or bite (Goodall 1986).
5. Aggressors tend to come from powerful communities whose members have gained increased reproductive success via improved access to either food resources (land) or breeding females (Williams et al. 2004). Thus the observed deaths of males (and one female) that were responsible for the demise of the Kahama community in Gombe resulted from attacks by males of the larger, dominant Kasekela community (Goodall et al. 1979). Males in the Kasekela community in Gombe have also killed individuals in the weaker Mitumba community and have made increasing use of the border area (Mjungu et al. 2010). In Kibale, the Ngogo community has killed members of a neighboring community and expanded into the neighbor’s range (Mitani et al. 2010). In Mahale a larger community dominated access to fruit groves contested with a smaller community (Nishida et al. 1985).
6. Finally, there is no indication that the decisions of individuals to participate in these attacks, or the intensity with which they do so, are influenced by social rewards or punishments. In theory the willingness of a female to copulate, or the probability of the alpha male offering coalitional support, could be increased for a

male who joins an attack or shows unusual ferocity, or a male who absents himself from a border-zone patrol might later be harassed by a coalition of high-ranking males. In practice no evidence has been reported to suggest that non-participants are punished or that participants receive social rewards. We conclude that individual decisions to participate in intergroup attacks are made without regard to the possible consequences for within-community social relationships.

Simple Warfare (Below the Military Horizon)

Here we review the same questions about simple warfare as considered above for chimpanzees. Simple warfare has been reported in both nomadic hunter-gatherers and small-scale farmers that lack institutional leadership (Boehm 1999; van der Dennen 2007). Our focus is on nomadic hunter-gatherers.

1. How often are intergroup interactions hostile? Surveys of the percentage of hunter-gatherers practicing warfare are confusing. All suffer from having to include studies of variable quality and duration. Some find a high frequency of war (78–92%: 88% practicing war, $n=56$, Hobhouse et al. 1915; 92% with war, $n=216$, Wright 1942; 78% with war, $n=9$, Otterbein 2004; 90% with war more often than “rarely or never,” $n=31$, Ember 1978). Others find a low frequency of war. Leavitt (1977) found war absent or rare in 73% of hunting and gathering societies ($n=22$) (cited by van der Dennen 2007), while Fry (2007:143) reported “the fact that simple nomadic hunter-gatherers typically are nonwarring.” Similarly contrasting conclusions have been drawn since such studies began in the nineteenth century (van der Dennen 2002). Three problems appear particularly responsible.

First is the fact that different authors mean different things by war. For instance Fry (2006) characterized the Andamanese as warless because they did not fight on a large scale. When war is used to mean to include group killings of members of neighboring groups, more hunter-gatherers are found to have war.

Second is the composition of the sampled populations. Surveys of war in hunter-gatherer societies often include groups that are neighbored by farmers and/or pastoralists but not by other societies of hunter-gatherers, such as the Mbuti, Semang, !Kung San, or Paliyan (Fry 2006, 2007). These cases remind us that warfare is not inevitable, but they do not answer the relevant evolutionary question, which is how nomadic hunter-gatherers would interact with neighbors living at a comparable level of subsistence (Headland and Reid 1989; Maschner and Reedy-Maschner 1998). Therefore we focus on nomadic hunter-gatherers bordered by at least one other nomadic hunter-gatherer society and exclude those who were settled (e.g., Asmat), equestrian (e.g., Comanche), or living in intimate relations with farmers (e.g., Mbuti).

Third, internal and external warfare are often not distinguished. Internal war is war with neighboring polities within the same society (Ember and Ember 1971). External war is war against other societies, where societies are groups with different dialects or languages and different cultural practices, occupying an identifiable area or territory (Otterbein 1994). The Andaman Islanders illustrate a particularly sharp version of the distinction. In the nineteenth century the eleven

Andamanese societies on Great Andaman Island were all nomadic hunter-gatherers: they had no farming neighbors (Kelly 2000). Radcliffe-Brown (1922:18) estimated their population in 1858, prior to epidemics of smallpox and measles, at ~4,950. Mean society size was therefore 450 individuals, and each society contained residential bands averaging 40–50 individuals (Radcliffe-Brown 1922:28). Relationships among neighboring bands within a society were often peaceful and cooperative, including joint hunting, feasting, dancing, exchange of gifts, adoption of children, and intermarriage, which everywhere promotes alliance (Chapais 2008; Kelly 2000). However, from time to time relations between bands deteriorated into temporary war (“internal war”). Internal wars occurred primarily as a result of competition over resources and revenge for homicide (Kelly 2000:102). They were carried out mainly by surprise raids in which the aim was to kill one or two men and then retreat (Radcliffe-Brown 1922:85). Peace was restored through explicit peacemaking mechanisms led by women.

External war, by contrast, occurred between societies. According to Kelly’s extensive study of the Andamanese, based on records dating to 1863, “external war is unremitting and constitutes a condition of existence that defines the boundaries of the niches exploited by two populations . . . peace was unattainable in external war” (Kelly 2000:118–119).

