Tolerance in intergroup encounters: Payoffs and plasticity in non-human primates and humans

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ABSTRACT

Primate individuals use a variety of strategies in intergroup encounters, from aggression to tolerance; however, despite the prevalence of tolerance in humans, recent focus on the evolution of intergroup contest has come at the cost of characterizing the role of tolerance in human sociality. Can we use the selection pressures hypothesized to favor tolerance in intergroup encounters in the non-great ape primates to explain the prevalence and plasticity of tolerance in humans and our closest living relatives? In the present paper, we review these candidate ecological and social factors and conclude that additional selection pressures are required to explain the prevalence of tolerance in human intergroup encounters; we nominate the need to access non-local resources in the human foraging ecology as a candidate pressure. To better evaluate existing hypotheses, additional, targeted data are needed to

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document the prevalence and plasticity of tolerance during intergroup encounters in some great ape species.

1. INTRODUCTION

Attempting to explain the prevalence of aggression between groups in primates, evolutionary anthropologists have focused extensively on the ecological and social factors favoring between-group contest and warfare. However, this has come at the cost of fully characterizing the variation in the strategies individuals use in intergroup encounters: for example, primates are also often observed behaving tolerantly towards out-group targets, or even coordinating with them in collective action (e.g., [1,2]; see also [3], Table 22-1). By identifying the social and ecological factors responsible for these varying strategies in non-human primates, we can better characterize the ancestral basis of intergroup relationships in the human lineage on which derived, unique features of human sociality were built. That said, as we note over the course of the present review, while theoretical approaches addressing incentives for contest in non-great ape primates provide insight into the prevalence and plasticity of aggression in the context of intergroup encounters in humans, approaches addressing incentives for encounter are insufficient to explain the prevalence and plasticity of tolerant human behavior. These approaches may also be insufficient to explain the variable strategies used in non-human great ape intergroup encounters[A], but we lack the field data to assess this possibility (see also [4]). With this limitation in mind, we will summarize the existing hypotheses regarding incentives for intergroup encounter in the non-human great apes and identify the types of field data needed to better distinguish among these approaches and to generate new hypotheses.

[A] Orangutans are excluded from this review, as they are semi-solitary and thus do not engage in intergroup encounters per se[27]; see section 4.

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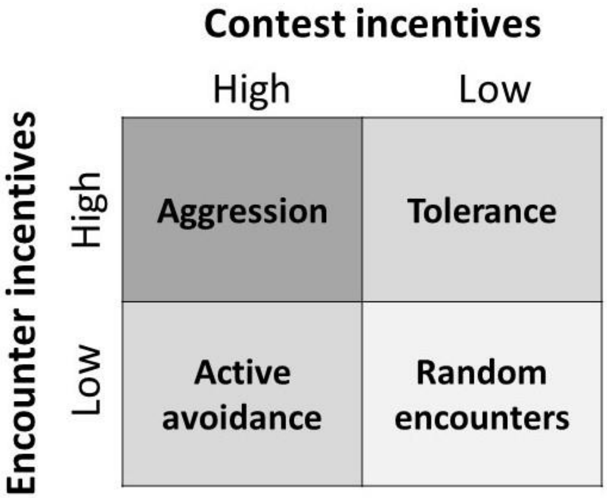

		Contest incentives	
		High	Low
Encounter incentives	High	Aggression	Tolerance
	Low	Active avoidance	Random encounters

Figure 1. Basic incentive structure for behavior towards an out-group target. Contest incentives include net benefits of defending food resources or mates. Incentives for encounter include net benefits of foraging in association, predation avoidance, and opportunities for mating and transfer.

Whether an individual exhibits tolerance towards a conspecific – that is, he or she has a visual encounter with a conspecific, has the option to leave, but remains in the encounter without engaging in an aggressive act (e.g., [5]) – is a function of two fitness-relevant dimensions: her incentives for contest and incentives for encounter with respect to the target individual (cf. [2]). When an individual has disincentive to engage in contest but incentive for encounter, she should exhibit tolerant behavior, all else equal (1st row, 2nd column of Figure 1); when she has incentive to engage in contest and incentive for encounter, she should exhibit aggression (1st row, 1st column). Existing theoretical approaches in the non-great ape primate literature suggest candidate selection pressures – features of the ecology and the strategies of conspecifics – that disfavor contest and favor encounter, resulting in tolerant behavior. How much of the variation in human behavior, and in the behavior of our closest relatives, can we explain using these existing theoretical approaches? Do we have appropriate data to assess their relevance?

To evaluate the explanatory power of existing frameworks from the non-ape primate literature regarding incentives for intergroup contest and encounter, in this review we will not focus on (1) the role of phylogeny; (2) competing incentives and constraints on individual-level behavior, such as rank, kinship networks, group size, and past experience (see Box 1); or (3) the proximate processes that produce tolerant behavior (e.g., hormonal responses to out-group exposure, features of our evolved psychology that regulate xenophobia, etc.). Instead, we will see how much traction we can gain using ecological and social frameworks commonly applied to non-ape primates and identify where more theory is needed to explain non-human ape and human patterns.

