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Bands of brothers and in-laws: Waorani warfare, marriage and alliance formation

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The root of modern human warfare lies in the lethal coalitionary violence of males in small-scale societies. However, there is a paucity of quantitative data concerning the form and function of coalitionary violence in this setting. Debates exist over how lethal coalitions are constituted, as well as the motivations and benefits for males to join such groups. Data from a lowland Amazonian population, the Waorani of Ecuador, illuminate three issues: (i) the degree to which raiding parties are composed of groups of fraternal kin as opposed to strategic alliances of actual or potential affinal kin; (ii) the extent to which individuals use pre-existing affinal ties to motivate others to participate in war or leverage warfare as a mechanism to create such ties; and (iii) the extent to which participation in raiding is driven by rewards associated with future marriage opportunities. Analyses demonstrate that Waorani raiding parties were composed of a mix of males who were potential affines, actual affines and fraternal kin, suggesting that men used pre-existing genetic, lineal and social kin ties for recruiting raid partners and used raiding as a venue to create novel social relationships. Furthermore, analyses demonstrate that males leveraged raiding alliances to achieve marriage opportunities for themselves as well as for their children. Overall, it appears that a complex set of motivations involving individual rewards, kin marriage opportunities, subtle coercion and the assessment of alliance strength promote violent intergroup conflict among the Waorani. These findings illustrate the complex inter-relationships among kin selection, coalition building and mating success in our species.

1. Introduction

While humans are not the only species to engage in lethal coalitionary aggression [1,2], the intensity and breadth of human warfare is unparalleled and remains a major vector for human mortality [3] and environmental degradation [4]. The impact of human warfare is not simply a product of our technological abilities; rather, our modular social organization that allows individuals and groups to form coalitions with others from beyond the local community increases the scale at which intergroup conflict occurs [5]. There is increasing evidence that the evolution of human inter-group violence is related to both social organization and ultra-sociality; however, debates linger over how these traits articulate and their consequences on human social life [5–18]. Examining the structure and function of raiding parties in tribal societies remains a fruitful lens for revealing its ultimate causation [6–12].

Historically, lethal coalitions in small-scale societies were assumed be based on fraternal associations of lineal kin: maternal and paternal brothers, fathers and sons, and other consanguineal male kin of ascending and descending

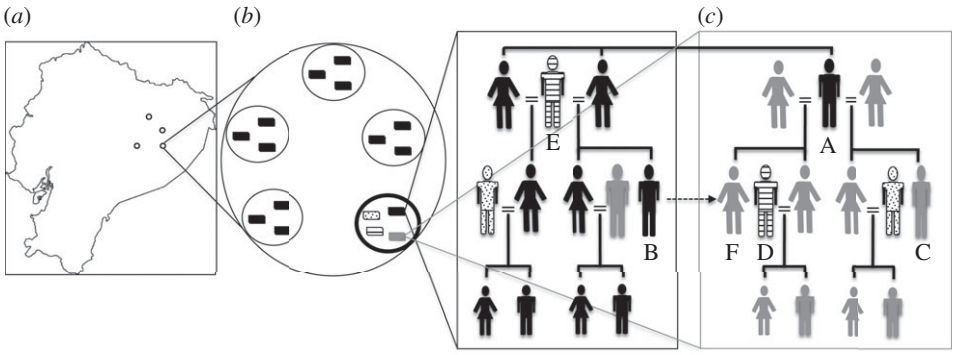

Figure 1. Image displaying relationships between (*a*) the four Waorani territories (not drawn to scale); (*b*) neighbourhood clusters composed of communal longhouses (*nanicabo*) within a territory; and (*c*) social organization within two communal longhouses. Individuals in (*c*) are shaded relative to the longhouse from which they originally grew up (referenced in the highlighted neighbourhood cluster in (*b*)). If A seeks to instigate a raid, he may solicit help from E and B with whom he shares affinal ties, with C who is his son, and with D who is his son-in-law. B may be motivated to join the raid because his father, E, is going and because he believes that doing so might provide marriage access to F. Whereas the raid relationship between A and E may be motivated by assessing alliance commitment, the relationship between A and C is motivated by lineal kinship, the relationship between A and D is subtle coercion based on affinal ties, and the relationship between A and B is individual level rewards. B and F are ideal marriage partners as they are bilateral cross-cousins (e.g. B's mother's brother's daughter).

