

1 **The evolution of intergroup tolerance in non-human primates and humans**

2 **[SHORT: Tolerance in intergroup encounters]**

3 Anne C. Pisor^{a,b*} & Martin Surbeck^c

4 ^a Department of Anthropology

5 Washington State University

6 Pullman, WA 99164-4910, USA

7 ^b Department of Human Behavior, Ecology, and Culture

8 ^c Department of Primatology

9 Max Planck Institute for Evolutionary Anthropology

10

11 *Corresponding author: anne.pisor@wsu.edu

12 **Anne Pisor** is an assistant professor in the Department of Anthropology at Washington State
13 University. She studies the origins, maintenance, and flexibility of between-community
14 relationships in humans, including flexibility in these relationships in response to changing
15 resource currencies among three populations of Bolivian horticulturalists.

16 **Martin Surbeck** is a group leader in the Department of Primatology at the Max Planck Institute
17 for Evolutionary Anthropology and director of the Kokolopori Bonobo Research Project. His
18 research examines the link between the ecology, social structure, reproductive strategies and
19 cooperation in the species of the genus *Pan*.

20

21 **ABSTRACT**

22 Primate individuals use a variety of strategies in intergroup encounters, from aggression to
23 tolerance; however, recent focus on the evolution of either warfare *or* peace has come at the
24 cost of characterizing this variability. We identify evolutionary advantages that may incentivize
25 tolerance toward extra-group individuals in humans and non-human primates, including
26 enhanced benefits in the domains of transfer, mating, and food acquisition. We highlight the role
27 these factors play in the flexibility of gorilla, chimpanzee, bonobo, and human behavior. Given
28 humans have an especially broad range of intergroup behavior, we explore how the human
29 foraging ecology, especially large geographic and temporal fluctuations in resource availability,
30 may have selected for a greater reliance on tolerant between-community relationships –
31 relationships reinforced by status acquisition and cultural institutions. We conclude by urging
32 careful, theoretically-motivated study of behavioral flexibility in intergroup encounters in
33 humans and the non-human great apes.

- 34 **Keywords:** intergroup encounter, tolerance, sociality, human evolution, hominoids, primate
- 35 behavior, cooperation

36 **1. INTRODUCTION**

37 Attempting to explain the prevalence of intergroup aggression in primates, especially in humans
38 (*Homo sapiens sapiens*), evolutionary anthropologists have focused extensively on intergroup
39 contest and warfare. In response, other evolutionary anthropologists have focused extensively
40 on peace systems in primates, especially in humans. Focusing on these two ends of the spectrum
41 – war or peacefulness – has come at the cost of fully characterizing within-species variation in
42 individuals' behavioral strategies in intergroup encounters (e.g., ¹⁻⁴; see also ⁵, Table 22-1).
43 Further, both of these approaches emphasize selection pressures that favor or disfavor
44 intergroup aggression; less researched are the selection pressures that, given disincentives for
45 intergroup aggression, favor *tolerant encounters* and the prolongment of tolerant encounters in
46 intergroup association.

47 In the present review, our goal is to call for explicit theorization about the individual-level
48 selection pressures that favored flexible behavior in intergroup encounters in humans and non-
49 human primates, especially the often-overlooked pressures that may favor tolerant encounters
50 and association given disincentives for aggression. We review how tolerant behavior toward
51 extra-group conspecifics in specific domains – such as food access, mating, and reconnaissance
52 before transfer – may have been favored by natural selection in non-human primates. In the
53 course of this review, we pay special attention to the group-living, non-human great apes – but
54 not because these species are necessarily the *best* analogies for intergroup behavior in humans.
55 We focus on these species for two reasons: first, humans and the non-human extant great apes
56 share a number of traits derived within the Primate order due to our common ancestry,
57 suggesting that there is (at least some) insight to be gained by drawing comparisons between

58 these species; and second, to highlight how little we still know about intergroup encounters in
59 the non-human great apes, especially gorillas and bonobos.

60 Given what has been observed of intergroup behavior in non-human primates, we assess
61 whether consideration of the potential selective benefits favoring intergroup encounter and
62 association in these species provides insight into human behavior. Our review of the literature
63 suggests that the particularly high prevalence of intergroup tolerant encounter and association
64 in humans may be derived, even within the great apes; we hypothesize that this high prevalence
65 reflects human reliance on resources that vary extensively in their availability across space and
66 time. Given that our field has invested much energy into studying the selection pressures favoring
67 or disfavoring intergroup aggression, we conclude by urging evolutionary anthropologists to
68 explicitly theorize about individual-level selection pressures that may favor intergroup tolerant
69 encounters, and even prolonged intergroup association, so that we can better understand the
70 variation in intergroup behavior within- and between-species.

71

72 **1.1 Defining our terms and assumptions**

73 To discuss tolerance in the context of intergroup encounters, we first define groups, encounters,
74 and tolerance (for brief definitions of the terms used in this paper, see Glossary). As commonly
75 defined in the primate behavior literature, groups are individuals “which remain [physically]
76 together in or separate from a larger unit” and interact with each other more than with other
77 individuals in the vicinity⁶ (p. 40). Because same-group conspecifics are competitors that can
78 negatively affect an individual’s reproductive fitness, the selection pressures that may have
79 favored group living across the Primate order are a subject of ongoing debate (for reviews of the

80 leading hypotheses, see ^{6,7}). For group living to persist, the fitness costs related to group living
81 must be outweighed by fitness benefits, e.g., predation avoidance. Indirect fitness benefits
82 generated by associating with same-sex kin may further amplify these benefits. In short, despite
83 conflicts of interest between an individual and a conspecific, an individual may remain in
84 association with this conspecific if there are net fitness benefits to doing so.

85 One of the benefits of living in a group, which can also be a benefit of association between
86 groups, is resource defense against conspecifics. If a resource is economically defensible – that
87 is, if an individual stands to gain net fitness benefits from defending it – an individual may
88 coordinate with others in their group to exclude third parties from the area of their range where
89 the resource is located⁸. Whether a resource can be economically defended by an individual or
90 individuals is a product of its characteristics, such as its distribution, density, size, and
91 predictability⁹; the individual's demand for the resource (e.g., her frequency of use¹⁰), as well as
92 the demand of third parties (e.g., as a consequence of population density¹¹); and the individual's
93 caloric or nutritional requirements. The degree of home range overlap between two neighboring
94 groups, especially the frequency with which areas of range overlap are used, can indicate that
95 relevant resources are less economically defensible and thus that there are diminished incentives
96 for intergroup aggression – at least at the edges of a group's home range. As such, range overlap,
97 or the frequency with which areas of overlap are used, is sometimes employed as a first-pass
98 approximation of opportunities for intergroup encounter¹⁰. However, while opportunity for
99 encounter is pre-requisite for encounters, it does not provide insight into *incentives* for
100 encounter; we focus on the latter here.

