

Combat stress in a small-scale society suggests divergent evolutionary roots for posttraumatic stress disorder symptoms

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Military personnel in industrialized societies often develop posttraumatic stress disorder (PTSD) during combat. It is unclear whether combat-related PTSD is a universal evolutionary response to danger or a culture-specific syndrome of industrialized societies. We interviewed 218 Turkana pastoralist warriors in Kenya, who engage in lethal cattle raids, about their combat experiences and PTSD symptoms. Turkana in our sample had a high prevalence of PTSD symptoms, but Turkana with high symptom severity had lower prevalence of depression-like symptoms than American service members with high symptom severity. Symptoms that facilitate responding to danger were better predicted by combat exposure, whereas depressive symptoms were better predicted by exposure to combat-related moral violations. The findings suggest that some PTSD symptoms stem from an evolved response to danger, while depressive PTSD symptoms may be caused by culturally specific moral norm violations.

PTSD | combat stress | moral injury | evolutionary medicine | cross-cultural psychology

Posttraumatic stress disorder (PTSD) affects individuals who have experienced traumatic events such as war, natural disasters, and interpersonal or sexual violence (1) and has long been associated with combat in industrialized societies. Combatrelated PTSD was first officially diagnosed in American veterans of the Vietnam War (2), but unofficial syndromes, such as "war neuroses" and "shell shock," date back to at least the First World War (3). An estimated 10 to 20% of American combat veterans of the wars in Iraq and Afghanistan have been diagnosed with PTSD (4, 5).

There are competing narratives of PTSD's origins (6). The implicit clinical view is that PTSD is a universal human reaction to dangerous events (7), with some positing that it has evolutionary origins that predate the human species (8–11). Others argue that PTSD is a socially constructed syndrome reflecting the social and political values of American, or at least Western, society at particular points in time (2, 12, 13) and that human responses to trauma are cross-culturally variable and will reflect a particular society's "idioms of distress" (14, 15). It has also been argued that combat-related PTSD may be unique to large-scale industrial societies that lack traditional systems of support available in small-scale societies (16).

However, distinguishing between these hypotheses has been challenging because the majority of research on trauma resulting from combat has been conducted with members of large-scale industrialized societies (14), which are not representative of most human groups (17, 18) and where combat experiences and moral norms of violence are less variable (19). Combat-related trauma has been described in non-Western industrialized societies among child soldiers (20–22) and survivors of war or mass violence (23–25). Local concepts of noncombat distress have been described in non-Western societies (14, 26–34). Together, these studies suggest that responses to trauma are influenced by cultural context. However, developing an integrated cul-

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tural and evolutionary account of combat stress would benefit from examining combat experiences of warriors in small-scale, nonhierarchical, nonindustrialized societies.

To help fill this empirical gap and better understand the ultimate causes (35-37) of combat stress, we examined the prevalence of PTSD symptoms among the Turkana, seminomadic subsistence pastoralists in Kenya who engage in lethal interethnic cattle raids. We surveyed warriors who live in the northern frontier of Turkana territory who frequently raid neighboring Toposa pastoralists in South Sudan and who are also frequently raided by the Toposa. Turkana in this area have a high degree of combat exposure, with approximately half of adult male mortality stemming from combat (with about 54% of the deaths from offensive raids and 46% while defending) (38). While only men participate in offensive raids, women and children are victims of violence when Turkana are attacked, actively participate in defensive support roles, and defend themselves from attack. The Turkana and neighboring pastoralists launch both "battle raids" involving hundreds of warriors in open combat and "stealth raids" involving fewer than a dozen warriors who try to capture animals undetected. The main goal of raids is to acquire livestock, but other motivations are gaining dry season pasture and wells along borders and retaliation for past raids. Cattle raiding is thought to have been ongoing for at least 200 y among pastoral groups in this region (39-41). Turkana do not generally raid other Turkana since raiding other Turkana is strongly

Significance

Did PTSD and combat stress evolve as a universal human response to danger? Or are they culturally specific? We addressed this question by interviewing 218 warriors from the Turkana, a non-Western small-scale society, who engage in high-risk lethal cattle raids. We found that symptoms that may have evolved to protect against danger, like flashbacks and startle response, were high in the Turkana and best predicted by combat exposure. However, symptoms that are similar to depression were lower in the Turkana compared to American service members and were better predicted by moral violations. These findings suggest different evolutionary roots for different symptoms which may lead to better diagnosis and treatment.

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condemned. Firearms began to proliferate and replaced spears in the late 1970s, which likely increased the lethality of raiding, although prefirearm raiding traditions persist.

Unlike state-level military operations, even large battle raids in Turkana are informal, voluntary, and implemented without centralized coercive authority and provide individual warriors with significant autonomy (38, 42, 43). Any warrior, leader, or diviner may propose to launch a raid and, if the idea gains traction, messengers are sent to announce the proposal and recruit participants from different settlements and subterritories. Those who plan to join encourage close friends, trusted raiding companions, and local age mates, cohorts of closely bonded similarly aged coequal men, to also join. Warriors are not professional and do not train for combat. No one has authority to coerce an unwilling person to join, although there is peer pressure to join if many of one's age mates are going. Prior to departure, raiders are exhorted by fellow combatants, celebrated by their community, blessed by the elders, and advised by prominent warriors. Animals are donated for communal feasts. Warriors dance to embolden and incite each other with songs of past successes and reminders of livestock lost when the enemy raided them. If the raid is organized by a diviner, the diviner details rituals and prohibitions that the raiding party must follow. Scouts who initiated the raid, renowned warriors, diviners, or settlement leaders may act as the raid leader, steering discussions, formulating strategies, and announcing plans, while informal age-group leaders communicate to and adapt plans for their constituents. Leaders have no coercive authority and social sanctions for violations are meted collectively by the community and age mates through criticism, corporal punishment, and fines of livestock.

