



Lethal Aggression in Mobile Forager Bands and Implications for the Origins of War

Douglas P. Fry and Patrik Söderberg

Science **341**, 270 (2013);

DOI: 10.1126/science.1235675

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and Weddell Seas (29, 31–33) (see supplementary materials), but total melting of 10 of the larger ice shelves is notably less here than in circumpolar models (7, 11). Discrepancies between model results and observations have been attributed to deficiencies in atmospheric forcing, the representation of sea-ice cover, the smoothing of bottom topography, and assumptions regarding cavity shape. Some models yield annual cycles and decadal variability (29) that can now be compared for specific periods with glaciological measurements, which need to be extended in time.

Our results indicate that basal melting accounts for a larger fraction of Antarctic ice-shelf attrition than previously estimated. These improved glaciological estimates provide not only more accurate and detailed reference values for modeling but also a baseline for similar future studies. Ice-shelf meltwater production exhibits a complex spatial pattern around the continent, with an outsized contribution of smaller, fast-melting ice shelves in both West and East Antarctica. Warm-cavity ice shelves along the Southeast Pacific coastline, predicted and observed to be sensitive to ocean warming and circulation strength (9, 34), were thinning rapidly in 2003 to 2008 (23). Nearly half of the East Antarctic ice shelves were also thinning, some due to probable exposure to “warm” seawater, with connections to ice drainage basins grounded below sea level.

Continued observations of ice-shelf velocity and thickness change, along with more detailed information on cavity shape, seafloor topography, and atmospheric and oceanic forcing variability are critical to understand the temporal variability and evolution of Antarctic ice shelves. Continued warming of the ocean will slowly increase ice-

shelf thinning, but if major shifts in sea ice cover and ocean circulation tip even large ice-shelf cavities from cold to warm (35), there could be major changes in ice shelf and thus ice-sheet mass balance.

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Acknowledgments: We thank three anonymous reviewers for their constructive criticism of the manuscript. This work was performed at the University of California, Irvine, and at the Jet Propulsion Laboratory, California Institute of Technology, under grants from NASA’s Cryospheric Science Program and Operation IceBridge (OIB) and at the Lamont-Doherty Earth Observatory of Columbia University under grants from the National Science Foundation and the National Oceanic and Atmospheric Administration.

Supplementary Materials

www.sciencemag.org/cgi/content/full/science.1235798/DC1
Supplementary Text
Figs. S1 to S4
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References (36–58)

29 January 2013; accepted 31 May 2013
Published online 13 June 2013;
10.1126/science.1235798

Lethal Aggression in Mobile Forager Bands and Implications for the Origins of War

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It has been argued that warfare evolved as a component of early human behavior within foraging band societies. We investigated lethal aggression in a sample of 21 mobile forager band societies (MFBS) derived systematically from the standard cross-cultural sample. We hypothesized, on the basis of mobile forager ethnography, that most lethal events would stem from personal disputes rather than coalitionary aggression against other groups (war). More than half of the lethal aggression events were perpetrated by lone individuals, and almost two-thirds resulted from accidents, interfamilial disputes, within-group executions, or interpersonal motives such as competition over a particular woman. Overall, the findings suggest that most incidents of lethal aggression among MFBS may be classified as homicides, a few others as feuds, and a minority as war.

A controversy exists regarding mobile forager band societies (MFBS) and warfare. Field researchers who have worked

with MFBS generally report that warfare is absent or rudimentarily developed (1–6). Fry (7) compared MFBSs with complex and equestri-

an foragers and found that most MFBS (62%) were nonwarring, whereas all of the complex and equestrian societies made war. On the other hand, Wrangham and Glowacki [(8), p. 7] developed a chimpanzee-based lethal raiding model, asserting that “humans evolved a tendency to kill members of other groups,” and they provided ethnographic quotations on MFBS to illustrate the model. They [(8), p. 8] define war as when “coalitions of members of a group seek to inflict bodily harm on one or more members of another group; ‘groups’ are independent political units.” Bowles (9) examined war deaths in eight societies, six of which were MFBS, and reported the occurrence of war in all eight societies, which he takes as confirmation that war has been pervasive during human evolution.

