ON THE EMERGENCE OF LARGE-SCALE HUMAN SOCIAL INTEGRATION

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Abstract

One of the universal features of human sociality is the fact that our social networks are highly integrated – human societies exhibit several nested social layers including families, bands and communities. Several factors have been identified as creating disincentives for hostile intergroup relations, including economic interdependence (trade), intermarriage (exogamy), cooperative defence against external adversaries (warfare), and lack of patrilocal residential groups coincident with external war (absence of patrilocality with external war). We provide a tests of hypotheses relating to the correlates of amicable relations between communities (i.e. absence of internal war) using the standard cross-cultural sample (SCCS) database and Dow (2007) and Eff and Dow (2009) software that controls for autocorrelation and imputes missing data. Intermarriage did not have any explanatory power, there was a nearly significant effect of trade on the establishment of intergroup tolerance, and the evidential basis for cooperative defence and patrilocal residence were strong when combed into a multiplicative effect. This analysis is complemented with an exploration of the evolutionary factors underlying elementary forms of meta-group organization in non-human primates.

Introduction

One of the universal features of human sociality is the fact that our social networks are highly integrated. The level of social integration seen in humans is unparalleled by any other primate. Social integration is achieved by interconnections among groups via crosscutting kinship and affinity ties as well as reciprocal exchange and cooperation ('ultrasociality') (Chapais 2011, Hill et al. 2011, Rodseth et al. 1991, Wiessner 1977). Humans are characterized by a nested and federated social system, whereby smaller units are embedded within larger ones (Foley and Gamble 2009, Grove 2011, Grueter, Chapais, and Zinner 2012, Hamilton et al. 2007, Rodseth et al. 1991). How such multilevel or modular societies have evolved has recently attracted a great deal of attention (Grueter et al. 2012). The three archetypical tiers comprising this system are the family[1], the band and the community or tribe[2] (Birdsell 1968, Brown 1918). This tiered social system has most likely evolved through the crystallization of nuclear families within originally multimale-multifemale/mixed-sex groups as a first step and the later aggregating of groups into communities (Chapais 2008, Grueter, Chapais, and Zinner 2012); but see Layton, O'Hara, and Bilsborough 2012). The functional reasons for the appearance of nuclear families have been

1 Lehmann, Lee and Dunbar (2014) argue that it is not the family *per se* that represents the basal layer of social organization, but an assortment of individuals characterized by strong emotional bonds which can include close family members but also unrelated friends (see also Sutcliffe et al. 2012).
2 This is a very rough categorization; Lehmann, Lee, and Dunbar (2014) distinguish among three levels of social organization above the band layer in hunter-gatherers, *viz*. community, mega-band and tribe (ethnolinguistic group).

treated exhaustively and shall not be restated here (see Chapais 2008, Chapais 2013, Grueter, Chapais, and Zinner 2012 and references therein). Instead, the emphasis we want to place here is on why human bands at some point in time started congregating into larger communities. This remains a fundamental issue in human social evolution and deserves scrutiny, especially considering that this large-scale social integration into a meta-group social structure with frequent opportunities for interactions has helped propel social learning and the accumulation of culture and complex technologies, resulting in our remarkable success as a species (Boyd and Richerson 1996, Henrich 2004, Hill et al. 2011, 2014; see also Pradhan, Tennie, and van Schaik 2012).

In order for such meta-groupings and intercommunity alliances to evolve, agonistic relations with neighbouring communities had to be overcome or discouraged. This is not to say that solidarity has replaced peace, as both phenomena are omnipresent in human societies. Intergroup violence characterizes traditional societies to varying degrees (Chagnon 1988, Ember 1978, Kelly 2000, Wrangham and Glowacki 2012) and archaeological evidence of war dates back to at least 12,000 years (Ferguson 2013, Kelly 2000) but violence involving individuals in different groups has probably much more ancient roots. Contrary to our closest relatives where intergroup relationships are first and foremost hostile (Aureli et al. 2006, Wrangham 1999, Wrangham and Peterson 1996), the ability to foster affiliative ties with other groups and expand the scope of our interaction networks must be derived traits characterizing humankind. Long-distance transport of lithic and other raw materials from their sources, indicating the establishment of tolerant relations between independent communities, can be traced archaeologically to ca 70,000 years (Ambrose 2010, Féblot-Augustins 1997, McBrearty and Brooks 2000; see also Layton, O'Hara, and Bilsborough 2012). Grove (2010) relied on archaeological evidence to predict that societies could have reached several hundred individuals by the time the genus Homo had evolved, but if this was the case, it is unclear if groups grew from inside or through amalgamation with neighbouring groups.

The ability to widen the social milieu and manage interactions across various social layers hinges on brainpower/cognitive competencies such as the ability to differentiate between individuals and social classes (e.g. friend and foe, in-group vs out-group members), but also on the ability to fine-tune one's behaviour in relation to others, attribute mental states to others (theory of mind) and reach agreement on goals and objectives (shared intentionality) (Chapais 2013, Gamble, Gowlett, and Dunbar 2011, Tomasello and Moll 2010). Another likely prerequisite for the formation of information exchange with neighbouring groups and of intricately unified meta-groups is a sophisticated communication system (e.g. Fuentes 2009, Lehmann, Lee, and Dunbar 2014). Moreover, favourable environmental preconditions have to be in place for large interlocking social groupings to materialize, e.g. a sufficiently large resource base that does not entail substantial per capita energetic costs (Kosse 1994).

What selective factors could have created the need for groups to (at least temporarily) fuse with other larger groups? Given that large social groups suffer from coordination problems and freeloading, the benefits of forming these must be substantial (Dunbar 1999, Lehmann, Lee, and

Dunbar 2014). While cooperative hunting (Hill 2002) and cooperative breeding (Hrdy 2009) are collective activities that include and unite members of lower-level social units, for large-scale social integration we have to look elsewhere. Fry (2012) lists a number of contributory factors to the emergence of socially integrated communities characterized by high levels of tolerance: (i) an overarching social identity, (ii) interconnections among subgroups, (iii) interdependence (ecological, economic, and/or defensive), (iv) nonwarring values, (v) symbolism and ceremonies that reinforce peace, and (vi) superordinate institutions and conflict management. Examples of such 'peace systems' include the Upper Xingu River basin tribes in Brazil, the Iroquois Confederacy, and the European Union. Some of these factors may explain the maintenance of peace systems, e.g. the use of symbolic markers and labels may have been crucial in allowing large and less individualized groups to form and retain integrity, as they facilitate demarcation of group membership (Kuhn et al. 2001, Moffett 2013, Richerson and Boyd 1998)[3]. In the following, we will examine three alleged key evolutionary drivers, i.e. interconnections (intermarriage) and interdependence (cooperative defence and trade)[4,5].