Raiding parties typically travel on foot 50 to 100 km outside of Turkana territory. En route participants may turn back as they become overcome by fear or premonitions of their imminent death and factions of warriors can announce that they are aborting the raid due to poor leadership or cohesion in the raiding party. Attacks are launched at the enemy's settlement during the night or dawn, in the pastures or watering points during the day, or when they are migrating. The raiding party organizes itself into wings based on age groups and aims to surround settlements from three sides, leaving the direction toward Turkana territory open for driving the escaping livestock. Women and children, although seldom targeted, can get caught in the crossfire. Warriors have substantial autonomy on potentially salient moral issues such as whether and whom to kill in combat, how much property damage to inflict, and whether to kidnap or facilitate the kidnapping of young boys for herding labor (43). Firefights can last from a few minutes to a full day and entail zero to scores of casualties, depending on whether the raiding party easily overcame a few herdsmen alone with cattle or the opponents ambushed the raiders, were numerous, or received reinforcement. In battle, a warrior may develop *ejokopi*, a state of incapacitating confusion in which he is unable to fight, escape, or recollect his name and needs to be guided out of the combat zone. A fallen opponent's firearm and other possessions can be retrieved by his killer, and these acquisitions become a source of pride. Injured men are carried back home when possible, although difficult decisions often need to be made to leave injured companions behind. Friends and age mates of a warrior who died in battle are often blamed by the grieving family for persuading him to go, for not protecting him during combat, or for not carrying him home when he got injured. The bodies of those killed in battle are left where they fell, but attempts are made to retrieve their firearms and possessions to preempt the opponent's side from taking them. Turkana in our study area did not personally know the majority of Toposa they raid; however, some had developed friendships with individual Toposa in peacetime who they sometimes might encounter in battle.

A successful raiding party can acquire hundreds of cows and is celebrated upon its return. Cattle won on a raid are divided between the participants. On a large raid, cattle are distributed to different age groups, who then divide it among themselves. Participants sometimes dispute their allocation, which can result in threats or interpersonal violence to resolve the dispute. On some raids, participants disregard division protocols and appropriate whatever livestock they could escape the battle with, causing men who stayed on fighting to feel betrayed. Afterward, there is continued discourse about the how the raid unfolded, with participants narrating details of the sequence of events to their age mates, family, and settlement members. Individuals are singled out and praised by their compatriots for turning the tides of battle, rescuing compatriots, assisting a weakened wing, or killing enemies in combat. Cowards, those who did not stand their ground or who fought from the rear, are identified by other raiders and criticized by the community, reprimanded by age mates, and after collective deliberations may be beaten by age mates or made to give up a prized bull. Rituals are performed to honor those who brought cows and, as we describe below, to honor men who killed or cleanse them to preempt haunting by dead enemy spirits. Individuals compose songs of their exploits that are sung at dances for years afterward and stories of remarkable losses and victories are retold to younger generations.

To explore the origins of combat stress, prior to data collection with the Turkana, we classified the 20 PTSD symptoms in the current edition of the *Diagnostic and Statistical Manual of Mental Disorders* (DSM-5) (1) into functional categories (Table 1) based on the adaptive problems they may have evolved to solve. These classifications suggest that some categories of PTSD symptoms will be culturally universal responses to dangerous combat situations, while others would depend more on cultural norms surrounding combat and be more culturally variable. While classifying symptoms in terms of proposed evolved function is not the norm in psychological or psychiatric research, it is considered a starting point for asking questions about the origins of psychiatric disorders in evolutionary medicine (9, 10, 36, 44–46) and

Table 1. DSM-5 PTSD symptoms organized by functional categories

Functional category	Symptom		
Learning	Memories		
	Nightmares		
	Flashbacks		
	Cued distress		
	Cued physical reactions		
Reacting	Hypervigilance		
	Startle		
Depressive	Low concentration		
	Detachment/estrangement		
	Irritability/aggression		
	Loss of interest		
	Negative beliefs		
	Negative feelings		
	Numbing		
Mixed	Avoiding reminders		
	Insomnia		
Others	Amnesia		
	Avoiding memories		
	Blame		
	Recklessness		

2 of 10 | PNAS https://doi.org/10.1073/pnas.2020430118 Zefferman and Mathew Combat stress in a small-scale society suggests divergent evolutionary roots for posttraumatic stress evolutionary behavioral sciences (11, 47–49). The reasoning for our classifications is detailed in *SI Appendix*, section S1; a comparison between our functional classification system and various clinical classifications, adapted from ref. 50, is in *SI Appendix*, section S2; and symptom descriptions that we used with the Turkana are in *SI Appendix*, section S3. Although a robust literature in cross-cultural psychology examines responses to trauma that do not conform to Western conceptions of PTSD (51), we conducted this study with the Western construction so that any contrast with Turkana would be most apparent.

Our first symptom category includes "learning" symptoms: nightmares, flashbacks, cued distress, and cued physical reactions. These symptoms had been previously hypothesized to have evolved because reexperiencing trauma could help individuals efficiently learn about acute hazards from a single traumatic experience (9, 10). Our second category includes "reacting" symptoms: hypervigilance and enhanced startle response. These symptoms had been previously hypothesized to have evolved because they prepare individuals to quickly respond to similar hazards in the future (9, 10). The symptoms in these two categories, which we refer to as learning-and-reacting symptoms, are thought to have evolved as responses to physical danger with origins that may predate modern humans (9, 10). Therefore, we expected that these symptoms would be cross-culturally prevalent and likely to be experienced by soldiers of state-level societies as well as warriors in small-scale societies such as the Turkana.