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There are two likely explanations for such divergent interpretations about warfare and MFBS: differences in how warfare is defined and differences in sampling procedure and composition (7, 8). Recognizing that definitional opinions differ, rather than making an a priori determination regarding which events are classified as manslaughter, homicide, feud, or war, we instead consider the salient characteristics of each and every actual event involving lethal aggression in a systematically derived, representative sample of MFBS.

There are numerous reasons to predict a paucity of warfare among MFBS (see supplementary materials). (i) In MFBS, group size is too small to support warfare. (ii) MFBS have egocentric social networks with descent generally figured bilaterally through both parental lines. This does not facilitate coalitional alliance formation useful in war. (iii) Group composition fluctuates over time, resulting in kinship and social networks that cut across different groups,

a factor that dampens intergroup hostility. (iv) MFBS tend not to be segmented into subgroups. In terms of residence, MFBS tend to be multi-local, not patrilocal, thus lacking a residential pattern known to facilitate coalitions among male kin useful for war. (v) The social order is egalitarian and leadership is lacking; no one has the authority to order others to fight. (vi) Foraging areas are large, population densities low, and resources spread-out, making defense of territory difficult or impossible. (vii) Boundaries often are controlled socially through use-requests and permission-granting. (viii) Typical spoils of war—material goods or stored food—are largely lacking, and the necessity of mobility makes the capture and containment of individuals against their will (e.g., slaves or brides) impractical (and runs counter to the MFBS ethos of egalitarianism). (ix) Conflicts within and between groups are easily handled by separation and other conflict-resolution mechanisms. On the basis of these foregoing characteristics, we

would expect lethal aggression in MFBS to be mostly interpersonal, not intergroup. Additionally, in mammals the killing of conspecifics is an atypical and infrequent form of aggression compared to displays, noncontact threats, and restrained aggression, so perhaps also for humans the development of an evolutionary model based on restraint as a widely documented phenomenon across species, rather than on rare killing behavior, merits consideration (10).

We extracted a subsample of purely MFBS ($n = 21$) from the standard cross-cultural sample (SCCS). To circumvent sampling bias, rather than self-selecting cases, we derived the sample of MFBS based on the published rating criteria of others researchers (11, 12). During data collection, we used only the principal authority sources (PAS) as the earliest, high-quality ethnographic descriptions available (12). We considered every instance of lethal aggression reported for these 21 MFBS (13).

The 21 MFBS produced a total of 148 lethal aggression events. The median number was 4 (mean = 7.05; SD = 14.64), with a range from 0 to 69. One society, the Tiwi of Australia, had an exceptionally large number of lethal events ($n = 69$). If the Tiwi case is removed, the median number of lethal events for the remaining 20 societies drops to 3.5, the mean is almost cut in half (mean = 3.95; SD = 3.69), and the range is reduced to 0 to 15.

Of 135 lethal events with unambiguous perpetrator and victim information, 55% consisted of one killer and one victim. In 23% of the lethal events, more than one person participated in killing a single individual, and in 22% of the events, more than one person participated in killing more than one person (Fig. 1). In only one lethal event (0.7%), did a single killer dispatch more than one person (table S4, case 18), and the two victims were children. Tiwi society reflects a different pattern wherein 44% of the lethal events involved one killer and one victim, whereas the corresponding figure for the other 20 societies combined was 64% (supplementary text).

Thirty-six percent of the lethal events took place within the local band; for example, between brothers, father and son, mother and child, in-laws, husbands and wives, companions, friends, clan “brothers,” neighbors, and so on (table S2). Six percent of all incidents involved husbands killing wives. In most lethal events (85%), the killers and victims were members of the same society. The remaining lethal aggression events involved persons from outside the society, such as shipwreck victims, colonists, missionaries, or neighboring indigenous cultures. Almost all of the killers were male, whether they acted alone or with others. Females were the killers or co-perpetrators in only 4% of the events.