101 When conspecifics from two different groups are in visual or vocal contact with one
102 another, they are involved in what we term an intergroup encounter (although there are notable
103 limitations to relying on vocal encounter data; see the Glossary for further discussion). If
104 conspecifics remain in visual or vocal contact without aggressing against one another, they are
105 exhibiting tolerance (cf. ²). We evaluate selection pressures that may favor intergroup tolerant
106 encounters, or even prolonged intergroup association, over the course of this review.

107 To generate hypotheses about the relevant benefits and costs of different kinds of
108 intergroup behavior, it is useful to begin by assuming that individual behavior is flexible and
109 reflects an optimal response to socioecological conditions^{3,12}. By this logic, natural selection
110 should favor features of primate psychology that are sensitive to the net benefits of association
111 with conspecifics in the current ecological and social context³, modulating tolerant and
112 aggressive behavior accordingly. Of course, a socioecological approach cannot explain all
113 behavioral variation; factors affecting the social strategies available to an individual include
114 phylogenetic inheritance, life history trade-offs, and collective action problems^{13–15}. It does,
115 however, allow first-pass theorizing about the underlying selective forces shaping the variety of
116 intergroup behavior observed both within and between primate species.

117

118 **1.2 From disincentives for aggression to incentives for tolerance**

119 Individual behavior in intergroup encounters is flexible, following a continuum from aggressive
120 to tolerant, and this flexibility reflects the local environment (e.g., the patchiness of resources,
121 seasonality in their availability, species' diet breadth), the qualities and condition of the
122 interacting individuals (e.g., sex, resource access, rank, the reproductive status of each), and

123 features of the interacting groups (e.g., the balance of power between the two, the presence and
124 number of estrous females in one or the other). However, despite evidence of this behavioral
125 flexibility, much of the existing literature on intergroup behavior in primates emphasizes the
126 release of selection pressures favoring aggression (e.g., the Dear Enemy Effect¹⁶), which allows
127 for either “random”¹⁷ or tolerant encounters (Figure 1); for example, other reviews have
128 provided thorough treatment of the selection pressures favoring (or disfavoring) aggressive
129 intergroup behavior in non-human primates and in humans^{3,5,15,18}. Our approach differs in that
130 we focus on individual-level selection pressures that, given selection pressures disfavoring
131 intergroup aggression, favor intergroup encounter and association over random encounter.
132 When incentives for contest with extra-group conspecifics are low, optimality theory would
133 predict that (1) if there are low benefits to encounter, an individual should randomly encounter
134 extra-group conspecifics¹⁷ (d, Figure 1); (2) if there are high benefits to encounter, an individual
135 should encounter extra-group conspecifics at a rate higher than chance (b, Figure 1). If individuals
136 gain net benefits from intergroup encounters, these encounters should be positively favored by
137 selection to increase in duration and to recur – to become intergroup associations.

138 The evolution of multilevel societies likely hinged on high net benefits to intergroup
139 tolerant encounter^{19–21}; theoretical work on the evolution of multilevel societies can inform our
140 understanding of why natural selection may have favored flexible tolerance toward extra-group
141 members at the individual level. For example, Kirkpatrick & Grueter¹⁹ considered how, given
142 reduced incentives for aggression due to food abundance, defending females against extra-group
143 males may have favored extended association in golden snub-nosed monkeys (*Rhinopithecus*
144 *roxellana*). Likewise, Schreier & Swedell²⁰ discussed both incentives for extended association and

145 disincentives for aggression in Hamadryas baboons (*Papio hamadryas hamadryas*), attributing
146 the former to predation avoidance and the latter to food abundance. Below, we draw on the
147 threads of this literature to organize observations of intergroup encounters in non-human
148 primate species with respect to potential selection pressures that may incentivize these
149 encounters.

150

151 **2. INTERGROUP TOLERANT ENCOUNTERS AND ASSOCIATION IN NON-HUMAN PRIMATES**

152 Drawing on the socioecological approach, theoretical perspectives on the evolution of multilevel
153 societies, and existing hypotheses put forward by field researchers, we have compiled a list of
154 benefits to intergroup tolerant encounter in Table 1, highlighting how these benefits are typically
155 realized. Note the first three of these candidate benefits are likewise benefits that may have
156 favored group living; selection pressures favoring the association with conspecifics within groups
157 can extend to association with conspecifics *between* groups. In a non-exhaustive list in column
158 three, we identify non-human primate species in which observations of intergroup interactions
159 are consistent with a given benefit. Assuming benefits from intergroup interactions can be
160 reliably obtained, intergroup encounter and association may be favored by natural selection, e.g.,
161 as was the case in the evolution of multilevel societies.

162 Two mechanisms can further enhance the net benefits of intergroup encounter and
163 association. First, the net benefits of interacting with extra-group members may be higher if
164 these individuals are relatives, as these interactions can have positive effects on inclusive
165 fitness¹⁵. Such kinship connections across groups arise due to past fissioning and dispersal events.
166 Further, there may be inclusive fitness benefits for adults if they tolerate subadult contact

167 between groups when their adolescent offspring are nearing transfer²². Second, partner
168 preferences across groups can help to enhance the net benefits of intergroup encounters. For
169 example, individuals appear to draw on memories of past experiences with specific extra-group
170 members to anticipate their behavior²³, selectively approaching individuals likely to be tolerant
171 and avoiding those likely to be aggressive¹⁵.