PTSD and depression are comorbid and have overlapping symptoms (52-54). We categorized as "depressive" the symptoms of PTSD that are related to low mood and depression: loss of concentration, detachment or estrangement from loved ones, irritability, loss of interest in enjoyable activities, negative beliefs and feelings, and emotional numbing. Unlike learningand-reacting symptoms, there is little prior evolutionary theory for why low mood should be a response to physical danger. However, there are existing evolutionary hypotheses of low mood and depression (48, 49, 55–57) including the hypothesis that these symptoms evolved to help solve complicated social dilemmas (56) and avoid social risks (57). Combat carries a particular type of social risk, the risk of violating moral norms concerning harm and violence. Violating moral norms can have evolutionary consequences when it results in social sanctioning or failed coordination (58), which can be especially salient in the life and death scenarios inherent in war (19, 38, 43). Furthermore, clinicians have begun to recognize that "moral injury," trauma caused by witnessing or participating in the violation of moral norms, either as participants or victims, (59) may be an important contributor to combat stress. Moral injury has also been proposed to have an evolutionary connection to depression (43, 60). The symptoms we categorize as depressive are similar to "dysphoric" symptoms in some clinical models (61-64) of PTSD symptomatology (SI Appendix, section S2). We hypothesized that witnessing or participating in potentially morally injurious events would be more strongly associated, in the Turkana, with depressive symptoms than with learning-and-reacting symptoms.

Since moral norms governing conduct in combat, including norms about killing of opponents and civilians, vary between societies, depressive symptoms should be influenced by a warrior's social and cultural context. For example, many American military veterans grow up in civilian society where they may not experience socially sanctioned lethal violence until adulthood and so may experience greater moral ambiguity about killing compared to combatants from societies without a distinction between "civilian" and "military" life. Also, combatants in small-scale societies where leaders have little to no coercive authority may have more autonomy to perform combat actions that align with their moral beliefs than soldiers who are embedded in a hierarchical command structure. They may also perceive broader support for their participation in combat than soldiers in societies where most people have never experienced combat or have prevalent antiwar sentiments. Because Turkana warriors have greater autonomy, raiding is widely endorsed, killing of opposing warriors in combat is unambiguously morally appropriate, and military and civilian societies are not separated, Turkana warriors should be better able than soldiers of nationstate societies to avoid combat experiences that violate personal or communal moral norms (43). Therefore, we hypothesized that Turkana warriors would have comparatively lower prevalence of depressive PTSD symptoms than soldiers of industrialized nation states.

Some symptoms did not fit into the learning, reacting, or depressive symptom categories. We classified two of these symptoms (insomnia and avoiding external reminders of a traumatic experience) as "mixed" because they could fit in multiple categories and classified five of these symptoms (selective amnesia, avoiding memories of the traumatic experience, blaming oneself or others for the traumatic experience, and recklessness) as "other" because we did not have predictions for how these categories will vary between societies or types of trauma. We do not claim that no functional evolutionary explanations are possible for these symptoms, only that we could not classify them in our framework. Additional information about the criteria for our functional classification is in *SI Appendix*, section S1.

To examine the cross-cultural similarity of combat stress symptoms, we compared Turkana PTSD symptom severity to an existing dataset of PTSD symptoms in treatment-seeking American service members who served in Afghanistan and Iraq (65). In both populations, following the PTSD Checklist for DSM-5 (PCL-5) (66), participants ranked how much each of the 20 PTSD symptoms bothered them in the previous month on a severity scale from 0 to 4, for a maximum total severity score of 80. Since we found that the American service members were more likely to respond with moderate values (1-3) and Turkana warriors were more likely to respond with extreme values (0) and 4) (SI Appendix, section S6), we compared the presenceabsence of each symptom using the standard cutoff (66) where a symptom with a score of 2 or more is classified as present. Since the American sample was of treatment-seeking service members, they had higher average symptom severity than American service members generally, while none of the Turkana were treatment seeking. Therefore, we also restricted our comparison to individuals from both groups who had a PTSD severity score of 33 or higher, the standard cutoff score for a provisional diagnosis of PTSD (66). The distributions of total PTSD severity scores for the Turkana (n = 62) and Americans (n =701) with high severity were similar (Turkana M = 47.1, SD = 9.6; American M = 48.8, SD = 10.2), allowing us to compare what symptoms were more or less likely to contribute to high PTSD severity among Turkana warriors and American service members.

Since we hypothesized that different types of combat experiences might contribute more to different PTSD symptoms, we also modeled total symptom severity, learning-and-reacting symptom severity, and depressive symptom severity in the Turkana using 10 predictors that capture a wide range of combat experiences and chose the best models for each symptom category type. The predictors are listed in Table 2 and described in more detail in *Materials and Methods*.

Results

We calculated descriptive statistics of Turkana combat exposure and reported PTSD symptom severity, compared the prevalence of Turkana PTSD symptoms to prevalence in a sample of treatment-seeking American service members, and conducted

Table 2. The 10 predictor variables used for statistical models of PTSD symptoms

Variable	Definition		
Combat exposure			
CE1	Combat exposure factor 1		
CE2	Combat exposure factor 2		
CE3	Combat exposure factor 3		
Combat outcomes			
AG	Gained animals		
AL	Lost animals		
Moral events (victim)			
MEV	Moral events victim scale		
Moral violations			
MS	Moral sphere scale		
MEP	Moral events perpetrator scale		
К	Killed in battle		
SS	Social sanctioning scale		

More details of these variables are in *Materials and Methods* and in *SI* Appendix, section S7.

a regression analysis to find the set of models that best predict Turkana PTSD symptom severity and the symptom severity of our main functional categories.

Turkana Combat Exposure and PTSD Symptoms. Turkana warriors in our study had a high degree of combat exposure. Subjects recounted participation in a median of three battle raids, one stealth raid, and two defensive raids. They recounted being ambushed by hostile forces a median of four times. A total of 72% reported having killed an enemy in combat and 26% had at least one visible bullet wound from enemy fire. Since, based on prior ethnographic experience, we expected subjects to preferentially report raids that are more recent, had more prolonged firefights, had high mortality rates, or involved substantial livestock gains or losses, the reported combat exposure is likely a lower bound on lifetime combat exposure, but should include the most salient combat events.