1.1 TOLERANCE

The majority of mammals are solitary; why then are groups so common in the Primate order, given that conspecifics may be competitors for food or may otherwise negatively affect an individual's fitness? There are several hypotheses favored in the literature for why primates may live in groups (see Box 2); in short, though an individual and fellow conspecifics have conflicts of interest, they may remain in association across time if the net benefits to be gained from doing so – in terms of resource defense and predation avoidance, for example – are high relative to incentives for contest over food and mates between these individuals. Perhaps unsurprisingly, groups are often composed of units of close kin of one sex and associated members of the other sex, as conflicts of interest are lower between close kin (see Box 1), augmenting the net benefits of remaining in association.

In most environments, individuals living in groups meet members of other groups, in what we term an intergroup encounter. We define an intergroup encounter as visual contact between at least one member of each of two groups. Why would an individual ever have incentive to encounter an individual from another group? After all, conflicts of interest between groups are usually higher than those within groups, as groups already fulfill a number of potentially fitness-beneficial functions. We will identify the benefits that can incentivize intergroup encounter over the course of this review; briefly, opportunities for transfer and copulation, as well as enhanced resource and predator defense, are some of the additional benefits to be gained from extended encounters. If there *are* benefits to intergroup encounters, then, why does an individual not remain in association with out-group members, fusing into a single group? The affordances of extended intergroup encounters for an individual may vary across time – for

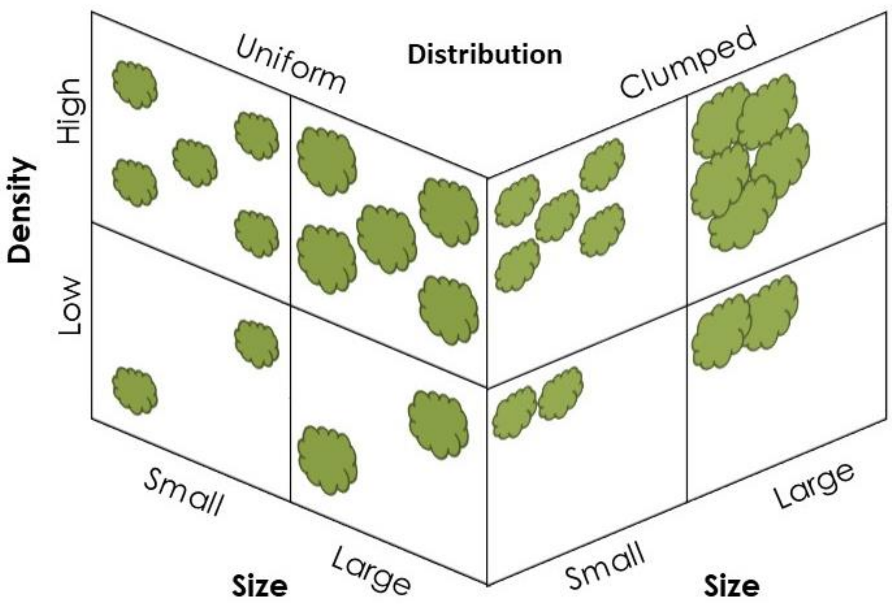

Figure 2. Visualization of distribution, density, and size as different facets of resource abundance; predictability is omitted. Adapted from [100].

example, by season, time of day[6], and out-group target (e.g., male vs female) – such that the net benefits to remaining in encounter diminish over time. Further, as aforementioned, competing interests may place constraints on individual behavior such that remaining in association is not possible (Box 1).

In the present paper, we will focus when possible on data on visual encounters between groups, turning to vocal encounter and home range overlap data as needed. This is because vocal encounter data provide less of a clear picture of the variable strategies group members may use in encounters: for example, high-ranking individuals may use long-calls to keep groups apart (2nd row, 1st column of Fig 1), not providing researchers the opportunity to examine how other group members behave towards out-group targets. We will likewise use data on home range overlap only as a complement to other sources of data. While home range overlap provides insight into factors affecting contest, overlap reflects only the *opportunity* for encounter (e.g., [1]), not incentives for encounter.

2. DISINCENTIVES FOR CONTEST COMPETITION

To make predictions about when an individual will exhibit tolerance toward an out-group target, we need to first identify the conditions under which incentives for contest are low (2nd column of Figure 1), conditions under which individuals are expected to either engage in aggression or active avoidance towards out-group individuals, all else equal. (For an in-depth review of these incentives, see [7].)

2.1 Food resources

As is true for all living things, the behavioral strategies used by members of the Primate order reflect local resource availability. Different primate species have different nutritional requirements and have preferred foods that provide these needed nutrients, which they may defend against conspecifics. The characteristics that affect the possibility of resource defense are the distribution, density, size, and predictability of resource patches (see Figure 2 for a visualization), which are often folded into a single metric of resource availability or quantity for ease of quantification (e.g., [8]). Clumped food resources, whether clumped in space or clumped in time, can encourage contest competition by incentivizing defense of food patches (i.e., territoriality[8]), especially if members of the local population are living at numbers close to the local carrying capacity[9]. When food resources are small, low density, and clumped (2nd row, 3rd cell from left in Fig 2), a single individual may defend them; when resources are sufficiently large and low density (2nd row, 4th cell), alliances of individuals that are constituent of groups may defend these resources against members of other groups[10]. However, the payoffs to intergroup contest can be limited, and incentives for intergroup contest low in turn, if clumped resources are too large and high density to defend (1st row, 4th cell in Fig 2) or an alternative resource is available[9] (e.g., patas monkeys[11]). In these cases, intergroup encounters are usually “random” encounters that result from attraction to these large resource patches[12].

