Warfare and reproductive success in a tribal population

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Intergroup conflict is a persistent feature of many human societies yet little is known about why individuals participate when doing so imposes a mortality risk. To evaluate whether participation in warfare is associated with reproductive benefits, we present data on participation in small-scale livestock raids among the Nyangatom, a group of nomadic pastoralists in East Africa. Nyangatom marriages require the exchange of a significant amount of bridewealth in the form of livestock. Raids are usually intended to capture livestock, which raises the question of whether and how these livestock are converted into reproductive opportunities. Over the short term, raiders do not have a greater number of wives or children than nonraiders. However, elders who were identified as prolific raiders in their youth have more wives and children than other elders. Raiders were not more likely to come from families with fewer older maternal sisters or a greater number of older maternal brothers. Our results suggest that in this cultural context raiding provides opportunities for increased reproductive success over the lifetime.

warfare | human behavioral ecology | reproductive success | pastoralists | status

The causes of warfare in small-scale societies continue to be debated. Most anthropological explanations have focused on causes that ignore the individual benefits warriors sometimes receive for participation (1, 2). However, evolutionary anthropologists have commonly argued that warriors may receive fitness benefits that ultimately motivate their participation (3–7). This hypothesis has a contentious history, in part because of concerns that a positive association between warfare and reproductive success may suggest biological proclivities to engage in violence (8, 9). Although such a relationship would be unsurprising in other mammalian species with similar patterns of lethal intergroup relations (10, 11), the fact that humans also have the capacity for sustained peaceful relations between groups has sometimes been interpreted as suggesting that warfare has a different function than intergroup conflict in other species (12–14).

Field data on the relationship between participation in small-scale warfare and reproductive success remain extremely sparse. Chagnon found that, among the Yanomamo of Venezuela, men who participated in killing an enemy and were then designated with a culturally specific label of *unokai* had greater reproductive success than non-*unokai*s (3). By contrast, data on raids from the Waorani, an Ecuadorian group of horticulturalists, found that more zealous warriors had decreased reproductive success (15), whereas a study of killers vs. nonkillers among the Ache of Paraguay found that the children of men who had killed had greater child survivorship (16). Because these latter two studies did not differentiate between intra- and intergroup killings, their significance is unclear for understanding whether participation in intergroup warfare is generally associated with greater reproductive success. Therefore, the extent to which men in small-scale societies tend to benefit reproductively from their participation in war remains unresolved.

Here we investigate whether participation in simple warfare is associated with increased reproductive success among the Nyangatom, an East African pastoralist society. We measure a warrior's reproductive success by the number of his wives and children. We also examine whether participation in warfare is a means for individuals to overcome constraints on marriage opportunities created

by their natal family composition. In this ethnographic context, men who have older maternal brothers or few maternal sisters are expected to have reduced access to bridewealth, resulting in increased reproductive competition. In groups similar to the Nyangatom, reproductive competition, including that provided by family composition, has been hypothesized to motivate participation in raiding as a means to improve reproductive prospects (17, 18). We then attempt to identify the likely pathways by which reproductive success may be affected by participation in raids focusing on access to bridewealth provided from successful raids.

Ethnographic Background

The Nyangatom are nomadic agro-pastoralists numbering ∼30,000 who inhabit a remote region along the southern border of Ethiopia and South Sudan. This region is one of the few remaining areas of the world in which warfare continues to occur largely free from commercial or state agendas.

The Nyangatom are members of the larger Ateker or Karamojong cluster, which includes the more populous and well-known Karamojong, Turkana, and Toposa (19, 20).

The Nyangatom have the social organization of a small-scale society. Many Nyangatom reside in mobile encampments ranging from a few families to several hundred individuals. There are also semipermanent villages in agriculturally productive areas, although membership is dynamic, as many individuals move between these villages and the temporary encampments. Local environmental conditions or the threat of conflict sometimes forces villages to relocate or disintegrate entirely, causing large areas of their territory to be uninhabited.