Contradicting the view that combat stress is unique to Western or industrialized societies (16), Turkana warriors have a high prevalence of combat-related PTSD symptoms. Of the 218 Turkana warriors we interviewed, 62 (28%) had total PTSD severity scores of 33 or higher (Fig. 1), which is a clinically defined threshold for a provisional diagnosis of PTSD in Western samples (65). However, since PTSD is not a validated clinical diagnosis in the Turkana, our results should not be taken to imply that Turkana participants have a clinically recognized mental health condition known as PTSD, only that symptoms associated with the Western conception of PTSD are also experienced by the Turkana. Selected participant descriptions of learning, reacting, depressive, and mixed symptoms are in Tables 3 and 4 with additional examples of these and other symptoms in *SI Appendix*, section S4.

We explored whether the functional evolutionary categories that we identified a priori were reflected in the data with a factor analysis of Turkana PTSD symptoms and found the categories, with a couple exceptions, reflected in the factors as reported in *SI Appendix*, section S5. We also explored a possible relationship between participant age and symptom severity (*SI Appendix*, section S12), as it is possible that PTSD symptoms would reduce with time since exposure to the traumatic events (67). We did not see an effect of age on symptom severity, which may be because symptoms persist long after particularly traumatic raid experiences, or because subjects are frequently exposed to traumatic raid experiences, or both.

Participant descriptions for 17 of the 20 symptoms consistently corresponded to the conception of the symptoms in the DSM-5, suggesting that most combat-related PTSD symptoms have cross-cultural validity, even if their prevalence may vary across societies. For all of the symptoms, except "recklessness," we were able to develop questions through this process that elicited responses which corresponded with the symptom descriptions in DSM-5. While participants understood specific examples of reckless behaviors, they did not seem to generalize these examples into a category of "reckless" behavior, suggesting that Turkana may not have such a predefined behavioral category of recklessness. In addition, post hoc descriptions of two symptoms, selective amnesia and loss of concentration, did not consistently correspond to the DSM-5 conception. Specifically, some respondents to the "selective amnesia" question reported memory loss due, at least in part, to old age, suggesting overreporting of that symptom. Additionally, we had very few reports of concentration loss (9 clear recordings of only 12 reports) with none clearly meeting the DSM-5 definition. Another round of back-translation confirmed that the question conveyed the intended meaning, so this symptom may simply be very rare in the Turkana. To account for potential validity problems from these symptoms, we conducted all subsequent analyses both including and excluding "recklessness," "amnesia," and "concentration." Results including these symptoms are in the main text; results excluding them are in SI Appendix, section S11 and are similar.

Turkana vs. American Symptom Prevalence. Similarities and differences between the relative symptom prevalence of Turkana warriors and American service members with high severity scores are shown in Fig. 2. Learning-and-reacting symptoms have similarly high prevalence in the Turkana and American samples, consistent with the hypothesis that these symptoms are responses to acute physical danger. Three depressive symptoms (negative beliefs, negative feelings, and emotional numbing), one mixed symptom (insomnia), and three uncategorized symptoms (amnesia, blame, and recklessness) also had similar prevalence between the two samples. The high prevalence of insomnia is also consistent with cross-cultural comparisons of PTSD in industrialized societies (14). However, five depressive symptoms (low concentration, detachment, irritability, loss of interest, and

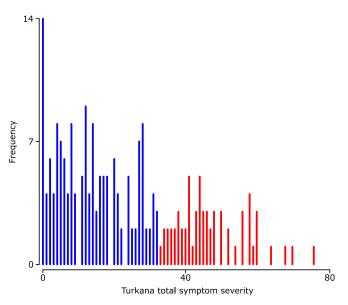


Fig. 1. Total PTSD severity scores for 218 Turkana warriors. Red bars correspond to scores of 33 or higher, the standard cutoff to qualify for a provisional diagnosis of PTSD (65, 68). Sixty-two warriors (28%) had scores over 33.

	Table 3.	Select participa	ant descriptions o	of learning-and-reactin	a symptoms t	ranslated from	Turkana to English
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Symptom	Participant description
Learning Symptom	
Memories	The death of my close friends, in-laws, cousins, and people of my clan makes me remember the raid frequently, even if I don't want to remember anything about it. It just comes to me unnoticed without me thinking about it. A woman who named her baby after me was also killed in the raid. This created a "death mood" in my life; whenever I see my namesake and other people who lost their beloved ones, I became too angry and emotional. The enemies did not manage to win even a single animal, although some of them were killed by bullets during the fight.
Nightmares	I dreamed about everything that happened in that raid, of how we engaged in a fight with the enemies. Sometimes I dreamed about walking together with my age mates who lost their lives in the raid. The image of my best friend, who deserves to be called "brother" not a friend, keeps on coming to my mind. While in a dream, I could hear him calling me: "Please, my brother, don't let me die. Come and stay with me. Why is it that there is nobody to stay close to me since you left me alone? You have turned against me in the last days of my life? Come on, brother, and give me company in this hostile place."
Flashbacks	I thought I was fighting after being caught by the owners of the goats [I had raided]. I took my gun and fired aimlessly into the night thinking that I was fighting with the enemies. I ran shouting, "Redirect the cattle! Quickly! Adeptly!" just like what had happened in the raid. I ran through my animals shooting, but after reaching the east side of our compound I realized that there was no fighting. It was a dream.
Cued distress	After that raid happened, I was very upset not only by the enemies. I also get upset by anyone from the community who reminded me of my brother, [name redacted], who taught me how to fight and go on raids. I became emotional and cried while grabbing the gun, ready to finish that person, thinking that he was the cause of my brother's death and the reason why my brother is no longer among us.
Cued physical reactions	When I am walking on the road, thoughts usually come and my body trembles. Once, after trembling, I remained standing alone in the field. The way I was standing while folding my hands together attracted the attention of people. They came to me and asked what I was going through in life, but I walked away silently from them.
Reacting symptoms	
Hypervigilance	After the raid, I became superalert. Whenever I go to the forest I monitor my movements. When I am in an insecure place, I don't step on the bare soil. I step on the shrubs and logs. This is because I don't want enemies to discover my footprints and follow me to where I went. While herding, I never sit down and remain in the same place. I am always keen and alert.
Startle	One day I woke up with my gun ready to shoot thinking that the enemy was creeping up to attack me while I was sleeping. Later, I realized it was a camel grazing close to where I was sleeping. Then I put the gun on safe and lowered it down. Some days later, again I woke up and got scared with a "kutukuut" (the sound produced by running donkeys). Because of that sound, I got up and shot abruptly, "puup," thinking enemies were running. Due to bad luck the bullet destroyed the forelimbs of the running donkey.