The distinction between internal and external war is a widespread feature among nomadic hunter-gatherers and other acephalous societies (Ember 1978; Otterbein 1994). Internal war was possibly not universal. Kelly (2000) cites the example of the Slave as a case in which there was no record of internal war, and Ember (1974) found that when hunter-gatherers were defined as having less than 20% of food from agricultural sources, two of ten societies had external war only (Kaska and Crow). To the extent that internal war “originates as an alternation of war and peace, that is, as a war/peace system” (Kelly 2000:118), it differs from the persistently hostile character of intergroup aggression among chimpanzees. By contrast external war as described for the hunter-gatherer societies of the Andaman Islands is analogous to chimpanzee intergroup aggression in being a permanent threat (Rodseth and Wrangham 2004).

How representative are the Andaman Islanders? Here we review six other culture areas where nomadic hunter-gatherer societies lived as neighbors: Tasmania, Australia, Tierra del Fuego, western Alaska, Canada, and New Guinea (Table 1). New Guinea is a marginal case, because although war is well-known there among horticulturalists (e.g., Dani: Heider 1997) and settled hunter-gatherers (Asmat: Zegwaard 1959) the ethnographic record of nomadic hunter-gatherers is very sparse. Roscoe (2002:156) concluded that “Contradicting the common stereotype that war is attenuated or absent among [semi- to fully nomadic] hunter-gatherers[,] fighting was endemic” in New Guinea, but he did not specify whether this applied to external war, internal war, or both. Other cases that could possibly provide information about nomadic hunter-gatherers living with other hunter-gatherers as neighbors include South America (e.g., northern vs. southern Ache; Hill and Hurtado 1996), the American Southwest and California (e.g., Yuki; Chase-Dunn and Mann 1998), and southern Africa (Bushmen; Cashdan 1983). However these culture-areas do not clearly fulfill our criteria because of such factors as isolation from other hunter-gatherers (Ache), largely

Table 1 Evidence for external war in nomadic hunter-gatherers bordered by another society of nomadic hunter-gatherers

	Shoot on sight, or trespass as cause of war	Ambushes and/or raids	Overt fear of strangers	Underused border zones or territory
Andaman Islands	[a] Kelly 2000:97	[b] Kelly 2000:139	[c] Kelly 2000:100	[d] Kelly 2005:15296
Australia	[e] Flood 2006:115; [f] Lourandos 1997:65; [g] Tindale 1974:78–79	[h] Warner 1931:457; [i] Basedow 1929:184	[j] Tindale 1974:33, 34, 43, 49	[k] Tindale 1974:59
Canada/ Great Lakes	[l] Graburn 1969:92; [m] Hickerson 1988:88	[n] Bishop and Lytwyn 2007:40; [o] Graburn 1969:76	[p] Bishop and Lytwyn 2007:50; [q] Graburn 1969:92	[r] Bishop and Lytwyn 2007:33; [s] Hickerson 1988:66, 88
Tasmania	[t] Jones 1974:328; [u] Jones 1984:41; [v] Roth 1890:83	[w] Tindale 1974:327; [x] Roth 1890:93	No mention found	No mention found
Tierra del Fuego	[y] Lothrop 1928:87, 165 (Ona, not Yahgan)	[z] Lothrop 1928:88	[aa] Lothrop 1928:92	No mention found
Western Alaska	[bb] Burch 2007:16	[cc] Burch 2007:19–20	[dd] Burch 2007:19	No mention found

Together with New Guinea, these six areas represent all known culture-areas where at least two societies of nomadic hunter-gatherers that did not have contact with pastoralists, farmers, or state societies had a common border, excluding groups that relied on horses or agricultural foods. Nomadic hunter-gatherers in New Guinea have been little studied (see text). Tasmania and Tierra del Fuego are also poorly known

Andaman Islands

^a “the Bea and Jarawa fight whenever they encounter one another and have no other form of interaction”; “Bea guides made it clear to the colonial parties initially exploring the interior that passage upstream beyond a certain point would provoke certain attack”

^b “The majority of incidents of armed conflict are spontaneous conflicts over resources, but adaptation to the prospect of this has led to a policy of attacking whenever a Jarawa hunting party has the advantage of surprise”

^c “the other eleven incidents are all readily interpretable as spontaneous attacks prompted by infringement of the Jarawa territorial domain rather than revenge”

^d “the maintenance of hostile intergroup relations is maladaptive under conditions commensurate with those found in the Andaman Islands . . . hostile relations shrink the utilizable area to the equivalent of 12 square miles, with a peripheral zone about one-third of a mile wide subject to border avoidance”

Australia

^e “These drove people into the territory of traditional enemies, who tended to kill strangers on sight”

^f “intergroup meetings . . . were most often held close to territorial boundaries so as to avoid trespass and therefore further conflict”

^g They said they would be killed if caught by themselves trespassing.” . . . “whenever a lone man was seen he was killed”

^h Warner details surprise raids and night attacks, including 35 deaths

ⁱ “the aggressors know that the most radical method to extinguish the enemy is to take them unawares, and to slaughter them before they can retaliate. For this purpose, it is best to either steal on them in the earliest hours of morning . . . or to lie in ambush at a place . . . where the enemy is sure to call”

^j “they attacked Strangers . . . not people with whom they had prior contacts. Their victims were people they regarded as alien.” “They [people from another area] were much dreaded and each tribal group in that area tended to attribute death in sleep to the secret attack by such an evil Wailo being.” “Tribes . . . register directions

of former arrivals of strangers, and thus the sources from which aggressive pressure may have been coming during the relatively immediate past”; “They use two different terms meaning south. . . . The latter term is widely used with a variety of meanings linked with the idea of strangers and aggressive visitors”

^k “A Kariara man considered Kulikuli ‘too near the boundary’ and therefore it was not much used by the Kariara. . . . Both tribes . . . preferred to camp further away from their neighbors”; “Men are believed to have used Kulikul in former days when out hunting but it was too near the tribal boundary for safe living” *Canada and the Great Lakes* (Some conflict involving Chippewa also occurred in what is now the U.S.)