Exogamy

Chagnon (1992, p. 160) remarked that "It is, in fact, by the exchange of women that independent villages extend kinship ties to each other." The concept of female exogamy, whereby female exchange can blunt violence and foster amicable ties between previously independent groups, has had a long history; precursors of this idea go back to Tylor (1888) and Lévi-Strauss (1949). Rodseth and Wrangham (2004) and Rodseth et al. (1991) re-emphasized the role of dispersing females in maintaining kinship bridges across groups. The most recent elaboration on the model of exogamy and alliance formation was carried out by Chapais (2008, 2010). He sees three ingredients as major phylogenetic causative factors to the establishment of inter-group alliances in the course of human evolution, i.e. pair bonding, paternal kin recognition and bisexual dispersal. As a first step, the capacity for bilateral kin and in-law recognition was amplified by the establishment of stable breeding bonds. By maintaining bonds with their natal group even after dispersal, intergroup bonds were cemented via both consanguineal kinship and affinal (in-law) kinship. An example of consanguineal ties are a transferred woman's children and their maternal uncles and grandparents living in the woman's natal group. Affinal kinship bonds also emerge because transferred individuals (women) upon marriage get acquainted with their husbands' kin in the new group, and by maintaining contact with their wives' natal kin, husbands are also in a position to recognize their wives' kin.

Widespread intermarriage is claimed to be a strong determinant of non-warring relations among the Iroquois and Upper Xingu peoples (Basso 1973, Fry 2006, Gregor 1990). There are other

3 On a proximate level, the in-group/out-group discrimination of individuals and parochial cooperation is modulated by oxytocin (De Dreu 2012).

4 Warfare/risk of raiding and resource/area trading (of which the latter is of particular importance at high latitudes under very difficult environmental conditions) were also recently hypothesized to constitute key drivers of community-level organization (Lehmann, Lee, and Dunbar 2014).

5 Hill et al. (2014) recently demonstrated that ritual relationships increase interaction rates between members of different bands in hunter-gatherers (Hadza and Ache).

ethnographic reports that ascribe a significant role to (female) exogamy in linking social groups. For example, Akin (1993) argued for the Kwaio of the Solomon Islands that marriages are fundamentally important in connecting the husband's and wife's groups in long-term alliances, and he also noted that marriages are further used strategically to form desired alliances. Podolefsky (1984) suggested that an increase in warfare in some highland areas of New Guinea might be the consequence of a decrease of inter-tribal marriages in the colonial and post-colonial era. Few quantitative tests of this hypothesis have been conducted, however. In a sample of foraging societies, the frequency of warfare is relatively low when the frequency of marriages between local communities rises above 60% (Kelly 2000). Contrarily, a cross-cultural test in which levels of feuding between exogamous and endogamous societies were compared did not provide any supportive evidence for the exogamy theory (Kang 1979). Hayano (1973, 1974) also did not find a pacifying effect of inter-marriage and exchange of women in the Tauna Awa in New Guinea.

Trade / Economic interdependence

Economic and ecological interdependence can constitute a disincentive against the waging of war (Fry 2012, Fry, Bonta, and Baszarkiewicz 2009, Keohane and Nye 1977, Kupchan 2010). The proposition that wars could be held in check by establishing trade, at least among democracies, was already expressed by Kant in his 1795 essay Perpetual Peace (Kant 1972) (for a thorough discourse see Barbieri 2002). Among modern nations, trade is negatively correlated with warfare (Gelpi and Grieco 2008). Interdependence can take the form of active trade of subsistence goods such as food or more passive forms such as mutually agreed permissions to utilize shared territories containing essential resources (although in the latter case gifts are exchanged to maintain rights of reciprocal access (Wiessner 1977)).

An example of trade-based interdependence are the tribes of the Upper Xingu who specialize in the production of particular goods, e.g. pottery and salt, which are then exchanged with neighbours (Gregor 1994). Trade may not always lead to permanent pacification, but may offer temporary relief from inter-group hostilities: The Iňupiaq in northwest Alaska organize annual trade fairs at which food resources and other goods from different areas are exchanged (Burch 2005). Evidence of long-distance trade in regional networks is also visible in the archaeological record in the European Palaeolithic and Mesolithic (Gamble 1989, Newell et al. 1990), and this also included non-utilitarian items used to establish contact with separate groups (Whallon 2006). A cross-cultural analysis revealed that trade was a weak inhibitor of war in simple political systems (independent communities, chiefdoms), but the pattern was reversed in states (Korotayev 2008).

Shared reciprocal access to resources can be of critical importance, especially in harsh environments with high resource uncertainty where constant conflict would be deleterious to fitness and render cooperation adaptive (Braun and Plog 1982, Kelly 1995, Whallon 2006). Examples of such large-scale social networks include small-scale foraging societies such as the Peoples of the Great Western Desert in Australia who resided in bands that were linked with each other as part of local groups that shared rights to use critical resources such as water and food

(Kelly 2005, Tonkinson 2004, see also Fry 2006). Also Kalahari Desert foragers (Ju/'hoansi') in southern Africa living in unproductive, unstable and unpredictable environments were characterized by large-scale networks of hxaro exchange acting as an insurance policy against resource failure in their area (Wiessner 1977, Wiessner 1982, see also Cashdan 1983). Similar exchange networks have been documented for other hunter-gatherers (Dentan 1968). A well-known ethnographic example of reciprocal gift giving is the Melanesian Kula ring where valuable objects such as shell-disc necklaces are ceremonially exchanged among different island communities, thereby stabilizing peaceful linkages among people (Malinowski 1920). Frequent visits and ceremonial gatherings, along with gift giving help to maintain ties and facilitate flow of information regarding the state of the environment (Whallon 1989, Wiessner 1984). That said, extreme resource unpredictability including natural disasters can also have an opposing effect, i.e. leading to war to take resources from enemies (Ember and Ember 1992).