The reasons for the lethal events varied. Given that most lethal aggression involved one killer and one victim, the large number of personal motives for killing is not surprising (Table 1 and

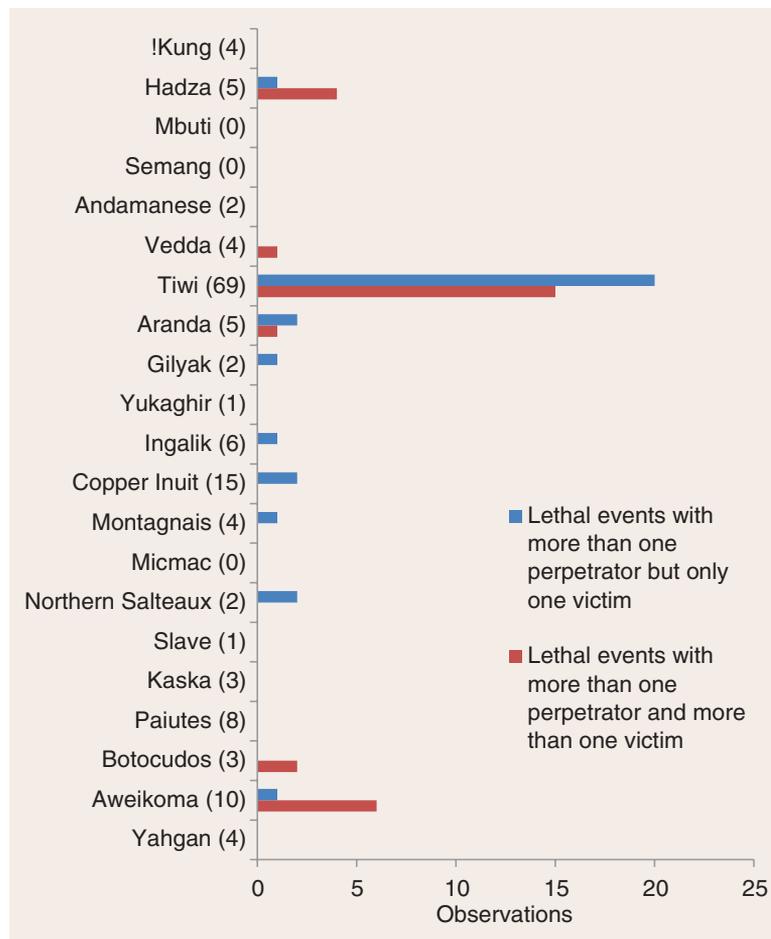


Fig. 1. Lethal aggression events with multiple perpetrators in 21 MBFS. The distribution of all lethal events that involved multiple perpetrators is shown, based on whether there was a single victim (31 events) or multiple victims (29 events), out of a grand total of 148 lethal events. The figure reflects how the Tiwi are more violent than the other MFBS. Nearly half of the sample societies (10 of 21) had no lethal events perpetrated by two or more persons. Three societies had no lethal events at all. For each society, the total number of lethal events is in parentheses.

table S3). Specifically, many lethal disputes involved two men competing over a particular woman (sometimes the wife of one of them), revenge homicide exacted by family members of a victim (often aimed at the specific person responsible for the previous killing), and interpersonal quarrels of various kinds; for instance, stealing of honey, insults or taunting, incest, self-defense or the protection of a loved-one, and so on. Additionally, in some killing events, another person or persons supported a companion who acted out of personal, not group, motives, such as when a friend assisted a husband in killing his wife's lover (see table S4, case 109).