2.2 Female access and defense

As female reproduction is calorically costly, females distribute themselves according to resource availability; the distribution of females influences male behavioral strategies in turn, including in the context of intergroup encounters[9,10]. Alliances of males may engage in contest to gain access to the food resources on which females depend and defend these resources against intrusion from out-group males (resource defense polygyny); however, as is true of food resources, if large numbers of females are clumped at high densities (1st row, 4th cell in Fig 2), the cost of resource defense polygyny may be too high even for alliances of males, disfavoring intergroup contest[10,13]. Further, if females rely on small, uniformly distributed, and low density resources (2nd row, 1st cell), they may be too dispersed for resource defense polygyny to provide net fitness benefits for males[13]. In this case, solitary males (e.g., geladas[14]) or kin-based alliances of males (e.g., pitheciines[15]) may herd females, forcing them to maintain distance from other groups (female defense polygyny; e.g., Japanese macaques[16]).

Out-group males may attempt to gain reproductive access to females by committing infanticide, thereby increasing incentives for resident males to engage in contest in order to protect their existing offspring. Occasionally out-group males may attempt infanticide without displacing resident males (e.g., Thomas langurs[17]); however, most instances of infanticide committed by out-group males occurs in the context of takeover, when out-group males displace resident males, becoming resident males themselves. To defend against infanticide and takeovers, males may remain in proximity to their male allies[15]. By coordinating male defense across reproductive units via extended encounter, males can improve their resource holding potential[B] against third parties (e.g., snub-nosed monkeys[12]) – in other words, there may be incentives for a male to remain in encounter with some out-group individuals to improve his chances of successful contest against *other* out-group individuals.

[B] For a review of the resource holding potential literature as it pertains to non-human primates, see [98]; for further discussion of how group size can generate individual benefits more broadly, see [36].

Females exhibit counterstrategies to both male defense and infanticide that reduce the net benefits of contest competition among males. Females may aggregate not only in space, but also in time by synchronizing their mating activity or their ovulation, reducing the relative availability of sexually-receptive females to males and thus increasing the cost of defense by males (see [18] for a review). They may also limit their availability by engaging in mate choice[18]. To reduce their susceptibility to infanticide by out-group males, females with infants may remain in proximity to resident males (e.g., yellow baboons[19]) or even mate with out-group males to confuse paternity (e.g., snub-nosed monkeys[12]).

3. INCENTIVES FOR ENCOUNTER

All else equal, when competition for resource access and female access are not worth the cost, we should expect individuals to either have low incentive to engage in intergroup contest or encounter, such that encounter rates are consistent with a random, null model[20] (2nd column, 2nd row of Fig 1), or to have incentive to engage in intergroup encounters at higher-than-random rates and exhibit tolerance in these encounters (2nd column, 1st row). If these random encounters generate individual net benefits, they can be positively favored by selection to increase in duration and to recur such that individuals are in visual contact with certain classes of out-group members more often than expected by chance (see also [21]). We identify several of these candidate individual-level benefits here.

3.1 Food resources

The benefits of associating at the location of a food resource include enhanced resource defense, improved foraging efficiency, and opportunities for social learning. Just as food resource defense is one explanation for group living in primates (Box 2), the possibilities of improved resource defense also apply to extended intergroup encounters: larger aggregations of individuals have more resource holding potential, such that there may be net benefits to the constituent members of these groups of remaining in the encounter. Even if two or more groups are feeding together at a resource patch by chance, the number of individuals present can deter other conspecific groups that could displace them (e.g., proboscis monkeys[12]). Once groups engage in passive resource defense by remaining in association, selection can favor cooperative, active resource defense, in which some individuals in both groups engage in contest against members of a third group that threaten to displace them[2C] – yet again, intergroup tolerance with some out-group targets can improve successful contest against other out-group targets.

While not being the focus of this review, interspecific extended encounters (i.e., polyspecific associations) may provide insight into the ecological and social factors that can increase incentives for encounters among conspecficics. For example, the foraging activities of some individuals in an encounter may improve the foraging returns of other individuals in the encounter as a byproduct (e.g., frugivores displace insects that insectivores eat[22]). Further, by remaining in visual contact, individuals can observe the location of food utilized by out-group members (e.g., red monkeys observing blue monkeys[23]) or can observe the objects or behaviors by which out-group members extract food[22]. We will re-visit the potential benefits of cooperative food acquisition and social transmission in our discussion of human behavior.