generations [5,13,19–23]. However, quantitative research examining raiding party composition in traditional societies suggests greater complexity underlies its social organization. Friendship [11] and affinal relations [9] play important roles in organizing lethal coalitions, suggesting that warfare may be a venue for creating strategic alliances [5,9,13]. The extent to which these findings generalize is unclear, as high-resolution data concerning coalitionary raiding in societies prior to the intervention of the state are scarce. Furthermore, if coalitionary raiding behaviour is structured by factors other than fraternal kinship, to what extent do individuals use pre-existing social ties to motivate others to participate [11] or leverage warfare as a mechanism to create them [9]? If individuals use raiding as a mechanism to create social relationships, who reaps the benefits associated with warfare? Research on tribal warfare suggests social benefits, such as marriage opportunities, should go to the participating member (e.g. [6,9–10,12]). However, in societies where kin arrange marriages, do the benefits go to other individuals, such as offspring? Here we evaluate questions regarding the composition of lethal coalitions, the motivations for joining raids, and the benefits to participation using data from a tribal society, the Waorani of Ecuador [24–26].

2. Site description

The Waorani are an indigenous Ecuadorian, lowland Amazonian population of approximately 2000 people today. At first peaceful contact (1958), they subsisted on manioc, banana and peach palm cultivation supplemented by hunting. At that time, approximately 500 individuals resided in four geographically separated, mutually hostile territorial groups each composed of neighbourhood clusters of communal longhouses (figure 1). Whereas neighbourhood clusters were separated from one another by a 1–2-day walk (i.e. 50–100 km), communal longhouses (*nanicabos*) within a cluster were separated from one another by a half hour to an hour's walk. Each *nanicabo* typically held an extended family composed of a senior man, his wives and unmarried children, as well as his daughters and their husbands and children (the Waorani practised uxorilocality—husbands moved into their wives' *nanicabo*). The senior males of the *nanicabos* in a neighbourhood cluster were often related as brothers, brothers-in-law or fathers-in-law/sons-in-law. Marriage was prescriptively with a bilateral cross-cousin and typically arranged by parents; however, couples could initiate marriage under the rule of the levirate and sororate. Most marriages occurred within the neighbourhood cluster; however, some involved individuals from unknown groups [25]. Both polygyny (usually sororal) and polyandry (always fraternal) occurred, usually as a response to fluctuating neighbourhood cluster sex ratios. The small population size, in conjunction with the large distances between settlements, made finding a wife who was not forbidden by the incest taboo problematic.

Revenge killings were common and raids were often motivated by vendettas [24]; however, reasons for raiding included the entrance of outsiders into their territory, obtaining iron tools and witchcraft [25]. Once an individual decided to carry out a raid, he enlisted followers from his own household or neighbourhood cluster. The individual would begin by shaving and decorating spears, each with its own distinctive size, shape and decoration. The reason for individualizing their weaponry was so that survivors of the attack would know who did the killing and fear them. Individuals were never compelled to participate, but were persuaded to join and could opt out at any time, including abandoning raids in progress. Consistent with many ethnographies (e.g. [6,9,18]), no raiders were killed or seriously injured while raiding. Typically raiders would remain hidden and wait until a very dark night to attack. They would approach the *nanicabo*, verify that everyone was sleeping or inattentive, and kill as many as possible before they could escape. Unless they had agreed beforehand to spare certain individuals, all inhabitants were killed. After the attack, the invaders would pillage the *nanicabo* for blowguns, machetes and axes, then burn the house. The raiders would then leave for home or continue raiding other *nanicabos* in the neighbourhood cluster.