Warfare / Cooperative defence

Already Darwin (1871) noted that intergroup hostilities could have an influence on the evolution of human socio-positive behaviour. Alexander (1990) proposed that between-group competition represented a major selective force for the evolution of large familial and suprafamilial groupings, complex coalitions and clan group solidarity. The need for cooperative defence against external threats may stimulate cordial sentiments to neighbouring communities. Multilevel selection provides an appropriate conceptual framework for understanding the evolution of cases of large-scale cooperation or prosociality such as collective defence against enemies (Richerson and Boyd 1998, Sober and Wilson 1998, Turchin 2011). This framework allows us for example to model the spread of a prosocial trait as a function of the intensity of (cultural) between-group selection pressures.

There is good evidence from the animal kingdom that solidarity within groups can be strengthened when agonistic support and concerted action of unit members is mandatory for group defence (Radford 2008, Radford 2011, Reeve and Hölldobler 2007). As for humans, early ethnographers recount that male camaraderie and cohesion increase when the risk of obliteration by enemy groups is acute (Langness 1967, Murphy 1957, see also Rodseth 2012). Game theoretic analyses have shown that certain forms of human cooperation surface or become intensified in the face of between-group contests (Bernhard, Fischbacher, and Fehr 2006, Puurtinen and Mappes 2009, West et al. 2006). A modelling approach coupled with ethno-archaeological evidence has demonstrated that the severity of intergroup conflicts has repercussions on the proliferation of altruistic group-beneficial behaviours in humans (Bowles 2009).

An example of between-society alliances for the purpose of mutual defence is the Iroquois confederation of Native American tribes (Dennis 1993). Rising population densities resulting in elevated levels of intergroup competition would have exacerbated the need for collective defence (Lehmann, Lee, and Dunbar 2014). New weapon technologies such as the bow in the North American Neolithic would also have made possible increases in the scale of warfare, thereby giving rise to large-scale social coalitions for defensive purposes (Bingham, Souza, and Blitz 2013). Turchin and Gavrilets (2009) reason that the emergence of large-scale hierarchically complex societies was the consequence of evolutionary pressures brought on by warfare (see also Turchin et al. 2013). Turchin and Gavrilets (2009) also state that European Union member states tend to be more unified and disciplined in times of outside threats and specifically refer to the phase when "Adversarial relations with the Soviet block … helped to suppress internal bickering among the member states" (p. 187). Another example given by Turchin (2011) are European settlers in North America that were initially divided based on geographic origin, ethnicity and religion and frequently quarrelled with each other (Silver 2008). Yet when their expansive tendencies were met with resistance from the Native Americans, the European settlers formed a common identity ('white people').

Patrilocality / Absence of aggression among local groups

The comparative study of Van Velsen and Van Wettering (1960) supports the view that patri- or virilocal power groups enhance intra-societal aggression between localized kin groups. This is supported by correlations of various measures of residence patterns and internal warfare in the standard cross-cultural sample (SCCS) database.

Aims

We use the standard cross-cultural sample (SCCS) to analyse the effects of inter-community food trade, intercommunity marriage and external warfare on the extent of conflict between communities. Rodseth et al. (1991) argued that the "principal means by which humans establish intergroup alliances is not the exchange of men among matrilocal groups but the exchange of women among patrilocal groups" (p. 230); we therefore distinguished between matrilocal and patrilocal societies. We predict that between-community solidarity and unification will be higher (i.e. conflict between communities lower) with increasing degrees of external warfare, trade, intermarriage and patrilocality. We also describe the results of a second prediction based on some of the effects of major asymmetries created by patri-local and patri-lineal social organization among humans, who extend recognition of paternal network links, and other primates, who do not. We modify our initially hypothesized model to include the interaction between external war and patrilocality. We close this essay with an exploration of the existence of antecedents of community integration in non-human primates.[6]

Methods

The SCCS includes 186 predominantly pre-industrial societies with a variety of subsistence strategies including hunter-gatherers, fishers, pastoralists, horticulturalists and agriculturalists. These societies were selected to be a representative sample of all geographic regions and cultural

6 It is also important to stress here that the factors that have selected for a trait and the factors that contribute to the maintenance of a trait may not be identical. For example, while trade maintains peace among societies nowadays, it is unclear whether this may have been the initial evolutionary trigger for the establishment of intergroup harmony. Factors may also have evolved sequentially, e.g. female exogamy may have brought initially distinct groups closer, and trade and cooperative defence may have ensued later on. Chapais (2013) argued that trade and economic agreements involve high levels of cognitive sophistication and are more likely to be a consequence rather than the root of between-group ties.

clusters (Murdock and White 1980, White et al. 2013). We used multiple regression analysis to examine the effects of SCCS variables #1 (intercommunity trade as food source), #72 (intercommunity marriage) and #1650 (frequency of external warfare) on the dependent variable #1649 (frequency of internal warfare). Variable #1649 is the most fully coded and robust variable measuring internal warfare/conflict between communities within same society. The variables had the following levels:

#1 (intercommunity trade as food source): 1 = no trade; 2 = food imports absent although trade present; 3 = salt or minerals only; 4 = <10% of food (90% from local extractive sources); 5 = <50% of food, and less than any single local source; 6 = <50% of food, and more than any single local source; 7 = >50% of food).

#72 (intercommunity marriage): 1 = local endogamy 90-100%; 2 = local endogamy 61-89% (agamous); 3 = local endogamy 40-60% (agamous); 4 = local endogamy 11-39% (agamous); 5 = local endogamy 0-10% (exogamy).

#69.d3 (marital residence): 0 = otherwise; 1 = patrilocal or virilocal - with husband's kin).