3.2 Avoiding predation

Extended encounters can protect against predation through several candidate mechanisms including by enhancing vigilance and diluting the risk of predation among individuals (for a review, see [22]); this is both a leading explanation for group living in primates as well as an incentive for intergroup encounter. By remaining in extended encounters, individuals engage in passive predation defense and may eavesdrop on the alarm calls of conspecifics, or even members of other species who are in association (e.g., Diana

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[C] Achieving active coordination across group boundaries requires further convergence of interests relative to passive association (e.g., coordinated mobbing of a predator, vs. remaining in association to discourage predation). With the exception of humans, few primates achieve successful intergroup collective action (e.g., [21]).

monkeys and species that associate with them[24]). Selection may also favor repurposing these extended encounters to meet additional fitness-relevant goals (e.g., aggregation to protect against predation may be repurposed for female defense in Hamadryas baboons[6]).

3.3 Transfer and copulation

Individuals may have incentives to engage in intergroup encounters to gain information about groups to which they might transfer, or to gain access to reproductive opportunities. Individuals on the brink of transfer are especially likely to behave tolerantly toward some members of candidate host groups[3]; individuals may even engage in a series of visits before emigrating to another group (e.g., ring-tailed lemurs[25]). These individuals are most commonly adolescents, but adult members of the dispersing sex may disperse again to avoid infanticide (e.g., Thomas langurs[17]) or seek reproductive opportunities[25]. Relatedly, individuals may seek matings with target out-group individuals by exhibiting tolerance toward them (e.g., capped langurs[26]). If females pursue this strategy, resident males may herd or otherwise defend resident females to preclude copulation (e.g., Japanese macaques[16]).

4. INTERGROUP AGGRESSION AND TOLERANCE IN NON-HUMAN GREAT APES

To what extent do the candidate selection pressures explaining incentives for contest and encounter in non-great ape primates apply to intergroup encounters in the great apes? Do we need additional explanatory frameworks to account for the prevalence and plasticity of tolerance in intergroup encounters in these species? In the section that follows, we focus on gorillas, chimpanzees, and bonobos, as defining social groups (and thus intergroup encounters) in orangutans is difficult (e.g., [27]). We start by briefly introducing each species and the spectrum of behavior observed during intergroup encounters, then focus on the relevance of the non-great ape primate models for explaining the variation observed.

4.1 BEHAVIORAL VARIATION IN NON-HUMAN GREAT APES

4.1.1. Gorillas

There are two recognized gorilla species, western gorillas (*Gorilla gorilla*) and eastern gorillas (*Gorilla beringei*). Reproductive groups in gorillas consist of one-male multi-female or multi-male multi-female groups, the latter being common only in eastern gorillas[28]. Generally, both sexes can emigrate from their natal group[29].

In both species of gorillas the home range overlap between neighboring groups varies extensively – the exclusive home range for a given group varies from 0% to 87% of their range – and the home range overlap between two neighboring groups seems to predict their encounter frequencies at feeding patches[30,31]. Western gorillas are more frugivorous than eastern gorillas, and fruit distribution is generally patchy; this may be why western gorillas have intergroup encounters at four times the rate of intergroup encounters in eastern gorillas, which rely more on evenly-distributed herbaceous vegetation[32]. In western gorillas relationships between groups can be affiliative, including peaceful intermingling and co-nesting[31]. In contrast, eastern gorilla males are usually aggressive in intergroup encounters[5]. This aggressive behavior includes infanticide[33] but also can have lethal consequences for participating adult males[34]. Nevertheless, in more than half of vocal encounters between eastern gorillas, tolerant behavior can be observed among some individuals of the interacting groups[5].

4.1.2. Chimpanzees

Chimpanzees live in multi-male multi-female communities whose members form temporal associations that vary in size and composition called parties (see Box 2). Males are philopatric and females generally transfer[35].

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Unlike gorillas, male chimpanzees cooperatively defend a territory against neighboring groups to increase the long-term reproductive success for all males in the group[36,37]. Consequently, dyadic home range overlap is rather small; for example, the chimpanzee communities of the Taï forest use an exclusive home range of 87%-93% and areas of range overlap are used infrequently[38]. In general, most of the encounters between neighboring communities are only auditory; when visual encounters occur, 40% involve at least some aggressive physical contact[39,40]. While physical encounters between males of different chimpanzee communities are always hostile and can be lethal for participating individuals[41], female behavior seems to be more variable[39].

4.1.3. Bonobos

Like chimpanzees, bonobos live in multi-male multi-female communities with fission-fusion dynamics and male philopatry. However, territory overlap is more variable – exclusive home range represents 50%-91% of bonobo home ranges[42] – and in stark contrast to chimpanzees, encounters with out-group members have been described at the center of bonobo home ranges[43]. While a third of visual intergroup encounters involve at least some physical aggression, similar rates to those seen in chimpanzees, the severity of this aggression seems lower and no lethal outcomes are known so far[41,44]. Furthermore, the phenotype of bonobo intergroup encounters seems more variable than that of chimpanzees: half of the visual encounters in the wild involve at least some tolerant interactions among adult members of different groups[44,45]. Unlike in chimpanzees, but similar to western gorillas, bonobo intergroup encounters can last for several days and can include nesting together ([46]; MS's own observation) and sharing food (Leveda Cheng and Liza Moscovice, personal communication).