Additional descriptions are in SI Appendix, section S4.

negative feelings), one mixed symptom (avoiding reminders), and one uncategorized symptom (avoiding memories) were lower for Turkana warriors than for the American veterans (Fig. 2 and *SI Appendix*, section S6). This is consistent with the hypothesis that depressive PTSD symptoms are more crossculturally variable than learning-and-reacting symptoms and suggests that aspects of Turkana warfare norms, moral beliefs, and social organization may be limiting the severity of these, mostly depressive, symptoms relative to those of American service members. Although, additional cross-cultural and longitudinal studies would be needed to strengthen the evidence for these hypotheses.

Predictors of Turkana Symptom Types. Statistical modeling suggests that combat exposure, combat outcomes, and moral factors influence PTSD symptom severity (Fig. 3 and *SI Appendix*, section S9). As predicted, when averaged across all models, PTSD severity scores were positively associated with combat exposure, losing animals, exposure to morally injurious events (where Turkana are both victims and perpetrators), greater moral spheres, and exposure to social sanctions. Gaining animals was negatively associated with PTSD symptom severity scores, as predicted.

Predictors associated with combat exposure and outcome were more strongly associated with learning-and-reacting symptoms (in terms of the total relative pseudo-Bayesian model averaging [pseudo-BMA] weight for models including those symptoms) than with total severity or with depressive symptom severity (Fig. 3). As predicted, higher levels of combat exposure, and loss of animals, are positively associated with learning-and-reacting symptom severity, while livestock gains are negatively associated. This is consistent with the hypothesis that learning-and-reacting symptoms are responses to the dangers of combat and potentially influenced by combat success or failure.

Predictors associated with moral violations were more strongly associated with depressive symptoms than with total severity or learning-and-reacting symptoms (Fig. 3). As predicted, exposure to moral violations as victims, having greater moral spheres, perpetrating moral violations, and exposure to social sanctions were all positively associated with depressive symptom severity. This is consistent with the hypothesis that depressive symptoms are related to violations of moral norms of behavior.

The relationship between killing in combat and PTSD is more complicated. Counter to our prediction, killing of opponents, despite being celebrated in Turkana culture, was associated with higher depressive symptom severity. Additionally, killing was ANTHROPOLOGY

Table 4. Select participant descriptions of depressive and mixed symptoms translated from Turkana to English

Symptom	Participant description		
Depressive Symptom			
Low concentration	[Although the wording of this question passed back-translation and a pilot with Turkana outside of our study area, we did not have a description of this symptom that clearly corresponded with the DSM definition among the nine translations we had from the 12 subjects who reported having the symptom.]		
Estrangement	I stayed away from the traditional dances and stopped joining other elders [for discussion] under the trees. Most of the time my heart recalled people who were killed by the enemies on the raid. I stayed away from other people, just like an animal. To tell you the truth, I am not from this area. I am from [another part of Turkana]. I am here because my people were killed.		
Irritability/aggression	Sometimes when people are talking about their own business, I think they are talking ill of me. I often get upset and say "Why do I even talk to people?" Even when a small child tells me something, my stomach always rejects it. When an animal keeps on disturbing me, I kill it because my heart is so harsh and brutal.		
Loss of interest	I avoided even the traditional dances that I used to participate in. I abandoned even footraces. I avoided even practicing how to fight with clubs. My heart has forsaken all of these activities. My heart now wants herding only. Then to sleep, or to go for a raid with other raiders, or join a group of scouts who go spy on a herd of [the enemy's] cattle during the grazing season.		
Negative beliefs	As I wrangled over the cow with another fellow, I was wondering, "What is bringing about all this? How does God treat me? How does he want me to live, or is it the devil that is responsible for all this? What led me deep into the fight while others were running away with the cattle? That I luckily came out of the raid with one cow, which I got by chance, but somebody has come now to wrangle over it with me? Or have I eaten that which belongs to the elders? So, those thoughts drove me to kill that cow.		
Negative feelings	My body develops negative feelings when remembering friends and other warriors who died in the battle. I become too upset and concluded that I will never participate in a raid again if this is the result and impact. I also had negative feelings about myself because of the enemies that we killed, as their blood flows like a river. I put a palm on my mouth as a sign of worry and wonder about people who we have killed, including innocent children. I felt pity for killing God's creation and destroying their houses.		
Numbing	Even when you meet with people, you do not laugh with them as is typical. You hardly greet them. You walk silently with each other. You keep going in opposite directions. Everything in the world taunts you because of the people who were killed by the enemies; your best friends, cousins. That weakens your body and you feel like, "What is my role here? Why should I laugh when people, many people, have been killed and did not return from the raids?"		
Mixed symptoms			
Avoid external reminders	Weapons and items that I used to own, I took them all and gave them to people, thinking that maybe these were making me remember the raid, the people who died, and the blood that was shed during the battle. The bags of the bullets, caps, a blanket that was left by a boy from our side who was killed in the raid; I gave away everything which I believed to be responsible for the bad thoughts.		
Insomnia	Sleep became a problem for me because I could not sleep. I was thinking that if I sleep an enemy will come for me and kill me while I am sleeping.		