#1650 (frequency of external warfare - resolved rating). The original code contained values 1 through 5; the code was subsequently revised to values between 1 and 17 by Carol Ember, Melvin Ember, and J. Patrick Gray (Carol Ember, personal communication to Anthon Eff). 1 = external warfare seems to be absent or rare (original code 1); 2 = original code 1.25; 3 = original code 1.5; 4 = original code 1.75; 5 = external warfare seems to occur once every 3 to 10 years (original code 3); 6 = original code 2.25; 7 = original code 2.5; 8 = original code 2.75; 9 = external warfare seems to occur at least once every two years (original code 3); 10 = original code 3.25; 11 = original code 3.5; 12 = original code 3.75; 13 = external warfare seems to occur every year, but usually only during a particular season (original code 4); 14 = original code 4.25; 15 = original code 4.5; 16 = original code 4.75; 17 = external warfare seems to occur almost constantly and at any time of the year (original code 5).

#1649 (frequency of internal warfare - resolved rating): 1 = internal warfare seems to be absent or rare (original code 1); 2 = original code 1.25; 3 = original code 1.5; 4 = original code 1.75; 5 = Internal warfare seems to occur once every 3 to 10 years (original code 2); 6 = original code 2.25; 7 = original code 2.5; 8 = original code 2.75; 9 = internal warfare seems to occur once every 2 years (original code 3); 10 = original code 3.25; 11 = original code 3.5; 12 = original code 3.75; 13 = internal warfare seems to occur every year, but usually only during a particular season (original code 4); 14 = original code 4.25; 15 = original code 4.5; 16 = original code 4.75; 17 = internal warfare seems to occur almost constantly and at any time of the year (original code 5).

Statistical analyses were performed in Galaxy CoSSci (http://socscicompute.ss.uci.edu), which implements methods that deal with imputation of missing data and with Galton's problem (White et al in press). DEf (Dow-Eff functions) (Dow 2007, Eff and Dow 2009) provide a generic solution to autocorrelation that controls for Galton's problem (i.e. that similar cultures could be due to borrowing, common descent, or evolutionary development). DEf computes an estimated variable Wy (network lag term) based only on the characteristics of the neighbours for each observation weighted by the closeness of their language and geographic (sometimes ecological) network connections. Added to an ordinary regression model, if the Wy variable leads to an error term with no significant correlations with the independent variables, as checked by the Hausman test, then it provides an appropriate measure of control for autocorrelation.

Results

The results in Table 1 involved iterating independent variables keeping variables #1 and #1650 (the initially significant variables) in the model. Variable #69.d3 (patrilocal/virilocal) was positively associated with internal warfare. Variable #1650 (external warfare) showed a significant association with intercommunity conflict, in the opposite direction as predicted. The coefficient for variable #1 (intercommunity trade) was negative and its p value almost reached statistical significance of 0.05. There was no improvement i.e., possible refinements that are more predictive, when variable #1 was dropped. Variable #72 (intercommunity marriage) was not a significant predictor of intercommunity conflict and hence dropped. The method of analysis (Dow 2007; exemplified in Eff and Dow 2009) and here and in Table 3 includes control for autocorrelation (distance and language) and imputation of missing data.

Table 1. Regression of trade #1, external warfare #1650 and patrilocality #69.d3 (independent variables) on intercommunity conflict (internal war). Independent variables with missing data are imputed for the n = 152 cases coded for dependent variable, #1649 (internal war). The Wald test (p = 0.61) shows that appropriate variables were dropped and no additional significant variables were detected in the dataset. The basic statistical criteria of exogeneity required for valid regression results are satisfied.

R^2 = 0.365 Internal War Dependent Var. Independent Variables:	**% Relative Importance**	**Standardized Coefficient**	**p**
(Intercept)	NA	NA	0.1742
#1 (Intercommunity trade) n=183	0.0132	-0.1392	0.0736 n.s.
#1650 (External warfare) n=154	0.2817	0.5233	0.0000****
#69.d3 (Patrilocal marital residence) n=185	0.0334	0.1788	0.0138*
Wy (Network lag term)	0.0349	0.0808	0.0006***

Levels of significance: * p<.56, ** p<.01, *** p<.001, *** p<.0001

The DEf results show that the external war variable #1650 has roughly 10 times the R^2 of any other variable in the model (a relative importance or relimp = 28% of the total variance, and a highly significant Wy or network lag term (Table 1). Autocorrelation is highly significant (p = 0.0006), with the percent of Wy autocorrelation that is linguistic is 77% compared to distance 23%, and no significant effect of ecological variables. Wy passes tests of non-significant variation from a normal distribution lacking heteroskedastacity (Shapiro-Wilkes p = 0.40, Breusch-Pagan p = 0.54) and the Hausman test of no correlation of residuals with the independent variables (p = 0.66), showing that autocorrelation controls are valid, which is the statistical evidence that Galton's problem is solved for this model. The model also passes tests for correct functional form of the model variables (RESET test p = 1.00). Our use of these tests were two-tailed with significance set at p = 0.06.

Discussion

The present cross-cultural exploratory analysis on the effects of trade, intermarriage and warfare on within-community cohesion has demonstrated a nearly significant effect of trade. The results suggest that trade could have been a pacifier, whereas female exchange and presence of external war did not contribute to pacification. In a similar vein, Korotayev (2008) did obtain a negative correlation between trade and warfare, but his analysis was for independent communities only and he used different variables, i.e. #819 (importance of trade) vs. #1 (intercommunity trade as food source).

Exogamy had no effect on intergroup conflict, a finding that is in concordance with Kang (1979). Internal warfare was found to be a greater issue in patrilocal societies, a finding that is consistent with Ember and Ember (1971; pp. 583-584): "The fact that warfare is at least sometimes internal appears to require patrilineally related males to be localized after their marriages. Or, in other words, if fighting occurs between neighbouring communities, families would want to keep their fighters at home for protection". New analyses of data on the Yanomamö have shown that marriage exchange is associated with lethal coalitionary aggression among men, implying that marriage exchange can actually lead to more internal warfare (Macfarlan et al. 2014). Marriage alliances thus form the bedrock for alliances that allow men to engage in internal warfare (Rodseth and Wrangham 2004).