4.2. DISINCENTIVES FOR CONTEST

4.2.1 Food resources

Low feeding competition in gorillas appears to facilitate home range overlap between different groups and tolerant encounters at feeding sites[5,47]. Greater reliance on clumped food resources such as fruits and mineral-rich forest clearings in western as compared to eastern gorillas seems to increase the rate of encounter[48]; dependence on these mineral-rich areas, which are not defensible due to their size, may disincentivize intergroup contest.

In chimpanzees, intergroup encounters are most likely to occur when individuals are eating clumped ripe fruits in the periphery of their home range[40]. However, direct resource competition does not explain the variation in the overall occurrence of male aggression during the encounters at such feeding sites[40]; instead, female aggressive behavior during encounters might reflect incentives for contest over resources (e.g., [49]). Consistent with this, a decrease in feeding competition is hypothesized to reduce the benefits of contest competition between chimpanzee groups, which may explain the variation in the occurrence of lethal aggression across different chimpanzee populations[39].

Relative to chimpanzees, bonobos may have reduced feeding competition between neighboring groups: their diet consists of a larger proportion of terrestrial herbaceous vegetation and large fruiting trees[50], resources less amenable to cooperative territorial defense[D]. High skew in paternity in bonobos, resulting in an uneven division of benefits of territorial defense, might additionally prevent this form of collective action[51].

4.2.2 Female defense

In gorillas, most of the aggression occurring between groups can be linked to male mating competition[5]. In western gorillas, for example, the more potential female migrants there are in a group, the less likely resident silverbacks are to engage in tolerance in intergroup encounters, presumably because they are engaging in female defense[47].

[D] Note that the characteristics of the bonobo diet are assumed, but usually not tested (for an exception, see [99]).

While male chimpanzees defend a territory (resource defense polygyny), they also seem to defend females against out-group males (female defense polygyny) – this is reflected in the fact that parties are less likely to travel to the periphery when accompanied by fecund females, suggesting a trade-off for males between female and territory defense[40]. That said, the variation in the severity of male aggressive behavior observed during a given encounter is not explained by the benefits of defending the associated females[40].

Relative to chimpanzees, bonobo males likely have reduced incentives to defend females, as female bonobos have more concealed ovulation than female chimpanzees, increasing the costs of defense[45].

4.2.3 Individual-level constraints and competing incentives

Further factors that have been linked to a reduction of the incentives to compete aggressively with males of neighboring communities include (1) close kinship between neighboring males in gorillas[52]; (2) a reduction in the imbalance in the number of individuals in encountering parties in chimpanzees (and potentially bonobos[37]), as the number of males present at the time of encounter influences a given chimpanzees party's tendency to move towards the out-group rather than retreat[40]; and (3) constraints imposed on males by female strategies, particularly relevant in bonobos where females have a higher social dominance rank than in gorillas or chimpanzees[53]. (For examples of these constraints in action in non-ape primates, see Box 1.)

4.3 INCENTIVES FOR ENCOUNTER

It seems unlikely that associations between groups observed in the great apes are a response to contemporary threats of predation: for example, prolonged association between groups have been described in bonobos at a site where natural predators seem absent[54]. We know of no data that indicate whether long-term associations in gorillas are associated with predation risk. That said, risk of predation may still be an incentive for group living in these species (see Box 2).

4.3.1 Food resources, transfer and copulations

To our knowledge, there are no studies investigating the potential benefits of extended intergroup encounters for foraging; however, female gorillas, chimpanzees, and bonobos use intergroup encounters to engage in reconnaissance in preparation for transfer, and to obtain access to out-group mating opportunities[39,46,47,55]. Furthermore, bonobo females are more likely than males to interact with same-sex members from other communities in the form of grooming or socio-sexual behavior[46]. It is unclear whether these interactions reflect the building of new relationships or existing kin relationships between females, as we do not yet have the genetic data to evaluate these possibilities[45].

4.4 SUMMARY: TOLERANCE IN INTERGROUP ENCOUNTERS IN THE NON-HUMAN GREAT APES

Data collected to date suggest that gorilla, chimpanzee, and bonobo intergroup behavior falls within the patterns observed with the other non-human primates. That said, while much research effort has been expended on analyzing the ecological and social factors promoting intergroup aggression among male chimpanzees, we know very little about whether the selection pressures that incentivize intergroup encounters in the non-ape primates apply with equal force to the great apes; our ability to evaluate this is especially hindered by a dearth of data on intergroup encounters in gorillas and bonobos, species in which extended intergroup encounters appear to be common.

5. INTERGROUP AGGRESSION AND TOLERANCE IN HUMANS

The study of incentives for intergroup contest in humans has taken the forefront in evolutionary anthropology (with only occasional attention to the disincentives for contest[56]), perhaps at the expense

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of research on incentives for encounter. This is despite the fact that humans have networks of social partners on scales unseen in non-human primates[57–59] that often span group boundaries[2,60,61], and the fact that humans use variable strategies in intergroup encounters across time, across contexts, and as a function of the out-group target him- or herself (see [62,63] for reviews). (For a discussion of the different kinds of relevant group boundaries in humans, see Box 2.)

Here, we will explore whether the disincentives for contest and incentives for encounter identified in the non-great ape primate literature explain human intergroup strategies (see Table 1 for an overview). We will use the term "extra-community" in lieu of "out-group" in this section to make clear that we refer to individuals who are not members of the smallest, local residential group (e.g., bands in hunter-gatherer societies, neighborhoods in post-industrial societies).