Historically, alliance building in Waorani society occurred for three purposes: vengeance, obtaining goods and marriage. With no domestic animals, no ownership of land, very minimal and impermanent residence groups, no political hierarchy outside the family, and social solidarity outside of the extended family being weak, there was little

Table 1. Descriptive statistics associated with Waorani raiding dyads ($n = 1041$) and raiders ($n = 81$).

variable	yes	no	*n*	mean (s.d.)	min	max	median
from same territory	736	305	1041	—	—	—	—
from same patriline	202	839	1041	—	—	—	—
from same matriline	184	857	1041	—	—	—	—
from neither lineage	778	263	1041				
coefficient of relatedness	—	—	1041	0.09 (0.15)	0	0.6875	0
absolute age difference	—	—	1041	13 (11)	0	56	11
no. of times dyad raided together	—	—	1041	2 (1)	1	12	1
age at first raid	—	—	81	18 (7)	6	36	17
raiding window (years)	—	—	81	31 (12)	11	67	28
no. of times ego raided	—	—	81	4 (3)	1	13	3
raiding network size	—	—	81	27 (15)	2	59	28
raiding network size: non-lineal members	—	—	81	18 (11)	2	50	18
ego married raid partner's female kin	58	23	81	—	—	—	—
no. of raid partners with whom ego arranged offspring marriages	—	—	81	1 (1)	0	5	1
ego's no. of offspring	—	—	81	8 (6)	0	28	8

else about for which to ally [26]. As such, they provide an ideal case study to examine the inter-relationships between raiding and marriage.

3. Methods

Genealogical information and coalitionary raiding data were collected over 18 months between 2000 and 2001 by S.B., P.E. and J.Y. via semi-structured interviews with nearly all Waorani men and women aged above 49 years ($n = 121$: 65 females, 56 males). Raiding data included the men who participated, the individual(s) who organized it, the victims and the rationale for attack. Marital and reproductive status were recorded to date individual raids and establish their relative chronology. Additionally, interviewees reported on the raid histories of their fathers, husbands and brothers. This process produced 550 raid reports (spanning 1916–1970) that were consolidated into 49 separate raids (44 of which were intra-tribal) involving 89 raiders. Raid group size ranged between 2 and 34 individuals (median = seven men) and average raider age was 27 years (min/max = 7/63 years; median = 26; $n = 360$).

Genealogical information was obtained from all 121 interviewed men and women, which was then cross-validated against two previous Waorani genealogic data sources (see [24]), resulting in a dataset containing 2172 individuals. Genetic relatedness and lineal kinship was calculated using Hagen's DESCENT software [27].

Statistical analyses were performed in STATA software [28]. To account for data structural autocorrelation around raid dyads and territorial membership, multivariate generalized estimating equations using robust standard errors were employed.

4. Results

If Waorani raids are organized around fraternal kinship, they should be composed of lineal kin. If they represent strategic alliances, they should be composed of men who can leverage raiding into marriage opportunities. Because of Waorani incest taboos and marriage norms, these men should be genetically related, but exist outside of patrilineal and matrilineal linkages. To adjudicate between these perspectives, we analyse raiding data at the level of the raid dyad ($n = 1210$) and the individual raider ($n = 89$). Because some men lacked sufficiently deep genealogies for estimating genetic relatedness and lineal membership, we truncate the dataset to include those with at least grandparental information ($n = 81$ men and 1041 raid dyads). Seventy-five per cent of raid dyads were from neither the same matriline nor patriline (table 1). A two-sample Kolmogorov–Smirnov test demonstrates the distribution of non-lineal kin in a warrior's raiding universe was substantially greater than the distribution of non-lineal kin in their kinship universe ($D = 0.25$; $p = 0.014$; $n = 162$). In only three instances were raid groups composed solely of fraternal kin. These raids involved the same two males who were fraternal brothers and raided in groups of size two (the minimum number for a raid group). Genetic relatedness among raiding partners was bimodally distributed. Fifty-seven per cent of raid dyads were not genetically related to one another, while 39% had a coefficient of relatedness of at least 0.0625. Of this latter category, the two most common raid partners were (i) genetically related males from different lineages (i.e. ideal marriage exchange partner) and (ii) males who shared lineage membership with a coefficient of relatedness of 0.25 (i.e. fraternal kin). Two two-sample Kolmogorov–Smirnov tests demonstrate the genetic relatedness between a warrior and his raiding universe was substantially higher than what would be expected given his relatedness to the entire Waorani universe ($D = 0.78$; $p < 0.001$; $n = 162$), but much less than what would be expected relative to his consanguineal kinship universe ($D = 0.23$; $p = 0.022$; $n = 162$). Furthermore, males formed raiding parties with similarly aged individuals (median age difference = 11 years). Consistent with the