The finding that external warfare is positively related to conflict between communities is contra the expectation. Some additional explanatory variable may have confounded the pattern, e.g. the presence/absence of fraternal interest groups, i.e. local groups of related males whose presence have been shown to be associated with proclivities toward internal warfare and feuding (Otterbein 1994).

White (1990), however, put the positive association between external and internal warfare in a different light by showing that there is also a very strong tendency for asymmetry between one of the off-diagonals (external war being far more frequent than internal war). This is true for the warfare variables of Wheeler's (1984) (variables #891/892 and 893) and those of Lang (1998) (variables #1746, 1747), with ratios in one off diagonal being respectively asymmetric by 150%, 250-300%, and 600-1200%. All three of Lang's (1998) tables where this is tested and both of Wheeler's tests confirm the same results, as shown in Table 2. The last of the table's findings, however, shows why this finding is not replicated with Ember and Ember's (1992) data (variables #1649/1650): their data are confounded by coder disagreement as to whether particular wars are internal or external. This often occurs when there is ambiguity as to which communities engaged in a war are local and which are not.

It is probably not that external war per se tends to repress internal war but that, consistent with Table 3 results, patri-oriented descent and localization – not other systems of residence and lineality – tend to push external war into more fractured internal conflicts because of breakdowns in segmentary structure while initially localized conflict among patri-oriented descent and localization groups spills into external war only with deep segmentary lineages or other special circumstances.

The original intent of White (1990) in showing the kinds of data in Table 2 on the asymmetries of external and internal warfare (demonstrated through cross-tabulations), with external war occurring much more often in the absence of internal war than the converse, was to show that the theory of Ross (1985, 1986) was mistaken: his view was that warfare begins with local orientations to violence and internal war and then spreads to external war. Smole's (1976) ethnography of the Yanoama of the highlands, however, shows a peaceful society, while the Yanomamö of the lowlands are not a "pristine" society but were beset by conflicts with traders, trappers, settlers, missionaries, and colonial administrators long before Chagnon's fieldwork. Ross (1968) extrapolates from Chagnon's (1992) Hobbesian theory that the Yanomamö represent an evolutionary prototype for internal violence that spreads to external war. The data of Table 2 might suggest that Hobbesian theories are mistaken when there are few societies that have internal warfare but little or no external war as contrasted with the converse. The lethal coalitionary aggression model of Macfarlan et al. (2014) for the Yanomamö, however, associated with formation of intracommunity female exogamous dual organization (Houseman and White 1998), might explain the low to moderate incidence of internal war without external war shown in Table 2.

To study off-diagonal inequalities in cross-tabulations requires eliminating the diagonals and computing the respective number of cases above and below the diagonals. Using R this can be done in commands such as table(dx$v1748,dx$v1747), where the leading dx$ of a variable retrieves the data from the DEf dataset. Ratios in Table 2 such as 40 : 8 indicate that per society there are 5 times as many societies with external rather than internal warfare frequency. The null hypothesis of equality is that the total frequencies are equal, in this first case 24 : 24 for a sum of 48. The Fisher Exact test then computes the likelihood that these two ratios do not differ from randomness, i.e. the expected equalities in the middle column.

Table 2. Are off-diagonals in the cross-tabulations of internal and external warfare asymmetric, i.e., many more cases of external war than internal war?

Cross-tabulations and two-tailed Fisher Exact	**Off-diagonal inequality**	**Expected equalities**	**Fisher Exact p**
Lang (1998) #1748 (Frequency of internal warfare involving non-territorially organized groups within unit of MaxPolAuth) (cross-tab) / #7147 (Frequency of external warfare)	40 : 8	24 : 24	0.00099
Lang (1998) #1749 (Frequency of violent conflict between groups within local communities) / #1747 (Frequency of external warfare)	48 : 6	27 : 27	0.000018
Lang (1998) #1750 (Frequency of violent conflict between groups within local communities) / #1747 (Frequency of external warfare)	42 : 3	22 : 22	0.0000042
Wheeler (1994) #891 (Frequency of internal warfare) (cross-tab) / #892 (Frequency of attacking)	51 : 21	36 : 36	0.017
Wheeler (1994) #891 (cross-tab) / #893 (Frequency of being attacked)	47 : 15	31 : 31	0.0050
Ember and Ember (1992) #1649 (Frequency of internal warfare between local communities within unit of maximal political authority) (cross-tab) / #1650 (Frequency of external warfare)	18 coders disagreed with others as 47 : 31	… to whether warfare is internal or 39 : 39	… external, i.e. the codes are confounded 0.12 n.s.

The present analysis shows that female exogamy (the greater dispersion of females at marriage with patrilocality than with matrilocality) is not associated with meta-group organization in humans, especially since patrilocality and patrilineages tend to segment kin groups rather than integrate them except perhaps in the lethal coalitionary aggression model of female exogamous dual organization. Consequently an exploration of the 'antecedents' of this factor in non-human primates may be rendered futile. However, constraints inherent in the data at hand (SCCS) may limit the power of the test provided, and results should be regarded as tentative; subsequent approaches may generate divergent findings, especially since the variables tested were limited above to those hypothesized.

Table 3 shows an instance of adjusting the model as hypothesized and examined in Table 1, which showed an effect of patrilocality now replaced in Table 3 by substituting an interactive term for patrilocality multiplied by external warfare. The standardized coefficient and p value are now 1.4 and 3.4 times greater and relative importance is 4.4 greater. The standard coefficient and relative importance of external war alone in this case is 1.4 less. This helps to explain that, for the off-diagonal asymmetries in Table 2, internal war is more likely to remain localized given patrilocality without external war, while internal war is more likely to increase in the case of patrilocality *with* external war. The result is to split the effects of #1650 on internal war into two parts, one including the product of #1650 and #69.d3 that has more internal war and a less significant effect on internal war without that those variables in concert. The comparative ethnographic scenario of Van Velsen and Van Wettering (1960) supports the view that patri- or virilocality enhance conflicts between localized kin groups, which is part of what we find for this model except that it is *viri-patrilocality and external war that help create fissile communities and greater internal war*. The theory of Ross (1986) that internal war causes or spreads to external war, using the Yanomamö as a prototype, is not supported.