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Table 1.

Disincentives for contest

	Consistent with non-human primate explanatory models	Additional theory required to explain patterns
Food resources	• Food abundance • Alternative foods	
Female defense	• Frequency of mate guarding sensitive to sex ratio • Partner choice and alliance formation as female counterstrategies	• Institutions can lower or raise the costs of defense

Incentives for encounter

	Consistent with non-human primate explanatory models	Additional theory required to explain patterns
Food resources	• Joint defense • Information transmission • Repurposed relationships	• Transfers of resources across boundaries enables human niche
Transfer/copulation	• Systems of transfer vary, e.g., by sex and age of transfer • Both men and women mate with other groups	• Intricate systems of exogamy • Norm systems make boundaries porous

5.1 DISINCENTIVES FOR CONTEST

5.1.1 Food resources

5.1.1.1 Utility of non-human primate explanatory models

Incentives for contest over food resources in humans are very similar to those seen in non-human primates. Like non-human primates, humans can better defend dense, predictable food resources than they can more dispersed food resources[64]; however, the availability of alternative foods reduces incentives for contest over food access, while approaching the carrying capacity increases these incentives[65]. Further, the human diet may include foods that are both defensible and foods that are not, such that humans may exhibit aggression in situations of extra-community encounter where one resource is contested but not another (e.g., while pre-contact Northwest Coast peoples sometimes defended salmon runs, they relied on extensive trade networks to obtain non-locally available resources (for a review, see [66])).

5.1.2 Female defense

5.1.2.1 Utility of non-human primate explanatory models

Like non-human primates, incentives for men to compete for access to women and, once access is attained, to guard women against extra-community men are magnified when there are few sexually-receptive women relative to sexually-receptive men[67]. Like non-human primate females, women utilize counterstrategies to undercut defense by men. For example, women can limit their availability through partner choice and alliance formation, reducing the payoffs to female defense[68].

5.1.2.2 Limitations of non-human primate explanatory models

Human institutions (see Box 1 for a definition of institutions) modify the affordances of female defense for men. In societies in which the movement of women is not restricted by social institutions, the costs of female defense may be too high[69], whereas the institutional restriction of women's movement lowers the costs of defending women against out-group males[70].

5.2 INCENTIVES FOR ENCOUNTER

5.2.1 Food resources

5.2.1.1 Utility of non-human primate explanatory models

Like non-human primates, even if humans are involved in food resource defense, individuals may be tolerant towards certain target extra-community members (e.g., the Turkana[71]). Encounters at large patches of seasonally-predictable, dense food resources can form the basis of extended encounters (e.g., tribes living near Fort Irwin[72]), and extra-community relationships forged in the domain of food production are often re-purposed for different goals[73]. Extra-community relationships in humans may also provide a conduit for social information relevant to the local ecology (e.g., hunter-gatherers adopting selectively adopting technology from pastoralist or agriculturalist neighbors[74]).

5.2.1.2 Limitations of non-human primate explanatory models

Relative to other great apes, humans have higher energy expenditure due to our large brains, making us prone to starvation[75]; we are also dependent on an array of micro- and macronutrients[76] and high quality foods to fuel our brains[77], resources for which rates of successful acquisition vary at different scales, from local (e.g., within an individual's day range) to non-local (e.g., between communities[78]). Accordingly, to ensure consistent access to these resources, humans are reliant on social connections that can buffer local shortfalls[64,78–80] and provide non-local food resource access[58,60,61] to a degree not observed in other primate species. Even if foods are available locally, but at lower densities than in another locale, humans can improve efficiency in resource acquisition by specializing and exchanging resources across community boundaries (e.g., Swat Valley[81]). To enhance the reliability of extra-community relationships, humans may use cultural institutions such as exogamous marriage (i.e., marrying outside the community[57,82]), trade partnerships[81,74], and fictive kinship, friendship, or ritualized relationships to solidify them[80,83]. Indeed, exchange of resources produced via specialization may be used to facilitate the maintenance of these extra-community relationships, which can be called upon in times of shortfall that threaten survival (e.g., the Yanomamö[84]).

5.2.2 Transfer and copulation

5.2.2.1 Utility of non-human primate explanatory models

Like non-human primates, humans have a diversity of systems of intercommunity transfer in which men, women, or members of both sexes may transfer[85]. Men and women may visit candidate new communities before emigration from their current location (e.g., the San[86]), and may not only immigrate to new communities at the age of maturity, but throughout adulthood. Also like non-human primates, humans stand to gain reproductive benefits by mating with extra-community individuals. In populations where men have higher variance in reproductive success than women, men may attain more mates by visiting distant locations (cf. the monogamous Maya[87]). Further, women may "gene shop" by engaging in extra-pair matings with individuals from different communities (see [69] for a review).