The Nyangatom have ongoing conflict with several neighboring ethnic groups including the Turkana, Dassanetch, and Suri, as well as occasional conflicts with other groups (21). Automatic weapons were introduced into the area in the late 1980s and are used throughout the region. Similar to neighboring pastoralist groups such as the Turkana (22), the Nyangatom have two types of offensive raids: stealth raids and battle raids. Stealth raids (sing. *emojirimónu*) are composed of a small number of men,
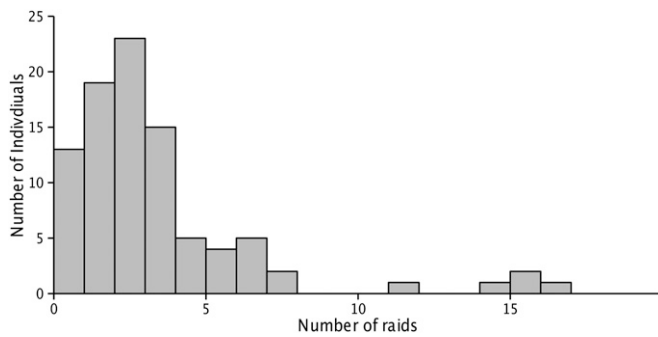
Fig. 1. Histogram of stealth raid participation during the study period for 91 nonelders.

usually 4–25, who attempt to capture poorly guarded livestock by stealth or sneak into an enemy village at night and steal livestock undetected. They may also opportunistically attack and kill individuals they encounter. Stealth raids are conducted primarily by young to middle-aged males and sometimes have informal leadership. Because warriors on stealth raids seek to minimize their risks and engage in livestock theft only when they are unlikely to be detected, stealth raids have a low casualty rate (22).

Battle raids (sing. *ajoré*) frequently include hundreds of participants and are intended to forcibly capture livestock or attack the enemy with overwhelming numerical superiority. Because they primarily rely on violent force instead of stealth, deaths for attackers are not uncommon. They commonly have leaders, which we here call "battle raid leaders." Battle raid leaders appear to take an especially active role in the conflict, coordinate participants, and provide tactical advice. However, as in stealth raids, participation in battle raids is not compulsory, and there are no chains of command or explicit sanctions for desertion or cowardice.

Similar to the neighboring Dassanetch, warriors commonly give livestock to their older paternal relatives after capturing them in stealth and battle raids (23). In such exchanges, the warrior is frequently reluctant to make the transfer, but succumbs to pressure from his relatives. The ethnographic context creates a lag between capturing livestock in a raid and accessing

them for personal use. Because captured livestock are generally given to paternal male relatives, the successful raider is unlikely to be able to use them for his own purposes over the short term.

The basic unit of social organization is the *nawi*, which refers to both the family and the settlement, which are commonly coextensive (19), although many villages are composed of multiple families. The *nawi* includes monogamous or polygynous families including the children of such marriages, adult offspring, and their wives and children. It may also include other adults such as the brothers of the family head, their wives and children, as well as other relatives and friends. Families are usually headed by an elder male who makes most decisions affecting the family, such as where and when to migrate. The family head is usually the owner of all of the livestock on which the family depends, although adults within the family sometimes own a few livestock individually. However, individuals commonly have stock rights to livestock owned by a family head. Stock rights are culturally recognized claims on livestock that allow the holder to claim livestock for certain reasons, including marriage and subsistence.

The Nyangatom are polygynous, with some men having as many as five or more wives. Marriage order within a family usually follows birth order, such that older sons marry before their younger brothers. Typically this applies across polygynous marriages, but the sons of first wives are sometimes favored above older brothers from the wives of subsequent marriages. Marriages, including cases of bride capture and elopement, do not occur without an eventual transfer of bridewealth, no matter how well regarded the groom is. When the bride's family accepts an offer of marriage, a few livestock may be transferred at once, but the majority of the bridewealth is usually given up to a decade later. Elders who marry polygynously commonly exchange bridewealth earlier than nonelders. The primary claims for bridewealth are usually against the family head of the groom and not the groom himself, unless he is the family head or owns a significant number of livestock. The amount of bridewealth required for marriage is not negotiated at the time of marriage but depends on several variables that may change before bridewealth is eventually paid. The number of livestock eventually transferred depends on the relative size of the herds belonging to the groom's paternal kin, the number and sex of the children produced by the marriage, and the number of the bride's male kin. It involves an exchange of more than 30 cattle and may reach up to