Table 3. Regression of trade as food source #1, external warfare #1650, and patri-virilocal residence with external war #69.d2X1650 (independent variables) on intercommunity conflict (dependent variable, #1649: internal war). Variable #72 (intercommunity marriage) was not a significant predictor of intercommunity conflict. All independent variables with missing data are imputed for cases coded for the dependent variable, n=152. The Wald test (p = 0.30) shows that appropriate variables were dropped and no additional significant variables were detected in the dataset. The basic statistical criteria of exogeneity required for valid regression results are satisfied.

R^2=0.369 Internal war dependent var. Independent variables:	**% Relative importance**	**Standardized coefficient**	**P**
(Intercept)	NA	NA	0.2952
#1 (Intercommunity trade)	0.0128	-0.1321	0.0591
#1650 (External warfare)	0.1863	0.3699	0.0000***
#69.d3X1650 (Patrilocal residence times external warfare): + Effect on internal war	0.1474 (in Table 1, patrilocality alone, this was 0.0334)	0.2577 (was 0.1788)	0.0040** (was 0.0138)
Wy (Network lag term)	0.0423	0.2183	0.0017**

Levels of significance: * p<.05, ** p<.01, *** p<.001, **** p<.0001

Autocorrelation (Wy) in Table 3 is again highly significant (p = 0.00004), with the percent of Wy autocorrelation that is linguistic 81% compared to distance 19%, and no significant effect of ecological variables. Wy passes tests of non-significant variation from a normal distribution lacking heteroskedastacity (Shapiro-Wilkes p = 0.30, Breusch-Pagan p = 0.39) and the Hausman test of no correlation of residuals with the independent variables (p = 0.73), showing that autocorrelation controls are valid, and indicating that Galton's problem is solved for this model. The model also passes the test for correct functional form of the model variables (RESET test p = 0.83).

The rudimentary forms of intergroup tolerance in non-human primates that are described below likely do not represent homologies with humans (are not precursors in the strict sense), but may rather have evolved in reaction to similar environmental and social pressures. Macfarlan et al. (2014) do suggest, however, in generalizing their Yanomamö model of lethal coalitionary aggression with female exogamous dual organization, that "it is still plausible that human and chimpanzee lethal coalitionary aggression share a common evolutionary origin."

Primates

Most primate societies are characterized by intergroup animosity, although there is variation on this theme, reflecting the sex of participants in intergroup interactions and the locally and seasonally varying importance of mate vs. resource defence. Intergroup conflict can also be relaxed in the context of mate quality assessments and extra-pair/group copulations (Cheney 1987, Cooper, Aureli, and Singh 2004, Crofoot 2007, Fashing 2001, Harris 2007, Korstjens, Nijssen, and Noë 2005, Perry 1996, Reichard and Sommer 1997, Robbins and Sawyer 2007, Saito et al. 1998, van Schaik, Assink, and Salafsky 1992, Wilson et al. 2012, Zhao 1997). There are also taxa in which instances of peaceful encounters, mutual tolerance and even temporary fusion between groups have been reported, e.g. western gorillas (*Gorilla gorilla*) (Bermejo 2004), mountain gorillas (*Gorilla beringei*) (Grueter, pers. obs.) and bonobos (*Pan paniscus*)(Furuichi 2011, Idani 1990). The only taxa where delineated social units stay in regular or permanent proximity to other units are those living in multilevel systems, i.e. geladas (*Theropithecus gelada*), Hamadryas baboons (*Papio hamadryas*), snub-nosed monkeys (*Rhinopithecus* spp.), douc langurs (*Pygathrix* spp.) and proboscis monkeys (*Nasalis larvatus*) (Grueter, Chapais, and Zinner 2012, Grueter and van Schaik 2010). Whether gibbons exhibit social and behavioral integration at the community level, i.e. modularity, is yet to be elucidated (Fuentes 2000, Whittaker and Lappan 2009), but there are for instance anecdotal reports of males of neighboring groups of Kloss gibbons (*Hylobates klossii*) engaging in (mutually beneficial?) choruses, assumedly an anti-predation strategy aimed at confusing human hunters (Tenaza 1976). There are also reports of long-distance alarm calls given by adult male Kloss gibbons (which are audible for much longer distances than needed for the immediate family) to warn neighbouring groups (possibly relatives) of danger (Tenaza and Tilson 1977). To what degree do the hypotheses for inter-group pacification outlined in this article apply to primates? An exhaustive treatment of this is beyond the scope of this article, but a systematic investigation on the factors promoting intergroup peace across primates would be desirable.

Exogamy

In primates, dispersal is often sex-specific, while bisexual dispersal is uncommon. Humans, however, have flexible residence patterns, with bisexual dispersal being particularly frequent in hunter-gatherers (Hill et al. 2011, Marlowe 2004). For friendly intergroup relations to become fully established, pair bonds coupled with paternal recognition (allowing bilateral kin and in-law recognition) have been identified as key ingredients (Chapais 2008). Moreover, humans maintain bonds with their natal kin even after transferring into another group to breed. This is basically absent in primates, in which kin lineages are isolated to single communities (Rodseth et al. 1991).

That said, there may be rudimentary forms of community integration in non-human primates. In modular colobines such as snub-nosed monkeys, female dispersal between interbreeding single-male units within bands may act as a unifying element; this may contribute to interunit tolerance and sporadic affiliation among females and thereby reinforce through females the maintenance of a modular society (Grueter, Chapais, and Zinner 2012). Gibbons are another informative example. While intergroup interactions are mostly agonistic or even lethal (Palombit 1993), many encounters are neutral or affiliative. There exist even reports of adult males playing with extragroup juveniles (Reichard and Sommer 1997). Shared descendance may be the source of reduced aggression between neighbouring groups. A combination of extra-group matings and short dispersal distances create a situation where adjacent groups may contain close relatives, thus facilitating the formation of affiliative intergroup relationships (Bartlett 2003, Reichard and Sommer 1997). These observations have led researchers to assume that gibbon groups (or 'households') actually exist as parts of larger communities (Bartlett 2003, Fuentes 2000, Reichard, Ganpanakngan, and Barelli 2012, see also Quiatt 1985) (Figure 1). Reichard, Ganpanakngan, and Barelli (2012) (p. 254) concluded: "The most dramatic change in our understanding of gibbons, as we see it, has been the shift from a socio-sexual monogamy model toward a dynamic community based-model in which individuals, although living in small social units and on small, group-specific home ranges, are connected to a much larger social sphere that involves permanent exchanges and interactions across core social unit's socio-spatial boundaries".