Additional descriptions are in SI Appendix, section S4.

associated with lower learning-and-reacting symptom severity. This could be because killing may signal gaining the upper hand in the firefight and thus may play a similar role in mitigating the response as gaining livestock. However, killing, as indicated by the narrow width of the associated bars in Fig. 3, was not frequently represented in the top models. Moreover, the direction of influence when it was represented was inconsistent (SI Appendix, section S9) even if it was overall positive for depressive and negative for learning and reacting (Fig. 3). The low importance of killing in our models indicates that killing is not as important a contributor to PTSD in Turkana as it is for American combat veterans (69, 70), consistent with our hypothesis. The overall direction of association being positive suggests that killing could still be a morally hazardous act despite cultural norms condoning it. Since our measures of potentially morally injurious events were based in part on scales developed for American combat veterans, they may have had a weaker association with depressive symptoms than measures based more specifically on Turkana moral beliefs, which differ from American beliefs in many respects (43).

Three of 30 associations were, when taking a weighted average across models, in a direction that did not fit our predictions. Gaining of animals (AG), while consistently negatively associated with total and learning-and-reacting symptom severity as predicted, was sometimes positively associated with depressive symptom severity. However, the coefficient for AG is not in any high-performing models and is inconsistent in magnitude and direction (SI Appendix, Fig. S3). It was also hypothesized to not be important for depressive systems, suggesting a weak or noncausal association. Social sanctions (SS), while consistently negatively associated with total and depressive symptom severity as predicted, were negatively associated with learning-and-reacting symptom severity. However, they were also not represented in high-performing models (SI Appendix, Fig. S4) and were hypothesized to be unimportant for predicting learning-and-reacting symptoms severity. The third factor of combat exposure (CE3) was negatively associated with depressive symptom severity. However, it was also not represented in the best-performing models (SI Appendix, Fig. S3) and combat exposure was hypothesized to be unimportant for predicting depressive symptom

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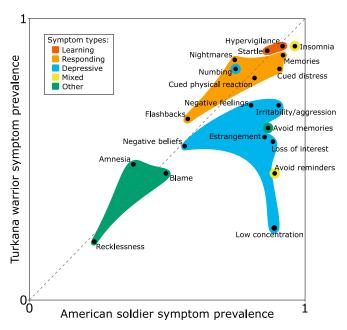


Fig. 2. Prevalence of each PTSD symptom in high PTSD severity Turkana warriors and American service members, measured by the fraction of each population who reported a severity score of 2 or higher. Symptoms are colored by category and the dashed line represents the 1:1 line. Turkana and Americans have similar relative prevalence for most symptoms, although Turkana have lower prevalence of five depressive symptoms, one mixed symptom, and one other symptom.

severity. Since all three of these predictors appear primarily in models with low pseudo-BMA weight for the relevant symptom category and were not expected to be important predictors for those categories, and two were not consistent in magnitude or direction across models, these results suggest weak or noncausal relationships.

Parameter estimates, confidence intervals, and pseudo-BMA weights for each model are in *SI Appendix*, section S9 and parameter estimates for the top 20 models for each symptom type are in *SI Appendix*, section S10. Fitted model results excluding the symptoms of amnesia, recklessness, and concentration are in *SI Appendix*, section S11 and are qualitatively similar.

Discussion

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Our findings demonstrate that combat-related PTSD symptoms are not limited to industrialized societies and can occur even in small-scale societies where warriors are venerated and socially embedded in tight-knit communities. In particular, learning-andreacting symptoms are potentially evolved responses to acute dangers such as those encountered in combat. These symptoms had high prevalence among both American service members and Turkana warriors. Moreover, among the Turkana, combat exposure and combat outcomes were more consistently associated with learning-and-reacting symptom severity than with depressive symptom severity.

Our findings have implications for understanding the roots of moral injury (59, 71, 72), trauma caused by "perpetrating, failing to prevent, or bearing witness to acts that transgress deeply held moral beliefs and expectations" (ref. 59, p. 695). For example, moral injury can occur when soldiers violate morally held beliefs against killing civilians (73). Moral injury might also be the primary cause of combat stress in drone pilots who, even though they are flying combat missions from a control room far from danger, have a high-definition view of the human suffering caused by their missile strikes (74). Our statistical models suggest a relationship between moral injury and

depressive PTSD symptoms in particular. Combat exposure and outcome measures are not as important predictors for depressive symptoms as they are for learning-and-reacting symptoms among the Turkana. Instead, predictors assessing exposure to moral violations as perpetrators or victims and experiencing social sanctions are associated with depressive symptoms. Additionally, having moral concerns for a larger segment of people from the opposing side was more strongly associated with depressive symptoms than with learning-and-reacting symptoms. All of this supports the idea that depressive symptoms may be a response to expected social sanctioning due to moral violations, which is consistent with some evolutionary theories of depression (56, 57). However, it is also possible that depressive symptoms, whatever their cause, may make instances of moral injury more salient to study participants. Additional experimental, longitudinal, and cross-cultural research may resolve the direction of causality.