Table 1. Regression models 1–4

Independent variables	Model 1 (hurdle model): Number of wives	Model 2: Number of children	Model 3: Number of wives	Model 4: Number of children
Number of raids (count)	1.07 [0.70; 1.30]			
Age rank (count)	0.97 [0.91; 1.00]			
Number of raids (zero)	0.96 [0.55; 13.29]			
Age rank (zero)	0.81* [0.61; 0.89]			
Number of raids		1.04 [0.97; 1.10]		
Age rank		0.97* [0.96; 0.98]	0.97* [0.96; 0.97]	0.96* [0.96; 0.99]
Top raiders			1.37 [0.53; 2.12]	1.74 [0.55; 2.62]
AIC	93.62	208.76	152.02	250.69
Log likelihood	−39.81	−100.38	−73.01	−122.35
Number of observations	91	52	91	91
BIC	111.19	216.56	159.55	258.23
χ^2	94.7	17.28	37.26	154.23
P value	<0.001	<0.001	<0.001	<0.001

Point estimates and 95% confidence intervals are incident rate ratios.
*Indicates statistical significance when 1 lies outside the bootstrap (10k) 95% confidence intervals (displayed in brackets).
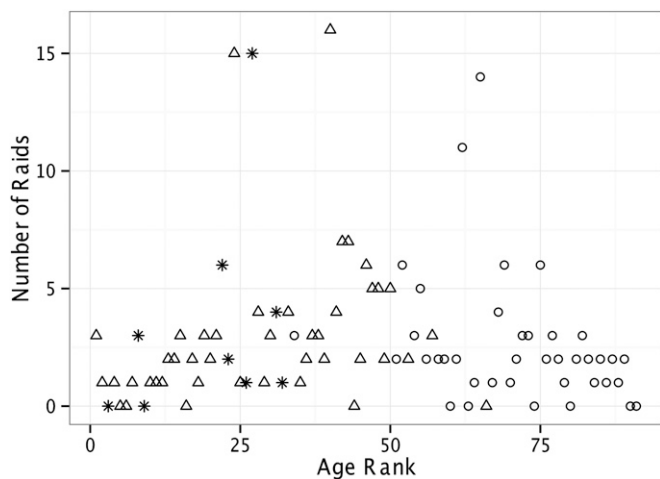
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Fig. 2. Scatterplot of the relationship between age rank and raid participation for nonelders with number of wives indicated by shape. Age rank ranges from 1 to 91, with 1 being the oldest individual in the sample and 91 being the youngest. Number of wives indicated by shape: ✳ = two wives; △ = one wife; ○ = unmarried.

100 cattle. Such a transfer can seriously deplete the herds of the groom's family, so men are expected to use a variety of means to obtain access to livestock to use for bridewealth, including raiding.

Acquiring bridewealth is complex and delays the age at first marriage until the late 20s to mid-30s, during which time virtually all men are married. For first marriages, males acquire bridewealth through accessing any livestock they personally own and by appealing to relatives and friends, although in practice men receive nearly all of their bridewealth allocations from their father and paternal uncles who are family heads.

Obtaining livestock for bridewealth for polygynous marriages is generally more difficult than for first marriages because relatives are less willing to provide livestock to the groom. Thus, to obtain additional wives after his first marriage, the prospective groom must own a herd of livestock or have significant stock rights on livestock owned by kin. Thus, the possibility of polygynous marriage is severely constrained for young men.

Men commonly generate stock rights through the marriage of a female relative. When females marry, their marriage generates incoming bridewealth in the form of livestock, although unmarried men usually cannot receive these livestock. Rather, they receive stock rights to a share of the livestock that they may claim later in life when they desire to marry. The number of livestock to which these stock rights pertain depends on the man's relatedness to the female who was married, with maternal brothers having the strongest claims to incoming bridewealth generated by their sister's marriage. Thus, men with few sisters are called "sister-poor," whereas men with several sisters are called "sister-rich" (18). In the same way, older brothers may use up much of a family's livestock through bridewealth payments, leaving younger brothers with little access to bridewealth. We call such men "brother-biased." Individuals who face shortages of bridewealth may seek strategies such as raiding to increase their access to livestock.

Stock rights are also generated through the compulsory gifts of captured livestock that men make to their elder relatives after a successful raid. Although young men "give" cattle they capture to their relatives, they may later invoke these gifts as stock rights. Commonly claimees resist fulfilling these stock rights due to their desire to use the livestock for their personal benefit, either for bridewealth or subsistence.

The death of a family head provides a means for the holder of stock rights to inherit livestock. Married men who have stock rights on livestock owned by the deceased can claim a share of the inheritance, and the stock rights held by unmarried individuals can transfer to the inheritors and be claimed later. Thus, the gifts of livestock to relatives that occur after a successful raid result in the possibility of a delayed return of livestock.