About one third of the lethal events involved disputes between people of different groups (Table 1). However, three-quarters (38 of 50) of intergroup disputes took place among the Tiwi alone. The percentage of intergroup disputes for the Tiwi exceeded 50% of their events, whereas the corresponding percentage for the other twenty societies was only about 15%. Another feature of the Tiwi data is the regular occurrence of strings of killings. Thirty-nine percent (27 of 69) of Tiwi lethal events occurred in seven separate strings (table S4, cases 129 to 131, 133 to 139, 140 to 141 and 145, 142 to 144, 146 to 149, 150 to 153, and 156 to 158), whereas only two strings of killings occurred in the other 20 societies (table S4, cases 10 to 13 and 82 to 89).

The findings suggest that MFBS are not particularly warlike if the actual circumstances of lethal aggression are examined. Fifty-five percent of the lethal events involved a sole perpetrator killing only one individual (64% if the atypical Tiwi are removed). One-person-killing-

one-person reflects homicide or manslaughter, not coalitional killings or war. Additionally, 36% of all lethal events occurred within the same local group (62% if the atypical Tiwi are removed), and violence within a local group is not coalitional war. Only 15% of the lethal events occurred across societal lines. Some such events might fall within a definition of war, whereas others might not (such as when shipwreck survivors were killed). Finally, very few lethal disputes were over resources. Overall, a consideration of reasons for lethal aggression reveals that most cases stemmed from personal motives consistent with homicide and, in some cases, family feuds, but much less often with lethal aggression between political communities, or warfare (supplementary text).

Approximately half of the societies had no lethal events that involved more than one perpetrator. This observation is incongruent with assertions by Bowles (9) and Pinker (14) that war is prevalent in MFBS or by Wrangham and Glowacki (8) that humans have an evolved tendency to form coalitions to kill members of neighboring groups. Additionally, two or more persons killing a third person might or might not occur in the context of a coalition against another group or war. In some instances, motives such as sexual jealousy (table S4, e.g., cases 29 and 109) or avenging the murder of a family member (table S4, e.g., case 157) are clearly personal rather than stemming from hypothesized general hostility toward other groups. Most mammalian aggression also is between individuals. A different evolutionary perspective supported by comparative mammalian data, game

theory on the evolutionary logic of fighting, and the observation that killing is an exceptional event in human societies leads to the counter-hypothesis that lethal behavior has been strongly selected against, not favored, in comparison to more restrained conflict behavior (7, 10, 15).

Taken together, the current findings contradict recent assertions that MFBS regularly engage in coalitional war against other groups (8), that "chronic raiding and feuding characterize life in a state of nature" [(14), p. xxiv], or that MFBS war deaths are substantial in recent millennia and in the Pleistocene (9) (supplementary text). Perhaps discrepancies between the foregoing propositions and the current findings can be accounted for by proposing that self-selection of ethnographic material may have exaggerated war (10). Additionally, methodological factors such as relying heavily on only a few secondary sources (8), or estimating war mortality on the basis of genocidal massacres and murders of indigenous peoples by armed ranchers and settlers (9), can lead to misimpressions in comparison to the use of systematic sampling procedures, reliance on primary ethnographic data, and a focus on the specific circumstances of lethal aggression cases in MFBS (7, 10).

In conclusion, when all cases are examined for a systematically drawn sample of MFBS, most incidents of lethal aggression can aptly be called homicides, a few others feud, and only a minority warfare. The findings do not lend support to the coalitional model. The predictions are substantiated that MFBS, as a social type, possess many features that make warfare unlikely. The actual reasons for lethal aggression are most often interpersonal, and consequently, the particulars of most of the lethal events in these societies do not conform to the usual conceptualization of war.

Table 1. Reasons for lethal aggression, from the personal to the communal. The atypical Tiwi findings are shown separately, followed by the other societies minus the Tiwi ($n = 20$), and the entire sample ($n = 21$), all in number of cases (with percentages in parentheses). A more detailed version of the table with case numbers for lethal aggression events is presented in table S3.