^l ^q “the natural reaction of anyone when he first sees a strange being is to flee or to kill it”

^m “if a hunting party of Sioux should venture upon this land, the report of a Chippewa’s being within its borders would frighten them off”

ⁿ “Their attacks are all by stratagem, surprise, and ambush”

^o “the Eskimos and Indians of the area had as little to do with each other as possible before the white man arrived, except when an opportunity presented for one group to surprise and kill the other”

^p “The primary motives for Cree raids in the eighteenth century derived from the fear and mistrust between two people”

^r “To the northwest, the region between the Nelson and Churchill rivers was an uninhabited ‘no-man’s land’ between the warring Cree and Inuit. To the southeast, the Nottaway River region was also avoided for fear of the Iroquois who raided into that area”

^s “Warfare . . . had rendered a large region west of Lake Superior unsafe for entry by anyone.” “Their dividing line may be considered 200 miles wide, for this tract of country lies untraversed by them”

Tasmania

^t “the usual causes for hostility were . . . trespass.” “Trespass was usually a challenge to or punished by war”

^u “The pattern of peaceful relations between bands . . . tended to be within such a tribal agglomeration and that of hostile ones or war outside it.” “Movements of bands outside this territory . . . were carefully sanctioned . . . trespass being usually a challenge to war”

^v Roth (1890) summarizes the cause of wars as being trespass by one tribe onto the lands of another tribe. Much of this was caused by the encroachment of whites

^w “the combats usually took the form of ambushes or personal fights”

^x “the perfection of their war was ambush and surprise”

Tierra del Fuego

^y “Organized warfare, during which any member of one group would kill at sight any member of another group, as among the Ona, was unknown to the Yahgan.” Also, “each group had definitely located hunting right[s] and to trespass on another’s territory was a cause for war”

^z “the first intimation of attack was the swish of hostile arrows and the first move was to run for shelter until the strength and nature of the attack could be determined”

^{aa} “If a stranger appeared at an Ona encampment unaccompanied by a member of it, he was likely to be deemed a poacher and promptly arrowed”

Western Alaska

^{bb} Although members of one group could at times use land belonging to another group, “trespass was considered a hostile act and, if discovered, was met with force”

^{cc} “The objective of surprise attacks and battles was to kill as many of the enemy as possible.” “Surprise attacks were of two basic types: ambushes and night-time raids. Both were reported from all parts of western Alaska”

^{dd} “Mistrust of foreigners, seem[s] to have been broadly applicable in western Alaska”

settled patterns (California), and long-term contact with powerful pastoralists (southern Africa).

External war has been described in each of the areas we reviewed based on evidence of intergroup killing, explicit fear of strangers, and/or avoidance of

border zones (Table 1). In some cases peaceful interactions were also found between neighboring societies. Thus in western Alaska there was considerable intermarrying between Eskimo and Athapascan speakers (Burch 2007), and in parts of Australia groups of societies could form sociopolitical alliances (Berndt and Berndt 1988; Lourandos 1997; Tindale 1974). During periods of economic hardship these were associated with sharing of food resources, and during good times, with communal feasting, ceremonies, and ritual exchanges.

Such examples show that the constant hostility of relationships among Andaman societies does not represent all recent hunter-gatherers. Even so, in every case intersocietal relationships were ordinarily tense, partly because unregulated trespass invited aggression. For example in Australia, in the words of Berndt and Berndt (1988:143), “there can be no question, no dispute, concerning Aboriginal ownership of land. . . . Members of such a unit were spiritually, emotionally and genealogically linked with that territory through consanguineal ties of kinship. They were the owners of that land.” Dixon (1976:214) noted that in northeast Queensland people could travel in alien territory but they needed a message-stick to do so: “without it they would be regarded as criminals and be liable to be killed.” Tindale (1974:20) concluded that similar patterns originally applied to the whole of Australia, though they disappeared quickly after colonialization: “The new situations arising from the presence of white men, representatives of the law, and the ready transportation of Aborigines to places never before seen, have diluted the strong sense of trespass which, in their untrammelled state, kept them from venturing into the territories of others save as armed raiders with malicious intent.”

In sum, whereas internal war was highly variable in frequency and clearly oscillated with relaxed peace, the relatively few cases of hunter-gatherers living with different societies of hunter-gatherers as neighbors show that the threat of violence was never far away. However, although the relationship was often one of war and could be permanently so, it was also often one in which members of neighboring societies were able to collaborate.