Here we evaluate the hypothesis that raiding provides reproductive benefits to warriors over the lifetime by testing four predictions: (*i*) among nonelders, increased raiding is associated with a greater number of wives and children; (*ii*) elders who were more active raiders in their youth have a greater number of wives and children; (*iii*) battle raid leadership is associated with a greater number of wives and children; and (*iv*) among nonelders, being sister-poor or brother-biased is associated with increased raid participation. We then use quantitative and qualitative ethnographic data to propose possible pathways between raiding and reproductive success.

Table 2. Regression models 5–8

Independent variables	Model 5 (hurdle model): Warriorship score	Model 6 (hurdle model): Warriorship score	Model 7: Battle leader	Model 8: Battle leader
Number of wives (count)	1.61* [1.04; 3.02]			
Number of wives (zero)	3.12* [1.06; 12.90]			
Number of children (count)		1.16 [0.63; 1.48]		
Number of children (zero)		1.52* [1.01; 2.21]		
Number of wives			2.76 [0.88; 8.79]	
Number of children				1.28 [0.90; 1.78]
AIC	92.08	88.47	29.67	27.35
Log likelihood	−41.04	−39.23	−12.83	−11.67
Number of observations	29	24	29	24
BIC	98.91	94.35	36.08	33.38
χ^2	14.28	6.14	6.46	2.01
P value	<0.001	0.046	0.03	0.15

Point estimates and 95% confidence intervals are incident rate ratios.
*Indicates statistical significance when 1 lies outside the bootstrap (10k) 95% confidence intervals (displayed in brackets).
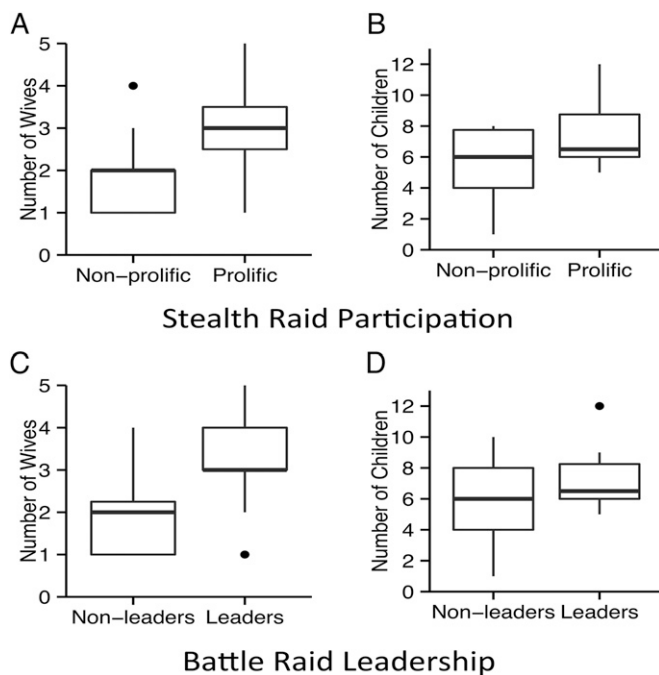
Fig. 3. Boxplots comparing the number of wives and children for battle raid leaders and prolific vs. nonprolific raiders. Prolific raider status of elders and (A) number of wives: nonprolific $n = 18$, prolific $n = 11$; (B) number of children: nonprolific $n = 14$, prolific $n = 10$. Battle-raid leadership and (C) number of wives: nonleaders $n = 20$, leaders $n = 9$. (D) Number of children: nonleaders $n = 16$, leaders $n = 8$.

Results

Study participants include 120 adult males residing at least seasonally in a group of settlements where the researcher was based. For analyses, subjects were divided into two culturally appropriate groups: elders and nonelders. Twenty-nine men were identified as elders by study participants with the local term for elder (sing. *ekasukout*). Because the primary determinant of being an elder is membership in a senior age group, we expect these individuals to be the oldest subjects, but we lack verifiable data on their ages. The remaining 91 men in our sample were members of younger age groups that we collectively call nonelders. We use their individual birth order (age rank) within the sample of nonelders to make age comparisons.