172 On Table 1, the non-human great ape species are highlighted in bold font. Note that
173 existing observations of the great apes are consistent with only two of the five benefits that may
174 favor intergroup encounter and association. This is not for lack of intergroup tolerant encounters:
175 while orangutans (genus *Pongo*) do not live in groups, making the question of intergroup
176 encounters moot, intergroup encounters have been observed in chimpanzees (*Pan troglodytes*),
177 bonobos (*Pan paniscus*), and gorillas (*Gorilla gorilla* and *Gorilla beringei*). Despite the presence
178 of intergroup encounters in all four species, we know vastly more about intergroup encounters
179 in chimpanzees than bonobos or gorillas. This disparity in research effort is predominantly
180 attributable to the use of chimpanzee intergroup behavior as a referential model for human
181 intergroup behavior: given chimpanzees are closely related to humans, they are often used as an
182 analogy for the Last Common Ancestor of humans and chimpanzees, and thus humans'
183 evolutionary heritage with respect to intergroup behavior. However, anthropologists' heavy
184 reliance on chimpanzee intergroup encounters as a referential model is short-sighted, for reasons
185 we detail in Box 1. As highlighted above, much can be inferred about the potential benefits and
186 costs of intergroup tolerance in humans, and even the less-studied non-human great apes, from
187 review of the existing literature on non-ape primates. Below, we assess the extent to which the
188 selection pressures potentially favoring intergroup encounters in the non-human primates,

189 detailed in Table 1 and Box 1, can explain the flexibility and prevalence of intergroup tolerant
190 behavior in humans -- or whether additional explanations are needed.

191

192 **3. HUMANS IN PRIMATE CONTEXT: PREDICTING INTERCOMMUNITY TOLERANT ENCOUNTERS**
193 **AND ASSOCIATION**

194 Humans have social networks on scales unseen in non-human primates^{24,25}, networks that often
195 span group boundaries^{1,2,26,27} – suggesting that incentives for association with extra-group
196 members must (at least sometimes) be high. To what extent may the domains highlighted in
197 Table 1 account for the flexibility and high prevalence of intergroup tolerance observed in extant
198 humans? We first briefly examine whether these domains predict contemporary human behavior
199 – in both small-scale and post-industrial societies – as documented in the social science literature.
200 Second, we ask whether additional selection pressures may have acted in the human lineage,
201 favoring a high prevalence of intergroup tolerant encounters and association. As have a handful
202 of behavioral ecologists and archaeologists before us, we highlight the relevance of non-local
203 resource access and the risk of resource shortfall in incentivizing intergroup tolerant encounters
204 and association in humans; we build on previous theorizing on the subject by addressing *why* the
205 human foraging ecology involves more risk of resource shortfall and reliance on non-local
206 resources than other primate foraging ecologies. Finally, we examine how the accrual of status
207 through intergroup connections and cultural institutions may support and reinforce resource
208 flows through between-group relationships.

209 To avoid misunderstanding, let us first clarify the use of the words “group” and
210 “community” with respect to humans. The word “group” has many connotations in the social
211 science literature, ranging from ethnolinguistic groups to gender-based groups to groups formed
212 in experimental contexts (for a discussion, see ²⁸). Some of these groups are separated in
213 geographic space; others are not. Because we are interested interactions between conspecifics
214 across space, we frame our review of the human literature in terms of “communities,” as Rodseth
215 and colleagues²⁹ use the term (see Glossary).

216

217 **3.1 Continuity: Primate-general patterns observed in humans**

218 **3.1.1 Resource holding potential and enhanced foraging returns.** Like other primate diets,
219 human diets often include foods that are both economically defensible and foods that are not.
220 As is true of other group-living apes (e.g., western gorillas), when resources are seasonally-
221 abundant and not defensible, these resources can provide the basis for the intermingling of
222 human communities³⁰, including in market contexts³¹ and, as Brewer and Caporael joke²⁸, at
223 scientific conferences. Further, individuals may have increased incentive to associate with extra-
224 community members when they can acquire social information that is potentially useful in the
225 local environment, enhancing returns to foraging and food production; social learning has been
226 especially important in humans, both for foragers^{32,33} and in other societies³³, given the diversity
227 of environments we inhabit. However, though intergroup association for resource defense has
228 only been observed in interspecific associations in non-human primates (Table 1), human
229 individuals in small-scale and even post-industrial societies sometimes associate with extra-
230 community members to defend a food resource against third-party communities, either passively

231 or in active, collective defense (see ³⁰ for small-scale examples). In this vein, research from
232 disciplines such as political science and psychology demonstrates that perceived national-level
233 resource threat – sometimes in interaction with other variables – can be correlated with a feeling
234 of common identity with co-nationals from other regions of the country and with increased
235 preferences to exclude immigrants³⁴.

236 Men may maintain relationships across community boundaries to defend females against
237 third-party communities, as has been observed among the Yanomamö³⁵. However, the
238 ethnographic literature suggests that between-community association to defend women is rare:
239 for example, when women are captured from other communities (e.g., bride capture, wife
240 stealing), if revenge or recapture occurs, usually only a woman's family or community are
241 involved (see ³⁶ for some relevant examples). This is similar to the non-human great apes, which
242 likewise show no evidence of female defense through inter-community association.

243 **3.1.2 Transfer and mating.** Women and men engage in visitation³⁷ and sometimes in
244 matings³⁸ with members of different communities. Both in small-scale³⁸ and post-industrial³⁹
245 societies, visitation permits individuals to try out a prospective community before emigrating.
246 The increased distances at which individuals can visit or make contact today, as fostered by
247 airplane travel and global communications networks, may also act to equalize cooperative
248 preferences with respect to members of different communities⁴⁰, allowing for additional transfer
249 opportunities. Mate search very often crosses community boundaries, as evidenced by the
250 ethnographic literature⁴¹ and bolstered by a decades-old literature on heterogamy across space
251 and ethnolinguistic and religious boundaries in economics, sociology, and demography⁴². In
252 ethnographically-studied societies, men – especially young, unmarried men, as observed among

253 the Agta – are especially likely to travel to and visit at greater distances⁴¹. Indeed, in societies
254 where men have higher variance in reproductive success than women, men may attain more
255 mates by visiting distant locations³⁸.