Table 2. Generalized estimating equation Poisson regression coefficients associated with the number of times Waaorni men raid together.

variable	IRR ± (RSE)	*z*	*p*-values
genetic relatedness	4.6 ± (1.3)	5.3	<0.001
dyad from same territory (0 = no; 1 = yes)	1.3 ± (0.05)	6.3	<0.001
absolute age difference	0.99 ± (0.002)	−3.9	<0.001
dyad from same patriline (0 = no; 1 = yes)	0.78 ± (0.08)	−2.5	0.013
dyad from same matriline (0 = no; 1 = yes)	0.82 ± (0.07)	−2.3	0.021
constant	1.3 ± (0.05)	9.0	<0.001

strategic alliance perspective, individuals formed coalitions with others who were genetically related but existed outside the lineal descent group. However, 25% of all raid dyads involved fraternal kin, with coalitions composed of fathers and sons, brothers, and lineal cousins and uncles.

Next we examine the factors influencing the number of times two men raid together. The fraternal interest group model predicts males should raid more often with lineal kin. The strategic alliance model predicts men should raid more often with those who can provide marriage opportunities. After controlling for data structural autocorrelation around dyads, a generalized estimating equation shows the incident rate for raiding together increases if men were similar in age, from the same territory, genetically related, and from different lineages (Wald $\chi^2 = 89.4$; $p < 0.0001$; n observations = 2082; n groups = 1041) (table 2). Consistent with the strategic alliance perspective, individuals raided more frequently with males who were genetically related outside the lineal group – i.e. ideal marriage exchange partners.

To probe the relationships between Waorani social organization, raiding and marriage we employ five generalized estimating equations examining the factors affecting a raider's (i) lifetime number of raids, (ii) raid network size, (iii) raid network size composed of non-lineal kin, (iv) probability of marrying his partner's daughter sister or half-sister, and (v) number of raid partners with whom he arranged marriages between their respective offspring. After controlling for the territory from which a man came, we find that longer windows between birth and pacification (i.e. raid windows) and earlier age at first raid increased lifetime number of raids (n groups = 4; n sample = 81; Wald $\chi^2 = 45.3$; $p < 0.0001$; raiding window: IRR ± (RSE) = 1.03 ± (0.007); $z = 5.2$; $p < 0.001$; age at first raid: IRR ± (RSE) = 0.98 ± (0.01); $z = -1.95$; $p = 0.05$). Second, we find that lifetime number of raids predicted a man's raid network size (n groups = 4; n sample = 81; Wald $\chi^2 = 48.8$; $p < 0.0001$; lifetime number of raids: B ± (RSE) = 2.8 ± (1.4); $z = 1.99$; $p = 0.046$; raiding window: B ± (RSE) = −0.07 ± (0.2); $z = -0.4$; $p = 0.7$; age at first raid: B ± (RSE) = −0.09 ± (0.2); $z = -0.37$; $p = 0.7$). Third, as the size of a male's raiding network increased so too did the number of raiding partners who were not lineal kin (n groups = 4; n sample = 81; Wald $\chi^2 = 344$; $p < 0.0001$; raid network size: B ± (RSE) = 0.7 ± (0.04); $z = 18.6$; $p < 0.001$). Fourth, as the size of a male's raiding network composed of non-lineal kin increased, so too did the probability that he married at least one of his raid partner's daughters, sisters or half-sisters (n groups = 4; n sample = 81; Wald $\chi^2 = 84.8$; $p = 0.014$; size of raid network comprised of non-lineal kin: OR ± (RSE) = 1.1(0.02); $z = 3.2$; $p = 0.001$; number of lifetime raids: OR ± (RSE) = 1.2(0.2); $z = 1.4$; $p = 0.16$; age at first raid: OR ± (RSE) = 1.03(0.05); $z = 0.5$; $p = 0.58$). Last, even after controlling for the number of children a warrior had, we find that as the size of a male's raiding network composed of non-lineal kin increased, so too did the number of raid partners with whom he arranged marriages between their respective offspring (n groups = 4; n sample = 81; Wald $\chi^2 = 28.1$; $p < 0.0001$; size of raid network composed of non-lineal kin: IRR ± (RSE) = 1.02(0.006); $z = 3.7$; $p < 0.001$; number of offspring: IRR ± (RSE) = 1.08(0.02); $z = 5.3$; $p < 0.001$). Interestingly, there appear to be reciprocal effects, as marrying a raid partner's female kin increased the number of raid partners with whom he arranged a marriage between their respective offspring (n groups = 4; n sample = 81; Wald $\chi^2 = 228.1$; $p < 0.0001$; ego married raid partner's kin: IRR ± (RSE) = 1.9(0.1); $z = 9.3$; $p < 0.001$; number of offspring: IRR ± (RSE) = 1.09(0.01); $z = 6.7$; $p < 0.001$). While consistent with strategic alliances, these analyses compress the temporal relationships between raiding and marriage, making it unclear whether Waorani men raided for marriage opportunities or if they were persuaded to go to war through the social obligations connected to affinal kin.