2. As in chimpanzees, killings tended to occur in interactions when there was a strong asymmetry of power between subgroups, as opposed to during escalated conflicts between facing lines. The Andaman Islanders again offer a crisp example. “The most elementary form of warfare,” according to Kelly (2000:4), “is a raid (or type of raid) in which a small group of men endeavour to enter enemy territory undetected in order to ambush and kill an unsuspecting isolated individual, and to then withdraw rapidly without suffering any casualties.” Because societies could number several hundred or a few thousand people, planned raids involving multiple bands could be large. For example Kelly (2005) records raids by more than 200 warriors. Kelly’s characterization of the Andamanese raid as a surprise attack summarizes the conclusions of numerous reviews of simple warfare among hunter-gatherers (Gat 2006; Otterbein 2004; Turney-High 1949; van der Dennen 1995). Everywhere the most frequent aim and expectation was to kill in a surprise attack.

Although simple warfare is defined as being dominated by raids and feuding, another important form of intersocietal violence was a spontaneous attack on outsiders encountered by chance. In the Andaman Islands men would be armed at

all times. When small parties from neighboring societies met by accident the typical reaction was for those in the larger party to shoot on sight (Kelly 2000). Similar accounts can be found in many nomadic hunter-gatherer societies from the Inuit to Australia (Burch 2005; Riches 1987; Tindale 1974). The Tiwi hunter-gatherers of northern Australia illustrate the attitude to members of other societies: “Outsiders who landed on the islands were massacred or vigorously resisted. . . they were not Tiwi and hence not real people, or at least not human enough to share the islands with the chosen people who owned them. . . . To such visitors from outside, the Tiwi were consistently and implacably hostile” (Hart and Pilling 1965:9–10). Among the Aché of Paraguay, strangers were shot on sight (Hill and Hurtado 1996). Even among hunter-gatherers whose economy was entwined with farmers the same could be true, such as the Agta of the Philippines: “All strangers are highly suspect and may be killed” (Griffin 1984:106).

- In nomadic hunter-gatherer societies battles have also been described. In western Alaska they occurred both in defense against raiders (on the lucky occasions when a raid was detected ahead of time) and as planned confrontations to decide a conflict. According to Burch (2007) the outcome was very sensitive to numbers. Groups that perceived themselves to be small tried to leave. If a melee eventually occurred, the victorious side would kill all except one or two who would be sent home to advise their group not to attack again (Burch 2005, 2007).
3. Compilations of rates of killing in hunter-gatherer war have not distinguished external from internal war, nor peoples bordered by farmers from areas in which hunter-gatherer groups shared a border. Very little can therefore be said of the rates of war death in hunter-gatherer culture-areas. A survey with those problems found a median death rate (from 12 hunter-gatherer groups) of 164 per 100,000 per year, which was similar to the rate of intercommunity killing in chimpanzees (69–287 per 100,000 per year: Wrangham et al. 2006).
 4. How dangerous was simple war for aggressors? Among nomadic hunter-gatherers the preferred tactics were hit-and-run ambushes and surprise attacks (Turney-High 1949; van der Dennen 1995). These are expected to give aggressors a large advantage in simple warfare. An extreme example is reported from the Waorani, an acephalous Ecuadorian horticultural society. A tally of 551 Waorani individuals over five generations revealed the highest death rate from violence recorded in any human population, accounting for 54% of all male and 39% of all female deaths (Larrick et al. 1979). Yet the complete raiding histories of 95 warriors, as well as the recollections of raids by 121 Waorani elders, produced no reports of a member of an attacking party being killed or badly injured in a raid (Beckerman et al. 2009). Chagnon (2009) likewise estimated for Yanomamö that “5% or fewer are killed or injured while raiding others and that most of these casualties would be wounds rather than fatalities.” Table 2 gives other examples in which aggressors were said to have suffered few or no casualties.

Nevertheless raiding carried two types of risk. First, defenders could fight back while under attack. During 13 attacks in external war among Andaman Islanders in which victims suffered six deaths and five wounded, return fire led to two aggressors being wounded by arrows (Kelly 2000:100). Second, if raiders were detected they could themselves be ambushed, sometimes with disastrous results (Table 2). For example in western Alaska, among 58 intersociety fights

Table 2 Examples of the relative numbers of attackers and defenders killed as a result of raids

Location	Deaths of attackers	Deaths of defenders	Notes	Citation
Alaska	0	Many	Waited until men left the camp before attacking	Burch 2007:22. Similar asymmetric massacres by attackers occurred in 31 of 58 conflicts (53%) reported by Burch (2005: App. 1).
Alaska	Most of raiding party	0	Raiding party was seen and ambushed	Burch 2007:20–21. See above.
Grand Valley, New Guinea	0	2	Surprise attack	Heider 1997:99
Grand Valley, New Guinea	0	1	Ambush	Heider 1997:98
Grand Valley, New Guinea	0	1	Surprise attack	Heider 1997:98
Grand Valley, New Guinea	0	1	Surprise attack	Heider 1997:99
Grand Valley, New Guinea	1	0	Raiding party was seen and ambushed	Heider 1997:99
New Georgia	1	0	Attacked village fought back	Zelenietz 1979:96
New Guinea	0	1	Ambush	Koch 1974:191
Solomon Islands	0	6	Surprise attack	White 1979:131
Wisconsin (Dakota)	0	2	Ambush	Hickerson 1988:84

These examples from both hunter-gatherer and horticultural societies show that death rates from interactions in simple warfare tend to be highly asymmetric. Although attackers tend to win, they face a significant risk of being killed when they are ambushed or confronted by a powerful defensive force

reported by Burch (2005: App. 1), attackers won in 40 (69%) but lost in 16 (28%), with the defeated side mostly being massacred (Table 2). Such numbers may be biased given the possibility of victorious survivors selectively forgetting their losses, or successful defenses creating especially acute memories. Even so, the risks for human aggressors in simple warfare appear higher than for chimpanzees.