During the study period, nonelders on average participated in nearly three stealth raids (mean = 2.91 raids, SE = 0.34, $n = 91$), whereas no elders ($n = 29$) participated in any stealth raids. Among nonelders, participation varied substantially: 12 men did not participate in any stealth raids, whereas 5 participated in more than 10 raids (Fig. 1). Although elders did not participate in stealth raids during the study period, all had done so during their youth. We therefore used a ranking task to evaluate the subjects' former participation in raids. This task consisted of asking elder males not in the study to identify the elders who had been prolific raiders in their youth. Men identified are called "prolific raiders," whereas men not identified are called "nonprolific raiders." We used the number of times an elder was identified as a prolific raider as their warriorship score. Elders also exhibited variation in their raiding histories, with 11 men identified as having been prolific raiders and warriorship scores ranging from 0 to 14 (mean = 2.71 warriorship score, SE = 0.68, $n = 29$).

We examined the relationship between raiding and reproductive success for nonelders, controlling for age using 3 y of raiding history as a proxy for participation in raiding over the life course. We did not find an association for nonelders between stealth raid participation and number of wives or children in models including age rank (models 1 and 2; Table 1 and Fig. 2).

We then examined the relationship between raiding and wife and child number in the top five raiders in our sample and also found no association between being a top raider and the number of wives or children (models 3 and 4; Table 1).

For elders, there was a positive association between raiding history and reproductive success. Elders who were identified as having been prolific raiders in their youth had more wives and children than nonprolific men (models 5 and 6; Table 2 and Fig. 3). Among men identified as prolific raiders, warriorship score was positively associated with wife number (model 5; Table 2). We examined the relationship between being a battle raid leader and wife and child number and did not find an association (models 7 and 8; Table 2 and Fig. 3).

Family composition had important effects but not in the direction predicted. We assessed the relative importance of age rank, the number of wives of the raider's father, the mother's wife number in a sequence of polygynous marriages, and the number of older maternal sisters and brothers on the number of stealth

Table 3. Regression models 9–10

Independent variables	Model 9 (hurdle model): Number of raids	Model 10: Number of wives
Age rank (count)	1.00	
	[0.99; 1.01]	
Number father's wives (count)	1.55*	
	[1.23; 2.19]	
Mother's wife number (count)	0.73*	
	[0.48; 0.92]	
Number older maternal sisters (count)	0.88	
	[0.62; 1.25]	
Number older maternal brothers (count)	1.19	
	[0.90; 1.56]	
Age rank (zero)	1.00	
	[0.96; 1.03]	
Number father's wives (zero)	1.46	
	[0.64; 3.02]	
Mother's wife number (zero)	1.16	
	[0.32; 4.89]	
Number older maternal sisters (zero)	1.02	
	[0.52; 2.25]	
Number older maternal brothers (zero)	0.59	
	[0.24; 1.83]	
Number older maternal sisters		0.85
		[0.63; 1.11]
Number older maternal brothers		0.91
		[0.71; 1.15]
AIC	399.01	187.57
Log likelihood	−186.50	−90.78
Number of observations	89	91
BIC	431.35	195.10
χ^2	34.91	1.71
P value	<0.001	0.43

Point estimates and 95% confidence intervals are incident rate ratios.
*Indicates statistical significance when 1 lies outside the bootstrap (10k) 95% confidence intervals (displayed in brackets).
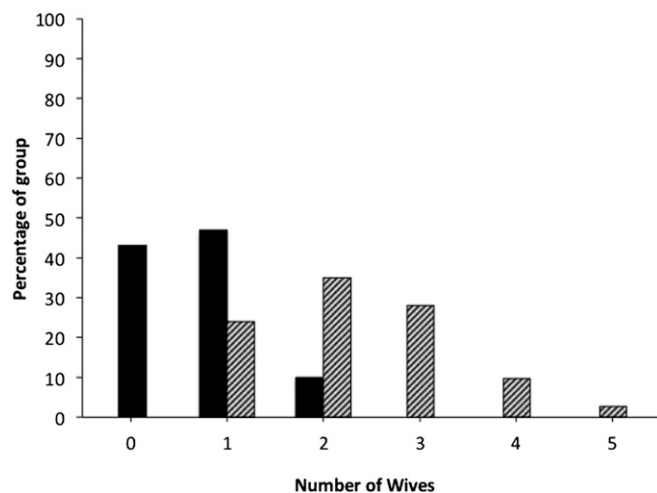
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Fig. 4. Histogram of distribution of the number of wives of study participants. Nonelders, solid bars (*n* = 91); elders, striped bars (*n* = 29).

raids participated in during the study period. Only the number of fathers' wives and mothers' wife number were associated with increased raid participation among men who had participated in raids during the study period (model 9; Table 3). This is consistent with the fathers of raiders having access to additional livestock allowing them to marry polygynously. We also examined whether the number of older maternal brothers and sisters limited the marriage prospects of nonelders. We did not find an association between the number of older maternal sisters or brothers and number of wives (model 10; Table 3). This result suggests that among the Nyangatom, natal family composition does not create significant limitations on the possibility of marriage for nonelders.