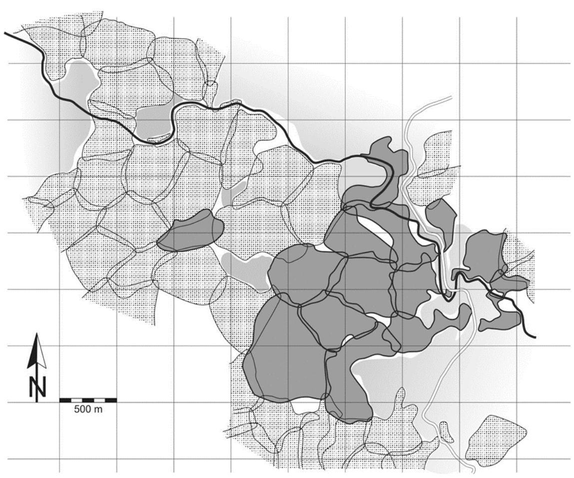

Figure 1. Home ranges of neighbouring groups of white-handed gibbons (*Hylobates lar*) in Khao Yai National Park, Thailand. Map courtesy of U. Reichard.

'Trade' / Economic interdependence

Intergroup trade sensu stricto does not occur in wild primates (although 'commodities' are exchanged between members of the same social group (Barrett and Henzi 2006, Yu et al. 2013) and captive primates have been coaxed into bartering tokens (Brosnan and de Waal 2005)). However, it is still conceivable that intergroup tolerance (as opposed to territoriality) and community interaction may be adaptive in situations where resource heterogeneity (on both spatial and temporal scales) is pronounced and neighboring groups of the same species are equally dependent on those resources. Highly localized and/or seasonal resources may act as magnets for social units. If resources are highly seasonal and/or clumped in distribution, it may pay a social unit to have a large home range encompassing a number of different habitats, as this would safeguard against food deprivation. The upshot is then that home ranges of separate groups overlap and this may be a basis for subsequent inter-group tolerance (Figure 2).

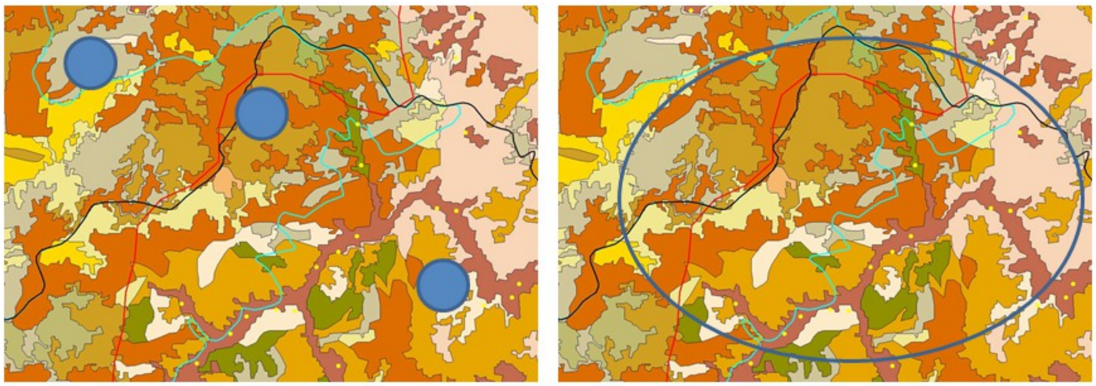

Figure 2. Hypothetical scenario depicting the adaptive benefit of a large home range shared among ancestrally isolated social units. Initially, a number of small social units occupied small (territorial) ranges (left). However, in case of extreme resource heterogeneity (as exemplified here by the habitat of black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) in Weixi County, Yunnan Province, China), a group may end up being confined to a single habitat type and may not have access to critical resources in other habitat types and at other times of year. This could act as an evolutionary incentive for groups to tolerate other groups in the vicinity and share a large non-territorial home range (right). Each colour represents a different ecozone or habitat type.

These arguments are reminiscent of the resource dispersion hypothesis which posits that, if there is spatial or temporal heterogeneity in the availability of resources, primary residents or primary units occupying a given area will have to cover a relatively larger area to include sufficient potential resource patches to exceed some critical probability of encountering enough exploitable patches over time. Groups per se (or higher level social associations such as module-based bands) may form with no or minor direct costs to the original residents or original units (Bacon, Ball, and Blackwell 1991, Carr and Macdonald 1986, Johnson et al. 2002). Johnson et al. (2002) point out that the resource dispersion hypothesis does not only apply to territorial species, but may potentially also explain the social organization of species that live in large non-territorial congregations, and that the resource dispersion hypothesis requires no cooperation among units. Experimental manipulation of food distribution in the Gunnison's prairie dog (*Cynomys gunnisoni*) revealed that increasing food patchiness in space and time was associated with increasing spatial overlap among individuals whereas overlap decreased as food became more evenly dispersed (Verdolin 2009). A comparison of five primate species in Kibale Forest, albeit relatively crude, showed that increasing variation in resource availability was reflected in a higher degree of spatial overlap of group activity ranges (Waser and Wiley 1979). Greater overlap in home ranges, and the resultant closer proximity of individuals to each other, may allow a higher frequency of social interactions among individuals, offering the potential for the evolution of increased sociality.

We conducted a preliminary test of the resource heterogeneity hypothesis on Asian colobines, a taxonomic group of primates that exhibits great variation in terms of intergroup tolerance and home range overlap. Some species are strictly territorial with no or limited home range overlap and respond mainly aggressively to intruders whereas others show up to 100% overlap in their ranges and high levels of tolerance towards neighbouring social units (modularity) (Grueter and van Schaik 2010). Resource heterogeneity was indexed by the coefficient of variation (CV) of (young) foliage availability, a highly sought resource for Asian colobines (e.g. Grueter et al. 2009). A simple linear regression showed a marginally significant effect of seasonal heterogeneity of foliage availability on home range overlap in a sample of Asian colobine species (estimate = 0.809, R^2 = 0.376, p = 0.079, n = 9; Figure 3). However, there was no statistical effect of CV fruit, another preferred resource type (estimate = 0.201, R^2 = 0.069, p = 0.495, n = 9). Systematic cross-species tests are needed to substantiate the association between resource heterogeneity (in both space and time) and intergroup tolerance.