Reason	Tiwi only	All others	Total sample
Interpersonal events	24 (34.8%)	50 (63.3%)	74 (50.0%)
Revenge against a particular killer(s)	9 (13.0%)	8 (10.1%)	17 (11.5%)
Over a particular woman	8 (11.6%)	6 (7.6%)	14 (9.5%)
Over a particular man	0 (0.0%)	1 (1.3%)	1 (0.7%)
Husband kills wife	2 (2.9%)	7 (8.9%)	9 (6.1%)
Wife kills husband	0 (0.0%)	0 (0.0%)	0 (0.0%)
Miscellaneous interpersonal disputes*	5 (7.2%)	28 (35.4%)	33 (22.3%)
Interfamilial feud	0 (0.0%)	6 (7.6%)	6 (4.1%)
Within-group execution	0 (0.0%)	3 (3.8%)	3 (2.0%)
Execution of outsiders	4 (5.8%)	3 (3.8%)	7 (4.7%)
Intergroup events	38 (55.1%)	12 (15.2%)	50 (33.8%)
Over borders/resources (e.g., fruit tree)	0 (0.0%)	2 (2.5%)	2 (1.4%)
Theft of women from another group	0 (0.0%)	2 (2.5%)	2 (1.4%)
Interclan revenge-seeking	17 (24.6%)	0 (0.0%)	17 (11.5%)
During a general fight	4 (5.8%)	0 (0.0%)	4 (2.7%)
Miscellaneous intergroup disputes*	17 (24.6%)	8 (10.1%)	25 (16.9%)
Accident	3 (4.3%)	3 (3.8%)	6 (4.1%)
Starvation cannibalism	0 (0.0%)	2 (2.5%)	2 (1.4%)
Grand total	69 (100%)	79 (100%)	148 (100%)

*For a listing of miscellaneous events, see table S3.

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Acknowledgments: Some of the data reported here were collected during research funded by the NSF (grant 03-13670). We are grateful to the Svenska Kulturfonden for assisting

with the costs of publication. The data reported in this study are located in the supplementary materials.

Supplementary Materials

www.sciencemag.org/cgi/content/full/341/6143/270/DC1
Material and Methods

Supplementary Text
Tables S1 to S4
References (16–127)

25 January 2013; accepted 10 June 2013
10.1126/science.1235675

Interactions of Multisensory Components Perceptually Rescue Túngara Frog Mating Signals

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Sexual signals are often complex and perceived by multiple senses. How animals integrate signal components across sensory modalities can influence signal evolution. Here we show that two relatively unattractive signals that are perceived acoustically and visually can be combined in a pattern to form a signal that is attractive to female túngara frogs. Such unanticipated perceptual effects suggest that the evolution of complex signals can occur by alteration of the relationships among already-existing traits.

Human perception of stimuli in multiple sensory modalities can positively influence signal detection, selective attention, learning, and memory (1). One example is “hearing lips and seeing voices” in the McGurk effect (2), which provided the foundation for speech auditory-visual research (3). Studies of multimodal communication in animals have often asked whether individual signal components in different sensory modalities are redundant or carry different information (4), but few studies have investigated how specific interactions influence signal perception (5).

Female túngara frogs base their mate choices on male mating calls. Specifically, males produce calls consisting of a whine alone or they may add up to seven chucks; they do not produce only chucks (6). Females exhibit phonotaxis (movement toward a call, a bioassay of call recognition and preference) to a whine only, but exhibit a fivefold preference for calls with a whine-chuck over a whine only [$N = 3662$ (11); see also Fig. 1A]. We tested female mate preferences in a series of two-choice tests. Synthetic male vocalizations were broadcast from two speakers, one of which was paired with a robotic frog that provided the visual stimulus of a calling male. Females were released equidistant from the two speakers (with a 60° separation relative to the female release point) and allowed to choose a stimulus. Because our experimental configuration differed from those of previous experiments, we replicated some studies and obtained similar

results (Fig. 1, A, B, and D). Females were tested only once.