- Fifth, the question of whether groups that are most often responsible for attacks tend to benefit does not appear to have been systematically reviewed. Certainly decisions about whether to go on a raid and whether to press an attack depend on warriors thinking it safe to do so, but even a militarily weak group can sometimes mount raids safely. The Jarawa and Bea were neighboring Andamanese societies in the nineteenth century, with the Bea having larger numbers (at least at first). However the Jarawa took over parts of Bea territory during a time when they repeatedly attacked and raided the Bea (Kelly 2000). The danger of such raids is the risk of a revenge attack. Burch (2007) records an Inuit group being repeatedly raided by neighboring Athapascans. In response the Inuit themselves raided. They gradually killed off and drove away their Athapascan neighbors, after which they occupied the emptied area. Bishop and Lytwyn (2007) reported a Cree group attacking Dene-speakers in the Hudson Bay area until the Dene left,

whereupon the Cree occupied the vacated lands. Such reports suggest the intuitively sensible conclusion that groups sometimes expand their domain as a result of successful raiding. Raiding could lead to territorial expansion even among hunter-gatherers who were not nomadic. The Wintu of California were village-living hunter-gatherers who would establish new settlements in areas used seasonally by the neighboring Hoka. If the Hoka objected, Wintu raids settled the matter (Chase-Dunn and Mann 1998).

Emic accounts of non-state war rarely report territorial expansion as a rationale for attacks; vengeance or retaliation are the typically stated purposes (Goldschmidt 1988). A similar generalization might apply to hunter-gatherers. For example, motives recorded for raiding among Canadian hunter-gatherers were primarily revenge, fear, and mistrust. Personal prestige and the possibility of capturing a wife were additional goals (Bishop and Lytwyn 2007). Still, in 11 of 13 attacks by Andamanese Jarawa on Bea, violence was apparently prompted “by infringement of the territorial domain rather than revenge” (Kelly 2000:100). Whether or not territorial gain was an explicit goal, it was clearly a possible consequence of successful aggression. The same conclusion applies to non-state societies in general: Ember and Ember (1992) found that victors drove the defeated from their land at least some of the time—in 77% of cases in which warfare occurred at least every two years ($n=30$).

6. Sixth, how far did explicit societal rewards and punishments influence hunter-gatherer men’s decisions to participate in war? Certainly men in nomadic hunter-gatherer groups could not be directed to fight, but motivations to join raids would not always have been entirely personal. Goldschmidt (1988) reviewed cultural influences on men’s participation in raids and warfare in 27 non-state societies, including three nomadic hunter-gatherer groups (Andamanese, Aranda and Chiricahua Apache) and at least four acephalous societies (Jivaro, Klamath, Mae Enga and Mundurucu). He concluded that rewarding, punishing, indoctrinating, and honoring men in relation to their warrior traits were characteristic of these societies. Elements of training included teaching of specific war skills, apprenticeship, games and contests, pain endurance tests, other endurance tests, and the use of legends and stories. It could begin early. Among the Jivaro, boys from the age of 6 onwards were instructed daily on the necessity of being warriors. Goldschmidt (1988) stressed that warriors did not always want to go on raids, citing cases where they lost their nerve while traveling toward an attack and therefore turned back (e.g., for Yanomamö: Chagnon 1992). Those fearful of combat were subject to ridicule. Goldschmidt (1988:53) concluded: “Most societies consciously inculcate military virtues in some ways, and I am confident that if our data were more complete, they would all do so in many ways. Where ethnographers have investigated the matter directly, we find elaborate schooling for the warriors.” Goldschmidt (1988) found no evidence of material rewards for Andamanese warriors, and only slight or rare rewards for Aranda. Material benefits, however, are not expected to be significant in nomadic hunter-gatherers compared with the social benefits, such as elevated status with its political and sexual implications.

In sum, while the pattern of warfare in culture-areas of nomadic hunter-gatherers is not fully understood, there was a strong tendency for hostility toward

members of different societies, and for killing to occur principally in asymmetric interactions. There is also some evidence that after warriors killed members of a neighboring society, the killers' group benefited as a whole via territorial expansion.

Discussion

Chimpanzees

First, do recent data on chimpanzee behavior challenge the chimpanzee model of intergroup aggression? Challenges could come from observations such as peaceful interactions among communities, attacks being made in circumstances that are patently dangerous for the aggressors, or aggressive communities losing access to resources. None of these has been seen.