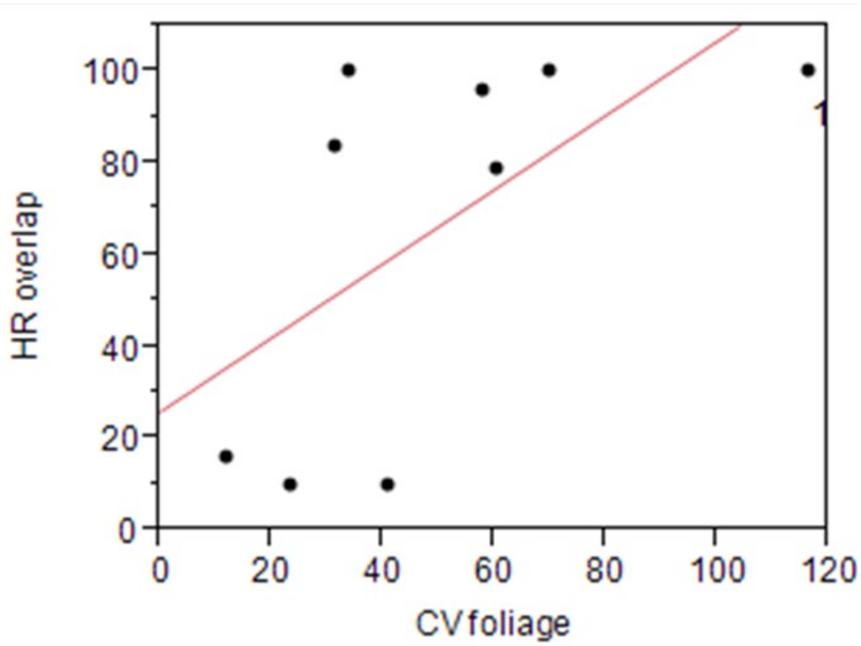

Figure 3. Home range overlap in Asian colobines as a function of CV foliage availability analysed by simple linear regression. Data on CV foliage from Tsuji, Hanya, and Grueter (2013), data on home range overlap from Grueter and van Schaik (2010).

Warfare

A link between intergroup conflict and within-group solidarity has been explicitly incorporated into the socioecological model of (female) primate social relationships (Sterck, Watts, and van

Schaik 1997, van Schaik 1989, Wrangham 1980). However, there is surprisingly little evidence in nonhuman primates that within-group cohesion is heightened by increasing conflicts between groups (Cheney 1992, Cords 2002, di Sorrentino et al. 2012, Grueter 2013). Examples of different social groups uniting against an external force are virtually non-existent[7], with the possible exception of multilevel systems of snub-nosed monkeys where the need for cooperative group defence against bachelor males can lead to tolerant or even cooperative relationships among units (Xiang et al. 2014)[8] (Figure 4). In Hamadryas baboons, males of different units within clans occasionally cooperate over access to females (Abegglen 1984). In both examples, though, interactions are restricted to family units and not higher levels of society.

Figure 4. Golden snub-nosed monkey (*Rhinopithecus roxellana*) males belonging to different social unit (one-male units) going on a joint patrol in pursuit of external threats. Photo taken by Hui Yao at Shennongjia Nature Reserve, China.

Conclusion

"The purpose of putting forth "stripped down" models is often misunderstood. Obviously, a rich mixture of special mechanisms and conditions was involved in any particular transition from a

7 In some bird species, male owners of neighbouring territories sometimes enter into an armistice and form temporary defence alliances in response to simulated territorial intrusion (Elfström 1997, Goodwin and Podos 2014). For analogous observations in an invertebrate, see Backwell and Jennions (2004).

8 Whether these collective acts represent genuine cooperation or mere simultaneous responses to the same stimulus remains to be elucidated.

simpler to a more complex society. However, history of science is emphatic: an attempt to build a theory that immediately tries to capture all this rich variety is self-defeating. Theories must be built from bottom up, starting from very simple propositions and then adding more complexity, while testing each step empirically. Only those components should be added that result in a substantial increase of the theory's explanatory power." (Turchin 2011:28-29)

We have attempted to illuminate some of the possible causes underlying the transition from intergroup rivalry to intergroup tolerance. Given the complexity of the phenomenon at hand, a multitude of explanatory factors are likely involved. The present exercise should by no means be seen as providing a definite answer; additional and refined empirical tests are needed. Nevertheless, we see great value in devising simple models as a starting point for elucidating a complex pattern such as large-scale social integration.

Cross-cultural analyses are not the only means by which hypotheses about the evolution of social integration can be scrutinized; what is also needed are more analyses focusing on single societies. However, with rapidly advancing anthropogenic changes that natural (and cultural?) environments are subjected to, obtaining quantitative data on several communities in intact traditional societies is getting increasingly difficult.

Multigroup cooperative networks and the coordination of whole social groups probably played a key role in the Upper Paleolithic expansion of human populations across the globe into marginal areas (Whallon 1989). Once intergroup pacification became established, our ability to innovate and transmit knowledge socially transcended the formerly independent group level and facilitated the accumulation of cumulative cultural technology that helped us in conquering (and exploiting) this planet (Boyd, Richerson, and Henrich 2011, Hill et al. 2011, Powell, Shennan, and Thomas 2009).

Trade may well to a certain degree contribute to peace in our contemporary world (Barbieri 2002, Gelpi and Grieco 2008, Russett and Oneal 2001). In fact an explicit incentive for the formation of the European Union was to abolish threat of war in the region (Staab 2008). This was to be achieved by progressively integrating the national economies (Fry 2009). However, while globalization may bring peace, it may over the long-term lead to accelerated resource depletion, thus creating conflict potential (Homer-Dixon 1994).

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