To explore the relationships between age and access to bridewealth, we focused on the associations between age and the number of wives (Figs. 2 and 4). All elders were married (mean = 2.34 wives, SE = 0.2, *n* = 29), and seven were married monogamously. Among nonelders, many individuals were yet to be married, and age rank was strongly associated with being married but did not predict having one wife or two wives (model 1; Table 1). These results suggest that age determines when a man can first marry but has little effect on the possibility of polygynous marriages for nonelders.

We examined returns from a sample of raids conducted by nonelders (*n* = 36) to explore whether captured livestock were kept by the raider so that he could use them for bridewealth. We found that captured livestock were more frequently given to paternal relatives than to the raider's in-laws or kept for their personal use [$\chi^2(2) = 18.67$, $P < 0.001$]. In 67% of cases, all captured livestock went to male paternal relatives. In 22% of cases, the raider personally kept some of the captured livestock, and in 11% of cases, captured livestock were distributed to the raider's in-laws as part of his bridewealth payment for a marriage that had already occurred. Together these indicate that captured livestock are generally unavailable to successful raiders over the short term.

Discussion

We found a positive relationship between raiding and reproductive success that depended on the life stage of the raider. Among nonelders, raiding was not associated with an increased number of wives or children. The most likely explanation for this result is that norms of livestock acquisition generally prescribe that a raider transfer captured livestock to his paternal kin, thereby making these livestock unavailable for the raider's own immediate bridewealth.

By contrast, elders who raided more in their youth had more wives and children than other elders. Thus, participation in raiding was associated with increased reproductive success over a lifetime. Because none of these elders had participated in a stealth raid

during the study period, we conclude that this was not due to their having access to recently raided livestock. Because participation in battle raids confers an elevated mortality risk (22), we expected that the additional mortality risk battle raid leaders faced would be compensated by battle raid leaders having greater reproductive success. However, battle raid leadership was not associated with having more wives or children in our sample.

Being sister-poor or brother-biased was hypothesized to limit access to bridewealth and to be associated with raiding as a means to generate livestock for bridewealth. Our analyses showed that the number of older male and female maternal siblings had no effect on the frequency of raiding. Our data therefore did not support the hypothesis that men used raiding to overcome challenges presented by having a high ratio of brothers to sisters among their older maternal siblings.

Our results differ from a previous study among East African pastoralists that found a positive association between commercial cattle raiding and the number of older sisters (18). We suggest that this stems from differences in the ethnographic context. In our setting, captured livestock are not immediately convertible to bridewealth: this presumably reduces the incentive to raid as a means to generate bridewealth over the short term. Additionally, Nyangatom men usually marry for the first time in their late 20s to early 30s, and by their mid-30s, nearly all men are married regardless of their family background. Therefore, it is unlikely that any male will be left unmarried because of lack of access to bridewealth or that raiding will substantially reduce the age at first marriage.

Together these findings suggest that raiding over a lifetime is associated with greater reproductive success. We consider three potential mechanisms for this relationship: immaterial cultural benefits, larger kin networks, and the delayed receipt of livestock from raiding.

Raiders may plausibly enjoy greater reproductive success because of immaterial cultural benefits (e.g., status, honorific names, and insignia). However, the opportunity for these to be converted into reproductive success is limited. Marriages do not occur without the eventual transfer of a significant number of livestock for bridewealth, even for high-status men. In theory, it is possible that warriors have more opportunities for extramarital affairs. However, adultery appears to be rare, because it is a serious and easily detected offense, and individuals who are caught are subject to sanctioning including fining and physical beatings. Consortships with unmarried females sometimes occur, but these opportunities are restricted by parental guarding, and females generally marry within a few years of menarche. These considerations suggest that, although status competition may be an important motivator for individual participation, there are few means for status to be converted into additional marriage opportunities because of the rigid requirements of bridewealth for marriage.