Chimpanzees tend to avoid territorial boundaries, yet in four of the five longest-term study sites deaths from intergroup aggression have been reported, and in the fifth they have been indicated. There is no evidence of aggressors having been seriously wounded. Males, the main intergroup fighters, have been killed at higher rates than females, and at three sites chimpanzee communities expanded into the ranges of neighboring groups following deaths that were definitely (Gombe, Ngogo) or likely (Mahale) caused predominantly by the invading group. Variation in killing rates is expected by the chimpanzee model since aggressive behavior should be sensitive to context, and this variation is indicated by the number of deaths from aggression in some well-studied sites being particularly high (Gombe: Williams et al. 2008; Wilson et al. 2004; Ngogo: Mitani et al. 2010), while in another it is strikingly low (Taï, Boesch et al. 2008).

Second, is the chimpanzee model compatible with evolutionary theory? Three kinds of adaptive explanation can in theory account for the evolution of chimpanzees' aggressive intergroup behavior: individual selection, genetic group selection, or cultural group selection. Genetic group selection cannot have significant influence if the number of successful intergroup migrants is greater than the rate of group extinction (Maynard Smith 1976; West et al. 2007). Since chimpanzees exhibit a high rate of intercommunity migration (50% to >90% of females per generation: Muller and Wrangham 2001a) combined with a low rate of group extinction, group selection must be a trivially weak force in chimpanzees. Cultural group selection depends on the presence of cultural practices that influence the behavior in question (Soltis et al. 1995). However no social traditions are known to affect intergroup aggression in chimpanzees, so cultural group selection does not appear relevant.

Natural selection acting at the individual level is therefore the only adaptive process that can explain the evolution of the predisposition for intergroup killing in chimpanzees. This might seem surprising given that individuals apparently do not receive benefits in proportion to their investment. Furthermore the costs of territorial defense and intergroup aggression, while low, are positive, including not only the marginal risk of being wounded but also the energetic costs of patrolling the territorial boundary, which can be high (Amsler 2010). However direct individual benefits could come from an increased effectiveness of attack when more aggressors

cooperate: for example, a greater likelihood of damaging or killing the opponent and a reduced likelihood of any members of the killing party suffering injury, with the concomitant benefits of reduced enemy threat and increased access to resources (Clutton-Brock 2009). Similar explanations apply to other species in which individuals regularly cooperate in intergroup interactions by supporting each other against neighbors, and in which larger groups tend to be more aggressive and more successful (e.g., lions [*Panthera leo*]: Heinsohn 1997; Loveridge et al. 2009; Mosser and Packer 2009; spotted hyenas [*Crocuta crocuta*]: Muller and Wrangham 2001b; wolves: Mech et al. 1998; and dogs [*Canis familiaris*]: Bonanni et al. 2010).

In short, without provocation male chimpanzees regularly form coalitions to safely attack and kill members of neighboring groups; individuals in the attacking community tend to benefit as a result; and individual selection is the only viable adaptive explanation accounting for the tendency to take safe opportunities to attack and damage vulnerable rivals. These points support the applicability of the “chimpanzee model” for chimpanzees.

Nomadic Hunter-Gatherers

The second question is whether the chimpanzee model of intergroup aggression applies to nomadic hunter-gatherer warfare. Note that we are not concerned here with explaining variations in war practices. Much is known about differences within and between societies in the nature and frequency of war, including correlations with hunting large animals (Otterbein 1994), fraternal interest groups (Boehm 2011), whether the society is segmented or unsegmented (Kelly 2005), the defensibility of resources (Dyson-Hudson and Smith 1978), and society size (Ember 1974). We ask only whether nomadic hunter-gatherers neighboring other nomadic hunter-gatherer societies tend to show the three key elements of the chimpanzee model: consistent intergroup hostility, safe killing, and benefits from intergroup dominance.

Although intrasocietal relations in hunter-gatherers sometimes include internal wars, these oscillate with periods of relaxed peace and therefore do not conform to the chimpanzee model. Peacemaking is readily explained by bands being members of the same society, with opportunities for linguistically negotiated intermarriage, trade, alliances, and migration between bands (Chapais 2008; Rodseth et al. 1991). By contrast, relationships between societies conform more closely to the chimpanzee model because they had external wars in all nomadic hunter-gatherer culture-areas. They also exhibited safe attacks by aggressors, and successfully aggressive groups at least sometimes gained resource benefits in the long term.

The hunter-gatherer context that fits the chimpanzee model most closely is the Andaman Islands. Because multiple societies were isolated in the Andaman Islands in the absence of agriculture, Kelly (2000:96) regarded them as an ideal natural experiment. However he also suggested that the fact that Andamanese had territories and were resource-limited was unusual for hunter-gatherers. Kelly’s caution looks out of place given that defense of territory was considered by Tindale (1974) to be universal even in Australia, where resources were often so limited that many societies developed elaborate systems for gaining access to each other’s temporary surpluses (Tindale 1974). We suggest that the Andamanese were unusual more in their failure to negotiate intersocietal cooperation than in their having resource-limited territories.