256 **3.1.3 Kin selection and partner preferences.** As is the case in non-human primates,
257 preferential interaction with kin and partner preferences can enhance the net benefits of
258 intergroup encounter in humans. Kin recognition permits individuals to modulate their behavior
259 towards kin or likely kin (e.g., the child of a dispersed sister) in other communities. Further,
260 humans have additional means to reap inclusive fitness benefits through interactions with extra-
261 community members. Exogamy (marrying outside the community), paired with long-term pair
262 bonding and between-community visitation, enables the recognition of affinal kin (kin by
263 marriage) and the application of kinship terms, and the norms of behavior associated with these
264 terms, to affinal kin^{24,43}. Frequent interaction with affinal kin can enhance an individual's tolerant
265 behavior toward members of their affines' communities, discouraging aggression or freeriding
266 against these individuals and facilitating investment in inclusive fitness interests (e.g., nieces and
267 nephews) across community boundaries^{24,25,29,35}.

268 Partner choice likewise enhances the net benefits of intercommunity tolerant encounter
269 and association in humans. An individual's expectations about extra-community members are
270 often informed by a combination of socially-transmitted information, including information
271 about extra-community members' aggressive behavior during past generations, as well as an
272 individual's own past experiences with extra-community members⁴. Repeated interactions, like
273 those that take place in markets, can enable strangers from different communities to transition

274 to relationships based on trust and reciprocity that generate greater benefits for the individuals
275 involved³¹.

276

277 **3.2 Humans the derived: Human-unique predictors of intercommunity tolerant encounters and** 278 **association**

279 The preponderance of between-community relationships in humans suggest that humans are an
280 outlier in the Primate order with respect to our intergroup behavior, even relative to more
281 distantly-related primates that, like humans, live in multilevel societies²¹. As is true for non-
282 human primates, resources that are not defensible disincentivize aggression in humans;
283 however, humans may even refrain from engaging in contest over an *economically-defensible*
284 resource in order to maintain extra-community relationships^{30,35,44,45}. Humans will even live in
285 home ranges in which needed or desired resources cannot be obtained, instead relying on
286 between-community relationships for access²⁵ – something not seen in non-human primates.
287 This raises the question: How did humans come to be such an outlier in the Primate order?
288 Evidence suggests that unique features of the human foraging ecology – our reliance on
289 resources that vary extensively in their geographic and temporal availability – may provide part
290 of the answer. The fact that individuals who move resources between communities³², e.g., big
291 men among complex hunter-gatherer societies⁴⁶, are accorded status in their home communities
292 underscores the importance of extra-community resource access; likewise, cross-cultural data
293 suggest that when between-community relationships generate individual-level benefits, cultural
294 institutions may further support and reinforce these relationships, further amplifying their
295 benefits.

296 **3.2.1 Buffering shortfalls and accessing non-local resources.** In the early 20th century,
297 functionalist anthropologists theorized about the importance of between-community
298 relationships for maintaining non-local resource access. These authors often leaned heavily on
299 the functions of cultural institutions but did not fail to attend to individual-level benefits of
300 participating in them. For example, Malinowski⁴⁷ proposed that the exchange of ritual goods
301 between islands in the Trobriand Islands, goods to which individual participants ascribed great
302 importance, enabled the exchange of resources they needed or desired in daily life. Radcliffe-
303 Brown⁴⁸ likewise noted that ritualized exchange with other communities permitted individual
304 Andaman Islanders access to valued non-local goods. The individual-level benefits accrued via
305 between-community relationships were later explicitly considered by human behavioral
306 ecologists^{30,44,45,49} and archaeologists^{32,43,50–53} (see especially ^{43,53}). Under these theoretical
307 approaches, the importance of managing resource access, including buffering the risk of resource
308 shortfalls and ensuring access to resources never locally available, provide incentives for
309 individuals to build and maintain relationships spanning distance. However, why access to distant
310 resources might be especially important to extant humans relative to other organisms – even
311 relative to the group-living non-human apes – was often left unstated.

312 Although between-community interactions in the group-living non-human apes are
313 understudied (see Box 1), initial evidence suggests the importance of between-community risk
314 management and non-local resource access in humans reflect human-specific adaptations¹. In
315 general, primates tend to rely on high-quality, high-risk foods¹⁴; however, humans' high energy
316 throughput, as related to the cost of our large brains (which may themselves be an adaptation to
317 our foraging ecology⁵⁴) and our high reproductive rates, created secondary selection pressures

318 on the effective management of the risk of resource shortfalls^{14,55}. The importance of specific,
319 sometimes difficult-to-acquire nutrients to the human brain⁵⁶, such as foods high in omega-3
320 fatty acids (see for ⁵⁷ a discussion), likely amplified the importance of access to non-local
321 resources.

322 One reason these foods and nutrients are risky and difficult to acquire for humans is that
323 they vary across space and time. In some ecologies, there is more asynchrony in resource
324 acquisition across space^{30,45} – that is, in the geographic scope of resource shortfalls⁴³. For
325 example, water availability can be asynchronous across distances of tens of kilometers in
326 Southwestern Africa⁴⁹ such that extra-community relationships become important sources of
327 water access in cases of local drought^{44,49}. When shortfalls are especially large in geographic scale
328 – for example, in the case of regional drought – extra-community relationships may span
329 hundreds of kilometers, as was the case for Aboriginal populations facing drought in Australia in
330 the 1960s⁵⁸. However, the frequency of these shortfalls also matters. The more frequent the
331 shortfalls, the more individuals may strategically utilize extra-community relationships to
332 maintain access to non-local resources – as evidenced by both within- and between-society
333 variation in the importance of these relationships^{30,44,45,50,52,53,59}. When shortfalls have a large
334 geographic scale but are rare, individuals may not maintain extra-community risk buffering
335 networks but instead use alternative strategies, including migration, opting out of their existing,
336 local buffering networks, or raiding neighboring communities^{32,43,53,59,60}. In short, if shortfalls in
337 the availability of a crucial resource occur at a geographic scale greater than the size of a
338 community and frequently enough that the possibility of their occurrence remains salient, extra-

339 community relationships may be an important component of individuals' risk-buffering
340 strategies.

341 Some resources important in a given ecology may not necessarily fluctuate in their
342 availability, but instead may never be available within a community's home range⁵³. For example,
343 preferred materials for toolmaking²⁵ and pottery^{48,61}, medicines⁶¹, and salt may never be
344 available locally (see ⁶² for a relevant review). Socially-transmitted information relevant to the
345 local ecology may have similar distributional features: extra-community individuals may be
346 sources of information about resource availability³², alternative methods of resource acquisition
347 and extraction³³, and, in societies with wage labor, even the availability of jobs⁶³. When
348 important resources, be they physical or informational, cannot be obtained within the local
349 community, extra-community relationships may be important for ensuring access. However, it
350 should be noted that extra-community relationships do not imply a complete absence of
351 between-community aggression; on the contrary, individuals may only be able to invest in and
352 draw upon these relationships during seasonal⁶¹ or periodic⁴ peacetimes.