A second explanation for the relationship between raiding and reproductive success is that more active raiders have larger kin networks providing them with more relatives from whom to recruit bridewealth. We found that the fathers of men who raided more had more wives and the mothers of these raiders were earlier in a sequence of their father's cowives. This finding is consistent with successful raids by a son allowing his father to obtain additional wives. However, it is unlikely that these additional marriages would result in significantly more opportunities for bridewealth for the raider through having larger kin networks. The reason for this is because bridewealth claims by men desiring to marry are generally made to consanguineal relatives and not the affines that would be created through the additional wives that a raider's father may have.

Finally, several pieces of evidence support the delayed receipt of livestock as a principal means by which raiders obtain additional wives. Raiding did not appear to result in short-term reproductive benefits among nonelders either by allowing them to marry earlier or marry polygynously. This result is consistent with our finding that captured cattle are generally not kept by the warrior but given to paternal kin.

Age alone is not sufficient for polygynous marriages. Among nonelders, age predicted being married but not having one wife or two. Further, many elders are married monogamously, whereas some nonelders have more than one wife. This variation indicates that being an elder is not sufficient for having multiple wives.

Bridewealth for polygynous marriages is commonly generated through the inheritance of livestock, allowing the individual to build a herd of his own or by having stock rights on the livestock owned by another individual. Inheritance and the receipt of stock rights depends on several factors including the size of the herds belonging to the individual's father and paternal uncles, the number of brothers an individual has, incoming bridewealth from the marriages of female relatives, and any contributions of livestock the individual has made to his relatives. This last factor is the principal variable by which individuals can improve their long-term access to livestock.

When warriors give captured livestock to paternal relatives, they generate stock rights they can later claim, or if the recipient dies, they may be able to inherit a portion of the deceased individual's livestock. Men that participate the most in raiding have more opportunities for stock rights and the inheritance of livestock. They may also benefit from the additional marriages their fathers may have as a result of their son's raiding. We found that the fathers of raiders had more wives and this may enable them to have more daughters. The marriage of these daughters generates incoming bridewealth that the raider may receive a share of and then use for his personal bridewealth. We suggest that these two pathways for the delayed receipt of livestock from raiding provide the most likely explanation for our results.

Conclusion

Nyangatom warriors who raided more often in youth had more wives and children when they became elders. The explanation for this relationship that is most consistent with our quantitative and qualitative ethnographic data are that raiders received delayed access to bridewealth.

Given the similarities of our ethnographic context to other pastoralist societies, our findings appear generalizable to other pastoralist groups practicing small-scale warfare (22, 24, 25), as they are consistent with accounts in similar cultures of the benefits that warriors receive for participation in warfare. We expect that in ethnographic contexts where raiding results in faster and more salient individual benefits, there will be greater incentives for individuals to participate in conflict. Increases in the benefits to warriors may contribute to an escalation of conflict intensity. This relationship may explain the escalated intensity of warfare that occurs among pastoralist groups that practice commercial cattle raiding. It also explains the lesser intensity of warfare commonly found among hunter-gatherers, who normally lack comparable incentive systems (6, 7). Overall, our results provide support for the more general proposition that warriors participating in small-scale warfare tend to receive fitness-enhancing benefits. However, the way in which benefits accrue will vary depending on specific cultural constraints.

Methods

Data were collected by L.G. from a Nyangatom conflict area along the Nyangatom-Turkana frontier during which time he resided at the field site for a total of 14 mo. The study participants consisted of 120 adult males recruited from a group of traditional settlements in which the corresponding author was based. All male residents of reproductive age residing in the study area during data collection were invited to participate in the study. These results exclude very old males and males still in puberty and adolescence. Approval for this study was obtained from the Harvard University Committee on the Use of Human Subjects, the South Omo Zone, Southern Nations, Nationalities, and Peoples' Region, Federal Democratic Republic of Ethiopia, and local elders. Informed consent was obtained from all participants.

Demographic and Reproductive Data. Natal family composition for nonelders and reproductive histories for both elders and nonelders were obtained through interviews with subjects.

Statistical Analysis. We use bootstrapped 95% CIs (10k samples) as our measure of significance for generalized linear model coefficients and report incidence rate ratios (IRRs) and 95% CIs. Analysis was conducted in R version 3.1.0.

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