5.2.2.2 Limitations of non-human primate explanatory models

Humans rely extensively on institutions to facilitate extra-community transfer. We have intricate systems of exogamous marriage that vary by population, and exogamy may have been the "glue" that initially held human multilevel societies together ([57,84]; see Box 2 and also [36]). In some cultures, norms of hospitality increase the porousness of community boundaries, facilitating visitation and potential immigration (see [88]). Indeed, although humans organize into ethnic groups, identity groups whose members trace their descent to a common ancestor and use markers to indicate their membership[81], these barriers are likewise porous: migrants often integrate by adopting the norm system of the target population (see [89] for a review). If an individual does transfer, social partners in the destination community may serve as sponsors, helping the immigrating individual integrate[83].

5.3 SUMMARY: TOLERANCE IN INTERGROUP ENCOUNTERS IN HUMANS

Tolerance toward extra-community members is prevalent in humans, but plastic: the extent to which individuals exhibit tolerance in intergroup encounters is upregulated and downregulated by an individual's own strategies (e.g., to attain access to mates or food resources) as well as the strategies of the target extra-community individual (e.g., to compete for mates or food resources). However, existing approaches addressing non-human primate behavior are better able to account for human incentives for intergroup contest than human incentives for intergroup encounter (Table 1). We suggest that the human foraging ecology likely increased the incentives for extended encounter with extra-community individuals, as they could act as sources of non-local resource access and buffer of local shortfalls[60,61]. To maintain resource access via extra-community social partners and re-purpose these connections to additional ends – acquiring non-local cultural knowledge, for example, or engaging in large-scale collective action – humans have utilized cultural institutions such as exogamous marriage rules, ritualized partnerships, and norms of hospitality to promote continuity of these relationships across time.

Characterizing the prevalence and plasticity of tolerance in human intergroup encounters has been hindered by the distribution of relevant data across the social sciences, as well as reduced attention to intergroup tolerance in evolutionary anthropological fieldwork. Field and experimental data from economics, political science, social psychology, and sociology under names such as "bridging social capital" and "intergroup contact" speak to the plasticity of tolerance in intergroup encounters, as does theoretical work from these disciplines (notable examples include [90,91]); however, this evidence is rarely marshalled to inform fieldwork by evolutionary anthropologists. Much field-based research on humans implicitly focuses on individuals' networks of kin and non-kin within their current community, often because of the time constraints on field researchers. We suggest that characterizing the relevance of social partners from other communities or other ethnic groups requires asking more questions about these individuals in ethnographic research and using the responses given to guide survey design regarding individuals' social networks.

6. DISCUSSION

Although currently popular depictions of the Primate order, and of humans within it, characterize primates as exhibiting aggression in intergroup encounters, evidence suggests that individual behavior in intergroup contexts is actually quite plastic. Here, we have examined the extent to which candidate selection pressures favoring tolerance in intergroup encounters in non-great ape primates – that is, the ecological and social factors creating disincentives for intergroup contest and incentives for intergroup encounter (Fig 1) – can account for the prevalence and plasticity in tolerant behavior in intergroup encounters in the non-human great apes and in humans. We noted that incentives for contest and incentives for encounter themselves are interrelated: individuals may exhibit tolerance towards one out-group target but aggression towards another (e.g., out-group male allies vs out-group males who pose a threat of takeover[6,12]). For brevity, we focused on inter-individual and intra-individual variation in tolerant behavior (that is, plasticity in an individual's exhibited tolerance across seasons, developmental stage, the sex of the out-group target, etc.) independently of his or her rank, group size and structure, local kin network, past experience, and other constraints.

We find that existing non-ape primate frameworks better explain the patterns of tolerance observed in non-human great ape intergroup encounters than in human intergroup encounters – that is, given the existing, sparse data for gorillas and bonobos. We propose that the increased prevalence of tolerance in intergroup encounters in humans is a product of the human foraging ecology[60,61]; the importance of buffering local risk and maintaining access to non-local resources increased the incentives for extended intergroup encounters in humans, connections that were then solidified and repurposed by human cultural institutions (Table 1).

Perhaps because of the emphasis on the evolution of contest and warfare in evolutionary anthropology, researchers may be overlooking an important feature of human and non-human great ape

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sociality. Here we have identified types of field data that will allow researchers to better characterize the prevalence and plasticity of tolerant behavior in non-human great ape and human intergroup encounters. In the great apes, this includes an increased focus on intergroup encounters in gorillas and bonobos, especially visual encounters when possible. In the case of humans, we need to attend to the relevant work produced by other social science disciplines, as well as collect more field data on individual's social network connections that span community or ethnic boundaries.

In order to evaluate the extent to which existing ecological and social approaches in the non-ape primate literature can explain variation in tolerant behavior in the non-human great apes and humans, we left aside the roles of constraints (see Box 1 for a list of candidate constraints), phylogeny, and proximate mechanisms in individual behavior. While we have chosen not to focus on the role of phylogenetic signal in explaining the patterns of tolerant intergroup behavior, the social factors identified here may be a product of phylogeny. Future work may further unpack the extent to which phylogeny accounts for patterns of intergroup tolerance in the Primate order. Likewise, we have omitted discussion of the proximate mechanisms that underlie the expression of tolerance towards out-group members, including hormonal responses and psychological mechanisms. For more information on these topics, we point readers to research produced in the disciplines of primatology, behavioral psychology, evolutionary psychology, and medicine, among others.