Consistent with the association in the Turkana between expected social sanctions and depressive symptoms, Turkana warriors with high symptom severity were less prone than American service members to experience some of the depressive symptoms of PTSD. This could be because the actual or perceived social risks of participating in war are lower for Turkana warriors than for American service members. Turkana warriors are venerated and there is widespread support from their community for going on raids and defending the Turkana from raids. They do not expect to face moral disapproval for participating in combat (43) (although they do face moral disapproval for cowardice and can be blamed for the death of comrades). In fact, those who have killed in combat are often celebrated in Turkana society with many warriors undergoing akiger, a ritual that scars the warrior's body to mark him as someone who has killed. Warriors with akiger scars are highly regarded by both men and women. Additionally, raid participation is high among Turkana men, so warriors are almost always in the company of other warriors with similar combat experiences. Many women and children too have experienced raids by other groups. As such, combat experiences are a commonly shared and a frequent topic of discussion in Turkana society. There is little to no stigma associated with sharing the details of combat (43).

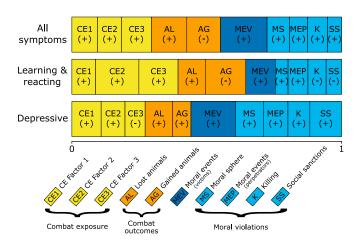


Fig. 3. Summary of total pseudo-BMA weights for models of each symptom severity type (total symptom severity, learning-and-reacting symptom severity, and depressive symptom severity). The bar length for each predictor represents the total pseudo-BMA weight for all models containing that predictor. The BMA weights are then normalized across predictors for each response variable so that they total one. Predictors labeled (+) have generally positive relationships. *SI Appendix*, section 59 shows pseudo-BMA weights, slopes, and confidence intervals for all fitted models.

By contrast, in the United States and other industrialized nation states, support for war and those who participate in war is often far from universal, and killing, even in combat, is rarely celebrated. American soldiers fight in foreign countries away from the civilian population and, upon returning, they may perceive disapproval of their experiences and actions from friends and family. Additionally, most Americans cannot relate to the experiences of those who have participated in combat. Consequently, warfare presents a moral conflict because what is considered a soldier's duty in combat can violate prevailing moral norms within the soldier's society. American soldiers may therefore have a heightened awareness of potential social repercussions especially as they integrate back into civilian life. Veterans' support groups and group therapy replicate some aspects of Turkana society by allowing veterans to share their experiences with each other, but Turkana warriors receive stronger signals of social support and understanding from all members of their communities.

Since most PTSD research has not focused on symptomspecific causes, moral injury research is relatively new, and combat trauma research has not taken a functional evolutionary perspective, there has been little attempt to associate depressive PTSD symptoms with moral injury in the Western context. A better grasp of symptom-specific patterns of PTSD in Western military personnel, as we have done with the Turkana, would be useful to further evaluate the proposed theory, delineate what moral injury manifests as, and assess how it relates to PTSD.

The effect of killing in combat on PTSD is more ambiguous in the Turkana than in American service members. While killing in combat is an important contributor to PTSD in American service members who served in Iraq and Afghanistan (70, 75), it was not present in the top models of total, learning-andreacting, or depressive symptom severity in the Turkana. On average, the direction of influence is to reduce learning-andreacting symptoms but increase depressive symptoms, opening the possibility that it might be a contributor to moral injury even in a population where killing in combat confers prestige. While this was counter to our prediction, it is consistent with some ethnographic observations. The Turkana, as well as neighboring pastoral groups, have culturally specific idioms of distress associated with killing in the war zone, including perceptions of being polluted, beliefs that killing portends future misfortune, and feeling haunted by the enemy's ghost, which suggest that killing of enemies is a potentially morally hazardous event (76). Among Samburu pastoralists, war zone mercy occurs even in circumstances where killing of the opponent would be normative, indicating that warriors may feel empathy toward their opponents (76) and can thus perceive killing as morally hazardous.

Our results imply that while killing is potentially morally hazardous across cultures, culturally specific institutions mediate its role in causing PTSD, which clarifies why killing is more risky for American service members than for Turkana warriors. First, norms regarding killing of individuals from the opposing side are less restrictive among the Turkana than in nation-state warfare. Unlike in nation-state warfare, the Turkana have a high level of moral autonomy in who they kill in combat, a pattern noted in other pastoral societies (76). Additionally, systems of social support within Turkana society may help alleviate its moral ambiguity. In particular, the Turkana have three postraid rituals that warriors can engage in that are specifically designated for those who have killed enemies in combat (43). In addition to akiger which is optional, akipur is a purification ritual which is viewed as mandatory for anyone who has killed an enemy in combat to protect them from weakening and slowly wasting away. Another ritual, ngitebus, protects a warrior from the ghosts of slain enemy warriors. It is considered optional, but it is almost always performed preventatively in conjunction with akipur. It can also be performed any time after a haunting occurs. For instance, one warrior, due to repeated hauntings, estimated that he underwent *ngitebus* 11 times over 20 y. These rituals, which require the participation of other community members, could serve as a cue to warriors that the community views their act of killing as morally acceptable. The lack of such rituals pertaining to killing, especially in populations with expansive moral beliefs and restrictive norms of killing in combat, may contribute to the heightened depressive symptoms and moral injury experienced by US military service members.