353 **3.2.2 Achieving status through between-community relationships.** Data suggest that
354 when non-local resource access was important in human history and pre-history, attribution of
355 status – analogous to rank in non-human primates, although often earned through prestige
356 rather than dominance⁶⁴ – to well-connected individuals supported between-community
357 resource flows. When the benefits of between-community resource access is sufficiently high,
358 the high costs some individuals pay for maintaining these relationships (for example, costs due
359 to risk of aggression from other communities or navigating difficult terrain³²) can be offset by
360 same-community members, e.g., in the form of payments³² or status⁵⁰. For example, Coast Salish

361 men with a greater number of between-community ties were accorded more status *within* their
362 communities, at least partially because these relationships provided access to non-local
363 resources⁶⁵. The importance of well-connected individuals for accessing non-local resources,
364 including resources such as jobs in post-industrial nations, is echoed in the literature on weak ties
365 in sociology⁶³. When the benefits of non-local resource access are outweighed by the costs of
366 between-community tolerant behavior, e.g., threat of extra-community aggression, different
367 traits should be accorded status. For example, in small-scale societies in which inter-community
368 ties are important, well-connected individuals may be rewarded with status; when inter-
369 community warfare predominates, warrior-like traits may benefit same-community members
370 and thus be rewarded with status⁶⁴.

371 **3.2.3 Cultural institutions.** The emergence of cultural institutions during human evolution
372 may have further enhanced non-local resource access via between-community relationships.
373 Cultural institutions act as external commitment devices that enhance the reliability of extra-
374 community partners and repurpose these relationships to additional ends. For example, inclusive
375 fitness benefits can be amplified, even across community boundaries, by institutions that
376 delineate appropriate behavior toward kin (and perhaps even enforce that behavior), or that
377 foster inclusive fitness interests (e.g., through exogamous marriage)²⁴. Fictive kinship, or
378 ritualized relationships (e.g., as seen above among the Trobriand Islanders⁴⁷ or in *hxaro* exchange
379 among the San⁴⁹), can co-opt these norms of behavior toward kin, often by enhancing feelings of
380 social closeness, and extend them towards non-kin extra-community members^{43,46,66}. Norms of
381 hospitality are similar in their mechanisms, requiring that individuals treat visiting extra-
382 community members as they would same-community members (see ⁴⁶ for ethnographic

383 examples). With respect to relationships based on reciprocity, research on the emergence of
384 markets suggests that initial between-community relationships often rely on simultaneous
385 exchange, as simultaneous exchange limits opportunities for defection^{32,67}. Once present,
386 simultaneous exchange can provide the basis for between-community divisions of labor⁶²; as
387 seen among the Yanomamö, this specialization can not only enhance the efficiency of production,
388 but even mitigate between-community hostilities³⁵. If individuals *do* defect on extra-community
389 relationships, theoretical work by economists and ethnographic data suggest that if between-
390 community relationships are valuable enough, same-community members may punish these
391 violations (see ⁶⁸ for relevant models and ethnographic examples).

392

393 **3.3 Studying humans: The limitations of existing research methods**

394 A weakness of existing theory on human intercommunity behavior in evolutionary anthropology
395 is the paucity of data used to inform it. For example, among fieldworkers studying living humans
396 (like AP), our focus on local, within-community risk buffering networks⁵¹; the low likelihood that
397 we observe rare events that require extra-community buffering⁵¹; and our tendency to use only
398 “complete” networks in social network analysis (which usually means including only same-
399 community individuals⁶⁹) have hindered our accurate representation of social relationships that
400 span human community boundaries, leading researchers to often conclude that humans tend
401 towards parochialism. To improve the accuracy of evolutionary anthropology’s characterization
402 of human intercommunity behavior, we suggest two things: first, that researchers attend to
403 findings from related disciplines (such as those highlighted above) that provide evidence of the
404 nature of the flexibility of parochialism and tolerance in humans, and second, that field

405 researchers working with living humans ask about relationships that span community boundaries
406 when collecting qualitative and quantitative data.

407

408 **4. DISCUSSION**

409 In evolutionary anthropology, and in disciplines influenced by it, a common current assumption
410 made by researchers is a “strong human universal toward parochial altruism” (p. 12702) – in-
411 group favoritism at out-group cost⁷⁰. Research focus on chimpanzees as a referential analogy for
412 human behavior⁷¹ tends to promote this perspective. However, evidence suggests that individual
413 behavior in intergroup encounters is actually quite flexible, both in humans (e.g., per the study
414 from which the preceding quote was drawn⁷⁰) and in the group-living great apes generally.
415 Disincentives for intergroup aggression have been thoroughly discussed by other reviews;
416 however, these disincentives provide insight only into when selection *could* favor individual
417 tolerance toward extra-group members, but not *why* it does under these circumstances. Here,
418 drawing on existing observations of non-human primates, we assembled potential fitness
419 benefits that may favor intergroup tolerant encounter and association (Table 1). Though
420 scientists know comparatively little about intergroup encounters in bonobos and gorillas relative
421 to chimpanzees – a situation that, as we argued in Box 1, should be remedied – the fitness
422 benefits we identified seem to account for at least some of the observed variability in intergroup
423 behavior in bonobos and gorillas.

424 Our review of the literature suggests that the benefits favoring intergroup tolerant
425 encounter and association in non-human primates can account for some, but not all, of the
426 flexibility of intergroup tolerance in humans. In both humans and non-human primates, mating

427 and transfer, as facilitated by visitation, and opportunities for social learning are potential
428 benefits to be gained from intergroup tolerant encounter and association. Likewise, across the
429 Primate order, kinship and partner preferences can further amplify the benefits and minimize
430 the costs of encounter. However, humans have a much higher prevalence of intergroup tolerant
431 encounters and association than do non-human primates – at least, as observed to date.
432 Evidence from anthropology and across the social sciences suggests that humans' reliance on
433 resources with extensive spatial and temporal variability has necessitated flexible interest in
434 between-community relationships as a means of managing the risks of resource shortfalls and
435 ensuring access to non-locally-available resources. When and where the benefits of between-
436 community resource access have been high, cultural institutions and social status have also
437 enhanced and reinforced these benefits. This is not to say that humans do not engage in
438 intergroup aggression – the ethnographic, archaeological, and contemporary records provide
439 ample evidence of parochialism and warfare – but rather that human intergroup behavior can be
440 both more tolerant and more aggressive than what we have observed in our closest relatives,
441 and that this flexibility in intergroup behavior is functional.