To uncover the temporal relationship between raiding and marriage we examine marriages between warriors and their raid partners' kin as well as between warriors who arranged marriages for their offspring. Of the 81 males, 75 married at least one female (mean number of wives = 1.7; range = 1–5) involving a total of 112 females and 125 marriages (13 women were married to more than one warrior). Five of the marriages were incestuous, resulting in 120 marriages that could be analysed to determine whether males marry their raiding partners' daughters, sisters or half-sisters. Seventy-five marriages (62%) involved a male who married the daughter, sister or half-sister of at least one of his raiding partners. Although retrospective interviewing of a population lacking calendrical account keeping poses uncertainty to reconstructing the timing of marriage and raiding, the data collection and cleaning process (see [24]; electronic supplementary material) resulted in 46 marriages where a male raided with his partner first, then married his partner's kin. Three cases involved a male who raided and married in the same year, and thus lacked sufficient detail to distinguish the relationship, while 26 involved a male who married first, then raided. The average time lapsed between raiding together and marriage was seven years ($n = 45$; min/max = 1/22 years). The average number of times an ego raided with his partners prior to marriage was two (min/max = 1/6 raids). A two-sample Kolmogorov–

Smirnov test shows that men who obtained spouses from raid partners were substantially more genetically related to their spouses (mean $r = 0.0527$) relative to those obtained from non-raid partners (mean $r = 0.016$; $D = 0.26$; $p = 0.039$; $n = 120$), suggesting that raiding promotes marriages that more closely match the cultural ideal of a cross-cousin.

Last, we examine all marriages occurring to the children of raiders to determine if raiders arranged marriages between their offspring. The 89 warriors produced 791 offspring (mean = 8.9 children; min/max = 0/28), 367 of whom were married to at least one spouse, totalling 432 marriages. Of these, 398 included a spouse whose father was known, representing 244 unique marriages, 81 of which involved two fathers who had raided together, 157 of which involved two fathers who either did not raid together ($n = 76$) or involved one father whose raid history was not elicited during interviews ($n = 81$), and six of which were incestuous marriages. Of the 81 marriages involving two fathers who raided together, 36 included information related to the date of marriage between their offspring. In every instance but one, these males raided prior to the marriage of their respective offspring. The average time elapsed between the timing of their first raid and the marriage of their offspring was 20 years (min/max = 2/40 years). After removing cases where individuals lacked insufficient genealogic information or included incestuous marriage, a two-sample Kolmogorov–Smirnov test shows that marriages involving the children of raid partners were much more likely to match the cultural norm of a cross-cousin marriage compared with those who were not raid partners ($D = 0.63$; $p < 0.001$; $n = 153$; mean spousal genetic relatedness between children of raid partners = 0.16; $n = 55$; mean spousal genetic relatedness between children of non-raid partners = 0.016; $n = 98$). Furthermore, a one-sample Kolmogorov–Smirnov test demonstrates the mean spousal genetic relatedness between the children of raid partners was substantially higher compared with the mean spousal relatedness across all Waorani marriages (mean = 0.023; $D = 0.98$; $p < 0.001$; $n = 55$).