We have also chosen not to pursue a comparative approach with non-primate species. While the intergroup behavior exhibited by non-human primates provides a useful initial framework for thinking about the origins and plasticity of intergroup tolerance in humans, this comparative approach has limitations, particularly with regard to explaining incentives for encounter. In some domains, human behavior may have better analogies among non-primate vertebrates or even insects[2]. That said, our goal in the present paper was to explore tolerance in humans in the context of the Primate order, rather than find the closest-match analogy for human behavior.

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BOX 1. CONSTRAINTS ON INDIVIDUAL BEHAVIOR AND COMPETING INCENTIVES

Sex and developmental stage are not the only individual characteristics that alter the relevant payoffs for tolerance in intergroup encounters. Other variables include a focal individual's rank, his or her kin relationships, the size and structure of her group, her past experience, and her competing incentives.

Rank. Individuals who are of lower dominance rank may be unable to exhibit tolerance toward out-group members because they are constrained by the behavior of dominants. Further, lower ranked individuals may be less likely to engage in aggressive intergroup encounters because they stand to gain fewer reproductive benefits from these interactions (e.g., by defending in-group females[7]).

Kin network characteristics. Inclusive fitness can also modulate the costs of aggression and the benefits of encounter. For example, close relatives are more likely to mount successful collective action in aggression (e.g., geladas[14]). On the other hand, an individual in Group A with a close relative in Group B may have reduced incentives to engage in contest with individuals Group B, if she would suffer indirect fitness costs from competing with the group members of her close relative; alternatively, she may have increased incentives for encounter with individuals in Group B if she can gain indirect fitness benefits from remaining in association with her close relative[52,82]. Further, inclusive fitness may favor a parent's tolerance of his or her offspring's interactions with out-group members before transfer (e.g., Thomas langurs[17]).

Group size. The number of individuals in each of two groups may modify the incentive structures for individual members of those groups: while in chimpanzees the group with the numerical majority is more likely to instigate confrontations and to “win” them by displacing the out-group or inflicting serious, sometimes lethal, harm on them[37,40], larger groups may be more prone to collective action problems in other species, lowering their ability to successfully defend resources[36].

Group structure. In theory, emergent properties of dyadic and triadic interactions and relationships can produce persistent group structure in non-human primates that constrain behavior[92], including behavior towards out-group members. That said, institutions are a component of group structure and are stable patterns of behavior coordinated and enforced by group members with the help of language; institutions thus appear to be a particularly human phenomenon[92].

Past experience. Some non-human primates can differentiate between familiar and strange out-group members, a necessary precondition for recalling interactions with these individuals; past encounters that were free of aggression can pave the way for tolerant future encounters (e.g., capped langurs[26]).

Competing incentives. In addition to rank, other constraints that may preclude intergroup encounter, even if an individual has an incentive to encounter an out-group target, include existing investment in reproductive ventures. For example, mate guarding can reduce the possibility of tolerant intergroup encounters for females, who may be prevented from approaching out-group members[7].

BOX 2. GROUPS

Groups are individuals “which remain together in or separate from a larger unit” and interact with each other more than with other individuals in the vicinity[93], p. 40). For example, reproductive units – where all individuals of one sex in the unit regularly interbreed with those of the opposite sex[21] – are the smallest type of group; two individuals drawn randomly from a reproductive unit will interact at higher rates with one another than will two individuals drawn from two different reproductive units. For reviews of the leading hypotheses as to why primates live in groups, see [93–95].

Reproductive units[21], not foraging parties, are the smallest type of group. Foraging parties are the product of fission-fusion dynamics, and the lines along which groups fission can vary from day to day. Parties in societies with fission-fusion dynamics are not groups: individuals in a party are no more likely to interact with each other than they are members of other parties[93] (see [21] for an in-depth treatment of this concept). In contrast, individuals drawn at random from the same reproductive unit will interact at higher rates than will individuals drawn at random from two reproductive units.

For two reproductive units to form a band, at least some tolerance is required between the constituent members of the two units[58,82]. The term “multilevel societies” refers to these nested group structures in which reproductive units are nested within bands, bands within clans, etc.[21] The nature of multilevel societies illustrates the limitation of using the term “intergroup encounter” to describe a meeting between two units of individuals. For example, when members of two different bands encounter one another, and both are members of the same clan, is that an intergroup encounter? (For an attempt to characterize this, see [96].) In cases such as these, we suggest taking the question back a step further: what are the social and ecological factors that may favor interband tolerance in this society? We address questions such as these in the main text.

Humans especially complicate the use of the word “group.” Humans can belong to a number of different groups simultaneously, and identify with these groups to varying degrees across time (see [97] for a review). The basis of human groups can be actual or presumed common ancestry (patrilines and matrilines, ethnic groups); common residence (residential groups, nations); common belief, values, or goals (religion, political parties, work cooperatives, sports teams); or common identity on a domain of salience (gender, sexual identity), among other bases. The constituent members of groups in which an individual is a member overlap to varying degrees; when groups are nested one within another, activing individuals' superordinate identities – that is, reminding them that their group is a constituent part of a larger group[90] – can promote large-scale collection action, such as efficient market economies[91].

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