442 We advance the hypotheses outlined in this review for testing by the evolutionary
443 anthropological community. Similar ideas with respect to the importance of between-community
444 resource access have been outlined by functional anthropologists, archaeologists, and human
445 behavioral ecologists previously – although usually without treatment of why between-
446 community resource access is of particular importance in humans. We hope that by
447 amalgamating these perspectives and building upon them, the present paper inspires newfound
448 interest in the flexibility of human and non-human great ape intergroup behavior, moving our

449 discipline beyond its current focus on parochialism. In addition to our larger hypothesis with
450 respect to the human foraging ecology, we wish to highlight other related questions to be
451 addressed by future work. (1) The higher the frequency of shortfalls, the more likely that
452 individuals will recall these shortfalls (whether via their own memories or even oral traditions)
453 and maintain between-community relationships accordingly^{43,52} – but how frequent must they
454 be? Is once every several generations enough? (2) Will the connections we drew between status
455 acquisition, cultural institutions, and the relative importance of between-community resource
456 access be supported by additional data? To date, the connection between status and between-
457 community relationships has been more theoretical than empirical. (3) Which poses the stronger
458 selection pressure in humans: benefits gained via intergroup tolerant encounters and association
459 in the currency of between-community resource access, or the cost of mortality risk from
460 aggression and warfare⁷², potentially reduced by intergroup tolerant encounters and
461 association?

462 To answer the above questions and improve the accuracy of our characterizations of
463 sociality in both humans and the non-human great apes, researchers will need to collect targeted
464 data assessing the predictors of intergroup behavior. For field researchers studying humans, we
465 urge caution with respect to reliance on observational data and “complete” social networks.
466 Asking participants about their social strategies for mitigating shortfalls⁵¹, their preferences for
467 same-community vs extra-community relationships^{26,27}, and their extra-community ties⁶⁹ may
468 provide a more accurate picture of the flexibility of human sociality. Further, the dedication of
469 increased research effort to intergroup encounters and association in gorillas and bonobos, as

470 well as habituation of neighboring groups, will improve our understanding of sociality in the
471 group-living non-human great apes.

472 In the present review, we opted not to unpack the nature of human “groups,” nor human
473 group psychology. Humans are adept at cognizing groups of various kinds – from groups formed
474 in experimental contexts to interest-based groups to ethnic or religious groups – and at
475 recognizing their boundaries. A number of the papers and chapters we reviewed here discuss
476 potential derived functions of group living in humans (e.g., ^{28,29,33,54}). Our larger point is that the
477 human reliance on resources that vary in their spatial and temporal availability often necessitates
478 relationships spanning distance; in general, the group-living great apes evidence flexible interest
479 in intergroup encounters and association (Box 1), and it is likely that this flexible interest became
480 even more important in the human lineage (Section 3.2). While relationships spanning distance
481 sometimes span ethnolinguistic boundaries, for example, or religious boundaries, they do not
482 necessarily. As such, questions of the proliferation of different types of human groups, and how
483 ethnic groups may have been built on the scaffolding of social relationships through which non-
484 local resources could be accessed (e.g., ⁶⁷), we leave to other papers.

485 Given the lack of attention the benefits of intergroup tolerant encounter and association
486 have received in evolutionary anthropology, the present review reflects first-pass theorizing
487 about these incentives; as such, we have not explored the roles of constraints, including
488 phylogeny and life history constraints, nor the affordances of a comparative approach with non-
489 primate species. Phylogeny and life history constraints likely affect the prevalence and flexibility
490 of intergroup tolerance in different species of primates. For example, the relationship between
491 intergroup tolerance and the ecological and social factors discussed here may partially reflect a

492 third variable, phylogenetic inertia. Whether such constraints explain existing observational data
493 is a question to be answered by future work. Further, we chose not to pursue a comparative
494 approach with non-primate species. Though the high incentives for intergroup tolerant
495 encounter and association observed in humans may have better analogies among non-primate
496 vertebrates or even insects², our goal here was to explore intergroup tolerance in humans in the
497 context of non-human primates rather than to find the closest-match analogy for human
498 behavior.

499

500 **5. CONCLUSION**

501 Intergroup behavior in primates is flexible, and the prevalence of intergroup tolerant encounters
502 and association varies across species. To be sure, incentives for aggression vary, as discussed
503 extensively in existing work; however, when incentives for aggression are low or absent, why
504 would natural selection favor tolerant behavior toward extra-group members – or even increased
505 rates of intergroup tolerant encounter and association? Drawing inferences from the existing
506 primatological literature, we highlighted benefits favoring intergroup tolerant encounter and
507 association across the Primate order, including in group-living non-human apes and humans, such
508 as transfer, mating, and enhanced foraging efficiency. Humans are unique among primates in our
509 high prevalence of intergroup tolerance, however, and data from across the social sciences
510 suggest the relevance of the human foraging ecology – especially the spatial and temporal
511 availability of resources on which we depend – in explaining the human pattern. Future research
512 should work to better document the variability in intergroup behavior in the group-living apes,

513 especially in gorillas, bonobos, and humans, using methods of data collection designed
514 specifically for this endeavor.

515

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521

522 **Data.** Data sharing is not applicable to this article as no new data were created or analyzed in this
523 study.

524

525 **GLOSSARY**

526 **Association.** Upon encounter, two conspecifics remain in spatial proximity to one another.

527 **Community.** For the purposes of this paper, we define communities as human individuals living
528 in close spatial proximity. While “community” is sometimes used to describe bonobo and
529 chimpanzee groups given their fission-fusion social structure²⁹, in our experience this causes
530 confusion among primate researchers; we use the word “community” only in reference to
531 humans to be clear that “between-community relationships” refer to relationships across
532 geographic space. Members of the same community are referred to as “same-community” and
533 members of other communities as “extra-community.”

534 **Contest.** An aggressive interaction between two conspecifics over access to a resource.