5. Discussion

We performed these analyses to understand the linkages between raiding, marriage and coalition building in a society prior to the incursion of the state. Our results suggest social competition and kinship structure Waorani raid groups and marriage opportunities. These systems are coupled and mutually reinforcing, where men use raiding as a venue to search for marriage exchange partners and use pre-existing genetic, social and affinal kin ties for recruiting raid partners. While other domains of social life (e.g. labour) probably impact coalition building, our data highlight the relationships between raiding and marriage.

Given our pattern of results, it appears Waorani raiding involves the creation of strategic alliances. Waorani raiding parties were composed of men from similar territories and age classes, across a range of genetic relatedness categories, and generally existing outside the descent group—these are ideal affinal kin. One way to increase exposure to potential wife-giving men is to raid over multiple occasions. However, simply maximizing raid participation is an inefficient route to achieving marriage [24], especially if one must cultivate trust with coalition members. Trust could be established through honest signalling of partnership intent [29] or the psychological sense of oneness that emerges from shared dysphoric experiences [30] stemming from multiple raids with the same individual. Waorani males appear to be strategic about whom they raid with over multiple occasions, selecting those from within the same territory who have greater genetic relatedness but emanate from different kin groups. These raiding dyads resulted in marriage and did so in a manner that matched Waorani cultural preferences for cross-cousins. What is most significant is that these raiding alliances produced marriage opportunities for both the self and one's children. These results support the notion that the evolution of human friendships lie in the alliances negotiated between non-kin who can provide benefits that kin cannot [31,32].

Waorani raiding coalitions also included fraternal kin. Individuals might seek fraternal kin because they live in close proximity, thereby lowering the costs of partner search, or because social kinship acts as a focal point for generating initial trust. Furthermore, fraternal kin provide an entry point for boys to learn the art of raiding and alliance building. Our interviews suggest some males brought their children or other young fraternal kin on their first raid to learn this skill. At the group level, fathers, brothers, uncles and nephews, operating as a descent group, can be in the marketplace for alliances with other similarly organized groups of men to exchange commodities. Alliances formed between entire descent groups provide the institutional matrix upon which future generations will tread to form new raid and marriage arrangements. Our analyses suggest this happened among the Waorani, as males who married their raid partners' female kin also arranged marriages between their children.

The causal arrow between raiding and marriage is not unidirectional. A number of marriages involved a male who married first, then later raided with his affinal kin. This suggests that the motivations for war can simultaneously involve individual-level rewards to participants (e.g. [3,8]) and subtle coercion (e.g. [7–8,14]) from affinal kin. This is particularly likely in lowland South America, where the bonds between father-in-law and son-in-law, and between brothers-in-law, are frequently reported to be close and intense (e.g. [6,9,24]).

The evolution of lethal coalitions is debated [15–23]. While territorial membership, age cohorts and maternal kinship structure chimpanzee border patrol coalitions [33], tribal raiding is predicated on living proximity, age cohorts, maternal and paternal kinship, as well as affinal kinship and friendship [5,9,11,13]. We speculate that fraternal alliances are the foundation upon which strategic alliances with non-lineal kin emerged. Fraternal alliances may have evolved away from a chimpanzee-like system once paternity recognition occurred in humans due to male consanguineal control of female mating. Once pair-bonding emerged, the evolution of social institutions related to marriage facilitated the extension of alliances to affinal kin.

In sum, Waorani raiding represents a mix of strategic alliances with potential and actual affinal kin, as well as fraternal groups. While the proximate motivation for raiding was vengeance, the ultimate rewards lie in the construction of alliances and marriage opportunities. However, the linkages between war and marriage are multidirectional, and suggest that a complex set of mechanisms related to individual rewards, kin rewards, subtle coercion and the assessment of alliance strength motivate behaviour.

Ethics. The research was approved by the Institutional Review Boards of Pennsylvania State University and the University of Connecticut. Informed consent was obtained from everyone interviewed.

Data accessibility. The datasets supporting this article are accessible via the electronic supplementary material.

Authors' contributions. S.B., P.I.E. and J.Y. designed the research. S.B., P.I.E., J.Y., J.R. and L.J. collected the data. S.J.M. analysed the data. S.J.M. and S.B. wrote the paper.

Competing interests. The authors declare they have no competing interests.

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