The acoustic component of a frog’s mating call is its most distinguishing feature, but visual

cues are also associated with the sexual display. Male frogs have inflatable vocal sacs that shuttle air to and from the lungs while calling. Similar to the movement of lips during human speech (2), they are a biomechanical consequence of the sound production system (7), but, as with lips and speech, they can also influence the perception of the call (8, 9). We have shown previously that female túngara frogs prefer a multimodal signal (a call associated with a robotic frog) to a call by itself (10), a result reconfirmed here (Fig. 1D).

In túngara frogs, the temporal relationship between acoustic components influences the signal’s attractiveness (11). When the chuck in a whine-chuck call is displaced by 500 ms, the call becomes merely as attractive as a whine only (Fig. 1B) and less attractive than a normal whine-chuck (Fig. 1C). The temporal relationship between the acoustic and visual components of the signal also influences the signal’s attractiveness

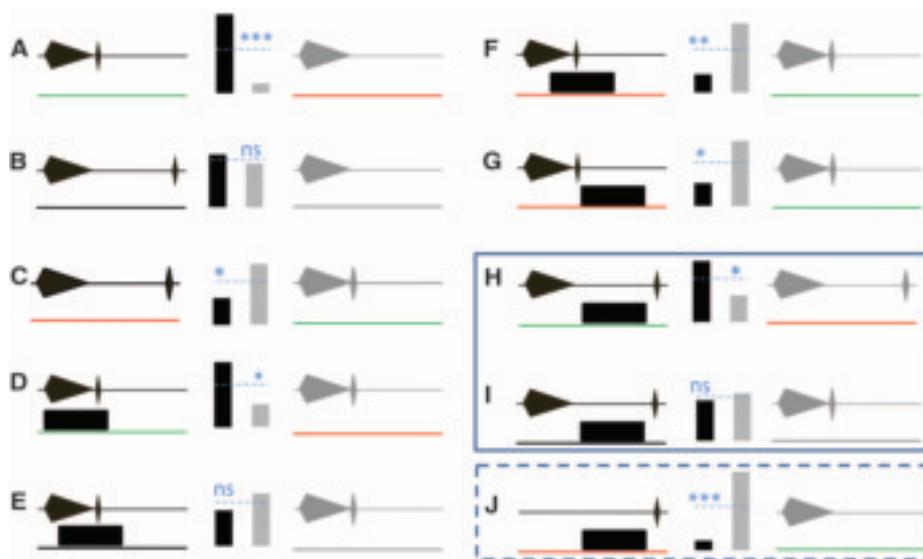


Fig. 1. Preference responses. Each portion of the figure illustrates the acoustic components of the túngara frog mating call: a whine only [(A, B, and J), right gray], a chuck only [(J), left black], or a whine-chuck (all other calls). The natural whine-chuck is depicted in (A), left black; (C), right gray; (D to G), all acoustic signals; and (I), right gray. The rectangle represents the inflation-deflation cycle of the robofrog’s vocal sac and its temporal relationship to the call [(D) to (J), left black]. The x axis represents 1000 ms, green indicates the significantly preferred stimulus, and red indicates the unpreferred stimulus. In each of the 10 experiments [(A) to (J)], 20 females were given a choice between the signal in black versus the signal in gray. The vertical black and gray bars represent the number of females that chose the respective signal, and the blue dashed horizontal lines represent the null hypothesis of equal preference. Experiments highlighted in the solid blue box are tests of the perceptual rescue versus template-matching hypotheses, and those in the dashed blue box are the test of the component substitution hypothesis. The results of binomial tests are noted as *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, ns (not significant) = $P > 0.05$. The exact P values for each experiment are as follows: (A) $P = 0.0003$, (B) $P = 0.744$, (C) $P = 0.019$, (D) $P = 0.034$, (E) $P = 0.323$, (F) $P = 0.0049$, (G) $P = 0.019$, (H) $P = 0.039$, (I) $P = 0.583$, (J) $P = 0.0001$.

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