In contrast to the Andamanese and chimpanzees, alliances occurred among other nomadic hunter-gatherer societies. Intersocietal alliances are a common feature distinguishing humans from chimpanzees, facilitated by features such as intermarriage, trade, and language (Chapais 2008; Rodseth et al. 1991). Their occurrence means that human intergroup relationships are normally more complex than among chimpanzees, but they do not eliminate intergroup hostility and territoriality. Jorgensen's comment about North Americans seems widely applicable: "One of the most obvious and interesting aspects of the cultures of western North America's Indians at the time of contact with Europeans was that so few societies actually engaged in persistent offensive warfare, or even raiding, yet the prospects of armed altercations deeply influenced the internal organizations and external relations of these aboriginal societies" (Jorgensen 1980:241, cited in van der Dennen 2007). The chimpanzee model of war thus fits the pattern of intergroup killing among Andaman Islanders and can account for intersocietal hostility among other hunter-gatherers.

The utility of the chimpanzee model of war for nomadic hunter-gatherers faces two important challenges. First is the existence of many peaceful hunter-gatherer groups (Fry 2007). However, Table 3 indicates that of the 21 nomadic hunter-gatherer societies listed by Fry (2007) as being peaceful, at least 13 (62%) interacted with pastoralist, farming, or state societies in ways suggesting that they were militarily and/or politically subordinate. Of the remaining eight, one was so isolated from other groups that it had no opportunity for war (Copper Inuit). Only two appear to be strong candidates for being warless (Columbia and possibly Sanpoil). Further investigation of unusually pacific groups such as the Columbia and Sanpoil is desirable.

Second, in the course of conducting a surprise attack hunter-gatherers were more likely than chimpanzees to have been wounded or killed. This means that the chimpanzee model must be either complemented by the cultural war-risk hypothesis or rejected in favor of the idea that humans are inherently more willing than chimpanzees to take risks in intergroup combat. The relative safety of aggressors in Andaman Islander societies is consistent with the cultural war-risk hypothesis. More such tests are needed in order to determine to what extent the similarity between chimpanzee and Andamanese intergroup violence is representative of general patterns of hunter-gatherers or is due to a specific feature such as their occupying thick tropical forest where attackers cannot easily be detected.

Alternatives to the Chimpanzee Model

Like the chimpanzee model, the parochial altruism model expects that nomadic hunter-gatherers fight over territory and in general do so when safe, but it differs by predicting self-sacrificial or excessively risky behavior, such as suicide missions or dangerous adherence to battle formation in the face of an opposing line, even in the absence of relevant cultural enjoinders (Choi and Bowles 2007). Although raiders certainly encountered risks from being ambushed or otherwise confronted, we have found no accounts of hunter-gatherer war that included deliberately risky behavior leading to death. Burch (2005) cites cases of warriors in western Alaska taunting the enemy by allowing themselves to be shot at. However, they were unharmed by the enemy fire, collected the spent arrows, and shot them back. Battles present a particularly clear opportunity for parochially altruistic behavior. Although battles

Table 3 Characteristics of peaceful hunter-gatherers listed by Fry (2007)

Name	Neighbors	Notes	Citations
!Kung	Bordered by larger pastoral and farming groups	Small-scale raiding occurred in the recent past.	Lee 1979
Batak Agta	State society	They were heavily acculturated and had been organized into political groups.	Warren 1975
Central Inuit	State society at time of ethnography	“their present attitude is well expressed in a speech. ‘In olden times we fought so that the blood ran over the ground. Now we fight with button blankets and other kinds of property.’”	Boas 1964:119
Chewong	Contact with state society	“they fled from marauding Malays.” No record of precontact behavior.	Howell 1988:150
Columbia	Foragers and fishers	No record of being attacked by other tribes or of offensive raids	Jorgensen 1980
Copper Inuit	Foragers, uninhabited land	“500 miles of barren coastline separated the Copper Eskimos from their nearest neighbors to the west, and hostile Indians barred the road southward; on the north was an uninhabited archipelago; while to the east, dotted at wide intervals along a coast not very prolific in game, were Eskimos . . . seldom encountered.”	Jeness 1921:549
Dorobo	Bordered by larger pastoral groups	It was permissible to kill members of other tribes. “Enemies were generally shot at from the cover of undergrowth.”	Huntingford 1954:134
G/wi	Neighbored by Bantu and European ranchers	There is no information on intergroup relations before the Bantu expansion.	Silberbauer 1972
Greenland Inuit	None/other Inuit	Blood feuds, raiding. Also, “The Eskimo migrations were not due to nomadic instinct but most—when enemy neighbors were not the compelling reason—to the desire to reach more favorable hunting grounds” (Rasmussen). “. . . as Arctic studies in the last 20 years have shown, there are no grounds for denying the existence of Eskimo, Thule, or Historic Inuit warfare” (Fossett).	Fossett 2001:49; Nansen 1893; Rasmussen 1919:181
Hadza	Bordered by larger pastoral groups	The Hadza had small wars with their neighbors in the recent past.	Marlowe 2010; Woodburn 1968
Kawaiisu	Foragers	Some small-scale warfare likely. “At least one Kawaiisu consultant referred to the hostility between the Kawaiisu and the Southern Youkuts” (Zigmond). See also Jorgensen for offensive raiding.	Jorgensen 1980:503; Zigmond 1986:399
Mbuti	Surrounded by forest cultivators	“The inseparability of the two people [forest cultivators] makes it . . . difficult to know where to begin.”	Turnbull 1965:26
Paliyan	Immediately bordered by state society and horticulturalists	“Paliyans have been in contact with powerful neighbors for millennia. . . their shy stance is an adaptation developed long ago.”	Gardner 2000:1, 2