Materials and Methods

M.R.Z. conducted semistructured interviews, with the assistance of experienced bilingual Turkana research assistants, over three 2-mo field seasons with 218 Turkana warriors who had each participated in at least one violent raid (either offensively or defensively). Participants were recruited by visiting local encampments and wedding locations and by approaching men passing through a semipermanent settlement. We requested interviews from any adult males we encountered and had a participation rate of more than 98%. Three potential participants refused to participate, but at least one of them participated in a subsequent field season. We did not include data from two interviews that we ended early because the participants provided inconsistent and unclear responses to introductory questions. We assessed participants' PTSD symptom severity using a version of the PCL-5 translated into Turkana. We piloted our study with 56 participants during our first field season with semistructured interviews. We used the results of this pilot in combination with ethnographic knowledge acquired in 13 y of research in the area by S.M. to develop questions for the remaining field seasons (n = 162) about each warrior's combat exposure and outcomes, morally salient events that transpired in battle, their moral beliefs governing conduct in combat, and their experience with social sanctions and rewards related to their combat conduct. Measures of combat exposure were based on the Combat Exposure Scale (77) and measures of morally injurious events were based on the Moral Injury Events Scale (78). Since both these scales were designed to evaluate Western combat veterans, we drew on our prior ethnographic experience (38, 42, 79) to tailor the questions to be more locally relevant. The questionnaires were developed with the assistance of the Turkana research assistants through an iterative process of translation, back-translation, and piloting of the questions (80) with Turkana pastoralists in an adjacent territorial section to our study area. Since these Turkana lived farther from the border areas, they had lower combat exposure. However, they spoke the same language, lived a similar lifestyle, were of similar socioeconomic status, and had a similar education level to that in our study area and interacted frequently with Turkana from our study area. The final survey was administered verbally in the Turkana language with the help of research assistants, who recorded answers on tablet computers. As a further check, participants who said they had experienced a symptom were asked to describe their experience with the symptom in their own words. We made audio recordings of some of these responses and translated the subset of recordings with clear audio into English. Survey questions in Turkana with English translations are in SI Appendix, section S3. This research was approved by the Arizona State University Institutional Review Board (00007315 and 00003958). Since most participants were not literate, consent was given verbally with an approved consent script.

Predictors. We constructed 10 predictors (Table 2) that captured a wide range of Turkana combat experiences. The survey questions we used for all predictors, and descriptions of how each predictor variable was constructed, are in *SI Appendix*, section S7.

Three predictors measured participants' combat exposure. Since we had several measures of combat exposure that were strongly autocorrelated (each warrior's exposure to offensive battle raids, offensive stealth raids involving combat, defensive raids, being ambushed, being shot at, being shot, hand-to-hand combat, and visible bullet wounds), we used a factor analysis to obtain generalized measures of combat exposure. We used the first three factors which loaded primarily on exposure to battle raids (CE1), defensive raids (CE2), and stealth raids (CE3). Factor analysis results are in *SI Appendix*, section S7.

We also used two combat outcome predictors, whether participants gained animals (AG) or lost animals (AL) during a raid. Raid success may protect individuals from some PTSD symptoms which might make them more likely to engage in raiding again, while loss may make symptoms more likely and deter future raid participation. Losing animals has been associated with

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biomarkers of stress among Turkana women (81) and with PTSD symptoms in Samburu pastoralists (34).

We used five predictors to assess moral injury risk. The first one is a measure of a subject's past experience witnessing or participating in potentially morally injurious events where the Turkana were victims (MEV). This includes seeing a Turkana die in battle, seeing a Turkana woman raped during a raid, friendly fire incidents, and feeling guilt over failing to save a life. Since events where Turkana are victims have both physical danger and morality, we expected this predictor to be associated with learning-andreacting, as well as depressive symptoms. The second predictor is witnessing or participating in potentially morally injurious events where the Turkana were the perpetrators (MEP). This includes acts of revenge, destruction of property, witnessing the killing of women and children, rape, kidnapping, and seeing the enemy get shot or die. We expected this predictor to be more strongly associated with depressive than learning-and-reacting symptoms. The third predictor is whether the participant had killed an opponent in battle (K). We separated killing from other potentially morally injurious perpetration events because of its special salience in American combat veterans (69, 75) and because killing, unlike other types of battlefield violence, is a source of prestige for the Turkana. Therefore, we expected that killing of opponents will not result in moral injury in Turkana warriors. The fourth predictor assesses the expansiveness of a warrior's moral sphere, as measured by how many of 11 demographic categories (e.g., young children or the elderly) the warrior says it is not permissible to kill in battle (MS). Having a larger moral sphere makes it more likely that a warrior performs acts in combat that violate his moral beliefs, and so we predicted that it would be more positively associated with depressive symptoms. The fifth predictor is a warrior's experience of social sanctions, such as criticism or ostracism, or not receiving the expected social approval for the warrior's actions (SS). This includes being criticized after a raid, being criticized for having done something the warrior believed was right, feeling betrayed or disappointed after a raid by community members who did not fight, and being denied the credit deserved for the warrior's acts of valor. More frequent experiences with these predictors would signal to a warrior that he is not receiving sufficient social approval or is facing social costs for his actions. This should elicit psychological responses associated with avoiding social risks, and so we expected it to be associated with higher prevalence of depressive symptoms.

Model Fitting. We fitted models using these 10 predictors to three response variables: Turkana warriors' total symptom severity for all symptoms, warriors' symptom severity for learning-and-reacting symptoms only, and warriors' symptom severity for depressive symptoms only. All models were zero-inflated negative binomial regressions with the linear component

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including every combination of the 10 predictors for 1,024 total models fitted to each response variable. Models were fitted using RStan (82) and the leave-one-out (LOO) R package (83). For each model we recorded the maximum-likelihood parameter estimates, credibility intervals for the parameter estimates, and pseudo-BMA scores with Pareto smoothing (84). Pseudo-BMA with Pareto smoothing is a computationally efficient approximation of widely applicable information criteria (WAIC) and (LOO) crossvalidation, rewards goodness of fit with a penalty for model complexity, and makes fewer assumptions about data structure than older information criteria model comparison methods (83, 84). Once pseudo-BMA scores were collected for each model, we calculated and recorded each model's pseudo-BMA weight. These weights give the relative goodness of fit for each model, penalized for complexity, compared to other models for the same response variable. Complete model specifications are in *SI Appendix*, section S8 and code for the analysis is available at https://osf.io/nzwhu/.

Data Availability. Anonymized Turkana data and code are archived in the Open Science Framework repository, https://osf.io/47htn/ (85). American service member data are maintained at the University of Texas Health Science Center at San Antonio in the STRONG STAR Repository. Requests for access to this data can be emailed to repository@strongstar.org.

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