535 **Encounter.** Visual or vocal contact between two conspecifics. When possible, we recommend
536 researchers study visual, rather than vocal, encounters when studying intergroup encounter for
537 two reasons. First, vocal encounters do not differentiate between the strategies outlined in
538 Figure 1. For example, individuals may use long calls to signal their group's position to extra-
539 group conspecifics either to facilitate *or avoid* encounter⁵ – vocal encounters do not allow us to
540 disambiguate these potential explanations. Second, from a logistical perspective, it can be
541 difficult for field researchers to distinguish within-group from between-group encounters in
542 fission-fusion societies, where parties may be foraging separately, unless they witness these
543 encounters. Because of these limitations, visual encounters are preferable sources of data.

544 **Group.** In the Primate order, groups are individuals “which remain [physically] together in or
545 separate from a larger unit” and interact with each other more than with other individuals⁶ (p.
546 40). This definition does not cover all uses of the word “group” in the social sciences (e.g., human
547 identity groups who identify with a common name or symbol may or may not interact with one
548 another more frequently than with other individuals). Because of this ambiguity, we use the word
549 “community” when referring to humans to better capture the notion of spatial proximity, per ²⁹.
550 Members of the same group are referred to as “same-group” and those from another group
551 “extra-group.”

552 **Intergroup encounter.** An encounter between at least two members from each of two groups.
553 An encounter in which only one individual from each group participates is often called a
554 “temporal visit.”

555 **Interspecific association.** An association between individuals from two or more species.

556 **Multilevel society.** Social organization in which basal units (often, but not always, reproductive
557 units and/or bachelor groups of males) are parts of larger groups²¹.

558 **Party.** An ephemeral association of conspecifics which does not meet the definition of a group²¹.

559 **Tolerance.** An individual has an encounter with a conspecific and can freely leave but remains in
560 the encounter without acting aggressively towards the conspecific. See Figure 1.

561 **BOX 1. Intergroup tolerant encounter and association in the non-human great apes: Referential**
562 **models for human behavior?**

563 In the last four decades, there has been extensive research interest in chimpanzees as potential
564 analogies for human behavior. Jane Goodall's observations of intergroup aggression in
565 chimpanzees at Gombe National Park inspired a generation of primatologists to further research
566 the topic (see ⁷¹ for a review), contributing to chimpanzees' status as one of the most-studied
567 non-human primates. Given the relatedness between chimpanzees and humans, this literature
568 often asserts that chimpanzees provide an analogy for humans – namely, that chimpanzees'
569 social behavior should approximate that of the Last Common Ancestor shared by chimpanzees
570 and humans, giving scientists insight into the evolutionary roots of human intergroup violence⁷³.
571 There is much debate as to whether this model, often termed the Chimpanzee Violence
572 Hypothesis⁷¹, provides a useful analogy for human behavior^{72,73}; however, this debate tends to
573 assess the fine-grained details of chimpanzees as a referential model, rather than explore
574 whether *other* species may provide analogies for, and thus insight into, human behavior.

575 Other candidate referential models for human intergroup behavior include non-human
576 primates and even invertebrates. As aforementioned, non-human primates living in multilevel
577 societies may provide a window into the evolution of intergroup tolerant association in
578 humans²¹. Polydomous ants offer a potential analogy for identity maintenance despite between-
579 group cooperation in humans². Further, the non-human great apes remain a source of insight.
580 Even if scientists disagree about the relevance of the Chimpanzee Violence Hypothesis for human
581 intergroup behavior, this does not imply that the great apes are devoid of useful analogies for
582 intergroup behavior in humans. Bonobos, for example, are as closely related to humans as are

583 chimpanzees. Bonobos have been described as largely peaceful⁷⁴; in reality, however, bonobo
584 intergroup encounters feature both tolerant and aggressive behavior⁷⁵, and the predictors of
585 these different behaviors may provide insight into the flexibility of human intergroup behavior.
586 Though not as closely related to humans, gorillas likewise exhibit a range of intergroup behavior
587 with clear differences by sex and rank. (See Box Table 1 for differences in intergroup behavior
588 between non-human great ape species.) In short, there are many candidate referential models
589 that might provide insight into the evolution of flexible intergroup behavior in humans, and useful
590 analogies need not all be found in the same species, or even the same clade.

591 Chimpanzees and bonobos have a very similar social structure: both live in social groups
592 characterized by fission-fusion dynamics and female dispersal. However, while the majority of
593 intergroup encounters in chimpanzees are hostile (see ⁷⁶ for exceptions), bonobo intergroup
594 behavior varies extensively, even within the same individual in the same intergroup encounter.
595 What predicts when tolerant intergroup encounters occur in bonobos? Recent studies find that
596 prolonged encounters between bonobos groups occur more frequently during times of high fruit
597 abundance, indicating that reduced feeding competition may be a precondition for these
598 encounters^{75,77}. However, as identified in Section 1.1, such findings address only disincentives for
599 aggression (see Figure 1); at this stage we can merely speculate on the actual incentives to *meet*.
600 Here are some of the candidate benefits (per Table 1) favoring intergroup encounter in bonobos,
601 given existing observational data:

- 602 • **Enhanced foraging returns.** New data indicate that bonobo groups may remain in
603 prolonged association when at least one of the two is foraging in a less familiar area,
604 suggesting that intergroup association might enhance foraging efficiency and

605 opportunities to socially learn the location of ripe food⁷⁷. Further, evidence from a
606 different site indicates the occurrence of food sharing between bonobo groups⁷⁸.

607 • **Extra-group mating.** During encounters, males and females will both initiate matings with
608 extra-group members; however, the function of these matings is unclear as they rarely
609 result in paternities^{75,79}.

610 • **Reconnaissance before transfer.** Encounters are used by young females to transfer
611 between groups; however, these females are unlikely to be responsible for initiating
612 intergroup encounters given their restricted influence on group movements⁸⁰. Although
613 not strongly emphasized in the literature on chimpanzee intergroup encounters, female
614 chimpanzees have also been observed to visit other chimpanzee groups, presumably in
615 preparation for transfer⁷⁶.