Table 3 (continued)

Name	Neighbors	Notes	Citations
Panare	Horticulturalists and foragers	Nearly exterminated due to conflict. Population dropped to four families as a result.	Henley 1982
Penan	Neighbored by a stronger group with superior technology and contact with state society	Very few precontact ethnographic materials. Neighbors have exterminated most groups.	Hose 1894
Sanpoil	Foragers but mostly allied tribes	Some raiding for horses (Ray). “So frequently did Plateau tribes, or segments thereof, participate together in various activities that Anastasio has characterized the entire congeries as a social entity, unified by consensus and reciprocal interaction” (Stern).	Ray 1980; Stern 1998:647
Semai	Bordered by farmers and state society	They “were eventually forced to give up their lands and to retreat into the hills in the face of Malay technological superiority. . . . Conceivably a series of defeats at the hands of the Malays led the aborigines to adopt a policy of fleeing rather than fighting.”	Dentan 1968:2
Semang	Interaction with state society	“the Semang have through intermarriage and trade relationships merged physically and culturally with them. . . . Trade with Malays and Chinese is important in the Semang economy.”	Lebar et al. 1964:182
Southern Paiute	Other foragers	Most groups had small-scale raiding with the exception of the Kaibab. “Several Southern Paiute groups . . . accused others of capturing women and children for sale as slaves” (Kelly and Fowler).	Jorgensen 1980; Kelly and Fowler 1986:368
Waiwai	Numerically superior foragers and horticulturalists; no neighbors to the northeast	“Waiwai history up to the present time is stamped by their almost complete extermination about the year 1890, and the subsequent heavy intermarriage with neighboring tribes.” “Peberdy, who visited the Waiwai in 1946 found . . . only four families or 27 individuals.”	Fock 1963:6, 236
Yahgan	Foragers	Little precontact ethnography. Attacks on and massacres of the early Europeans. “Their culture was much modified before they could be studied.” No mention of intertribal war.	Lothrop 1928:116

This table is adapted from Fry’s (2007) list of “Warless Societies.” We have excluded groups that were not nomadic hunter-gatherers who obtained most of their subsistence from foraging; redundant groups where references indicate similar patterns for all groups (e.g., Point Barrow Inuit, Polar Eskimo); groups with inadequate precontact ethnographic materials; and groups that did not consist of a single small-scale society (Andaman Islanders, Australian Aborigines)

among nomadic hunter-gatherers were generally rare (apparently absent in Andaman Islands: Kelly 2000), Burch (2005: App. 1) reported that 7 of 51 raids conducted

among hunter-gatherers in western Alaska led to battles. Battles can lead to standoffs in which no one is killed, to massacres in which all are killed on one side and none on the other, or to deaths on both sides. A systematic review that searches for evidence of self-sacrificial behavior in societies practicing war but lacking a militarized culture would help to resolve whether parochial altruism is a characteristic trait of warfare in general or results from cultural influences that encourage high-risk or suicidal behavior (e.g., Atran 2003; Atran and Norenzayan 2004; Dunbar 1991).

The parochial altruism model is one of several that could challenge the chimpanzee model by showing that humans have evolved psychological traits for warfare that are not found in chimpanzees. For example, revenge-seeking is a principal motivation for war among hunter-gatherers that has not been evidenced among chimpanzees (Boehm 2011). If traits such as parochial altruism or revenge prove to be evolved characteristics distinguishing humans from chimpanzees, the chimpanzee model will not apply directly to hunter-gatherers. However it will remain a useful starting-point for considering the biological evolution of human war psychology.

An alternative set of interpretations would suggest that warfare among hunter-gatherers was not adaptive. Thus naturally peaceful intersocietal relations might be disturbed from time to time by competitive tendencies that originated in pathology, individual selfishness, or maladaptive ideology. Such ideas could be supported by nomadic hunter-gatherer societies that fail to take advantage of favorable power differentials, or by evidence that where cultures are least militaristic, warfare is particularly variable in style and frequency. Our review did not support these expectations, which were inconsistent with the Andaman case and the pervasive evidence of external war. They could also be supported by evidence of reluctance to kill, as found in modern war (Goldschmidt 1994; Roscoe 2007; Smith 2007). Again we did not find any evidence of such reluctance. The reluctance-to-kill hypothesis makes sense in complex warfare, where warriors are routinely coerced to fight. Even in complex warfare, however, soldiers are not always reluctant to kill: Bourke (2001) reports that in World War II allied soldiers had to be bribed with promises of ice-cream or extra leave to stop killing Japanese prisoners. The reluctance-to-kill hypothesis could be tested by a careful review of the behavior of warriors in simple warfare. Similar considerations apply to the hypothesis that killers tend to suffer post-traumatic stress disorder (Grossman 1995; Smith 2007).

In sum, nomadic hunter-gatherer warfare tends to conform to the chimpanzee model, but whether humans have also evolved species-specific adaptations for war is uncertain. The chimpanzee model therefore appears to be a useful starting point for analyzing the cultural evolution of warfare, and possibly its biological evolution as well.

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