616 It is possible, per Section 2, that close kinship between females in different bonobo groups
617 facilitates tolerant encounter; however, we do not have the genetic data to evaluate this
618 possibility. In general, to better assess the relevance of bonobo intergroup behavior as a
619 referential model for that of humans – as well as to better understand why bonobo intergroup
620 behavior differs so much from that of chimpanzees, despite their close relatedness and similar
621 social structure – more data are needed. Bonobos have a smaller population size than
622 chimpanzees and are located at sites often inaccessible due to political constraints, hurdles to
623 studying this species. Targeted data collection among these sometimes hard-to-reach
624 populations, further facilitated by habituation of neighboring groups such that encounters can
625 be documented from multiple vantage points, will better elucidate the factors influencing
626 bonobo intergroup behavior.

627 While researchers tend to focus on our closest relatives, chimpanzees and bonobos, as
628 analogies for human sociality, gorillas are another great ape species that may provide insight into
629 the evolution of tolerant intergroup behavior in humans. While western gorillas tend to be more
630 tolerant toward extra-group members than mountain gorillas⁸¹, peaceful interactions such as
631 play or touching behavior also occur between members of different mountain gorilla groups⁸². In
632 western gorillas, mutual attraction to mineral-rich forest-clearings may disincentive aggression⁸³
633 – though, as noted above, this observation does not provide insight into incentives for tolerant
634 encounter. Reconnaissance before transfer is one possible benefit to tolerant intergroup
635 encounter in gorillas: like bonobos and chimpanzees, western gorilla females may visit other
636 groups before transfer⁸¹. Additionally, males may also benefit from reconnaissance with respect
637 to the competitive abilities of future rivals⁸¹. Relatedness or familiarity between male silverbacks
638 in neighboring groups may further enhance the net benefits of tolerant interactions between
639 these individuals⁸⁴ (but ⁸⁵). A recent study in mountain gorillas suggests that tolerant intergroup
640 encounters might be more frequent than previously appreciated⁸². New data such as these will
641 permit researchers to better assess the extent to which intergroup behavior in the great apes can
642 provide analogies for human tolerant intergroup behavior.

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852 **Table 1.** Potential benefits to tolerant intergroup encounter and association are highlighted in the below table. In the second column,
 853 we identify how these benefits are typically realized; where benefits are more likely to accrue to individuals of a given sex or rank, we
 854 note this in parentheses (“m” for male, “f” for female, “high” for high rank, “low” for low rank). In the third column we provide a non-
 855 exhaustive list of primate species in which interactions consistent with the hypothesized benefit have been observed. One set of
 856 observations of interspecific intergroup encounters, rather than intraspecific (as it the focus of this paper), is indicated with a *. Where
 857 relevant, we cite existing reviews providing further details on how benefits can be realized.

Benefits of tolerant intergroup encounter	Association with extra-group individuals permits:	Non-human primate examples
Increased resource holding potential	Actively or passively deterring third-party extra-group members from accessing a contested resource (m/f) ^A	Tamarins (genus <i>Sanguinus</i>) ^{86*}
	Passively defending mating partners against third-party extra-group members (m high)	Baboons (genus <i>Papio</i>) ⁸⁷ Golden snub-nosed monkeys (<i>Rhinopithecus roxellana</i>) ¹⁹
Enhanced foraging returns	Knowing which resource patches have been depleted by conspecifics (m/f)	Yunnan snub-nosed monkeys (<i>Rhinopithecus bieti</i>) ⁸⁸
	Learning the location of food or methods of food extraction (m/f)	Tamarins (genus <i>Sanguinus</i>) ⁸⁹
Reducing predation risk	Enhancing vigilance and diluting the per-capita risk of predation (m/f)	Hamadryas baboons (<i>Papio hamadryas hamadryas</i>) ²⁰
Reconnaissance before transfer	Gaining information about groups to which individuals might transfer ¹⁵ (m/f low)	Ring-tailed lemurs (<i>Lemur catta</i>) ⁹⁰ Vervets (<i>Cercopithecus aethiops</i>) ²³ Chimpanzees (<i>Pan troglodytes</i>) ⁷⁶ Bonobos (<i>Pan paniscus</i>) ⁹¹ Gorillas (<i>Gorilla gorilla, beringei</i>) ^{81,92}

Extra-group mating	Confusing paternity to avoid infanticide (f), shopping for good genes (f), or gaining additional opportunities to sire offspring (m)	Ring-tailed lemurs (<i>Lemur catta</i>) ⁹⁰ Bonobos (<i>Pan paniscus</i>; mixed evidence⁷⁵) Chimpanzees (<i>Pan troglodytes</i>)⁷⁶
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858 ^A Resource defense can be passive, consisting solely of a numerical advantage, or active, if groups in association aggress against third
859 parties that threaten to displace them².

860 **Table Box 1. Reported differences in intergroup behavior in the group-living non-human great ape species.** WG indicates western
 861 gorillas; MG indicates mountain gorillas.

	Chimpanzees	Bonobos	Gorillas
Home range overlap ^A	7-13% ⁹³	9-23% ⁹⁴	13-100% ^{84,95}
Encounter duration	hours (single females with offspring may stay longer) ⁷⁶	up to several days ⁷⁷	up to several days ⁹²
Occurrence of encounters (% of observation days)	3.33-5% ⁷⁶	0.2-30% ^{75,77,78}	WG: 2% ⁹⁵
Lethal outcomes	occur ⁹⁶	not reported ⁹⁶	WG: not reported MG: occur ⁹⁷
Patrolling and other territorial behavior	occur ⁹⁸	not reported	not reported
Within-group coalitions	occur ⁹⁸	occur ^B	WG: not reported MG: occur ⁹⁷
Between-group coalitions	not reported	occur ⁹⁹	not reported
Copulation between groups	occur ⁷⁶	occur ¹⁰⁰	not reported
Food sharing between groups	not reported	occur ⁷⁸	not reported
Grooming between groups	not reported (except during female visits) ⁷⁶	occur ¹⁰⁰	not reported

862 ^ASee Section 1.1 for the limitations of this measure. ^BPersonal observation by MS.

863 **Figure 1.** Basic incentive structure for behavior towards an extra-group conspecific. Contest incentives include the net benefits of
864 defending food resources or mates, among others. Incentives for encounter include the net benefits of foraging in association,
865 predation avoidance, and opportunities for mating and transfer.

		Contest incentives	
		High	Low
Encounter incentives	High	a Aggression	b Tolerance
	Low	c Active avoidance	d Random encounters

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