Correlates of individual participation in boundary patrols by male chimpanzees

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20 Group territory defense poses a collective action problem: individuals can free-ride, benefiting

21 without paying the costs. Individual heterogeneity has been proposed to solve such problems, as

22 individuals high in reproductive success, rank, fighting ability, or motivation may benefit from

23 defending territories even if others free-ride. To test this hypothesis, we analyzed 30 years of

24 data from chimpanzees (*Pan troglodytes*) in the Kasekela community, Gombe National Park,

25 Tanzania (1978-2007). We examined the extent to which individual participation in patrols

26 varied according to correlates of reproductive success (mating rate, rank, age), fighting ability

27 (hunting), motivation (scores from personality ratings), costs of defecting (the number of adult

28 males in the community), and gregariousness (sighting frequency). In contrast to expectations

29 from collective action theory, males participated in patrols at consistently high rates (mean ±

30 S.D. = 74.5 ± 11.1% of patrols, n=23 males). The best predictors of patrol participation were

31 sighting frequency, age, and hunting participation. Current and former alpha males did not

32 participate at a higher rate than males that never achieved alpha status. These findings suggest

33 that the temptation to free-ride is low, and that a mutualistic mechanism such as group

34 augmentation may better explain individual participation in group territorial behavior.

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35   Many group-living mammals defend group territories (e.g., meerkats, *Suricata* suricatta [1]; free-

36   ranging dogs, *Canis lupus familiarus* [2]; lions, *Panthera leo* [3]; ring-tailed lemurs, *Lemur catta*

37   [4]; white-faced capuchins, *Cebus capucinus* [5]; chimpanzees, *Pan troglodytes* [6]; primates in

38   general [7,8]). These territories provide benefits to group members, including resources such as

39   food, water, and shelter [9–12], and safety from intergroup attacks [13]. These benefits are public

40   goods, because group members can obtain these benefits regardless of whether they have paid

41   the costs of production [14]. This poses a collective action problem [15]: insofar as territorial

42   effort is costly, individuals will be tempted to free-ride, benefiting from the public goods without

43   paying the costs. But if all individuals free-ride, the good will not be produced. A group

44   composed entirely of free-riders eventually will have no territory to defend. What motivates

45   individuals to participate in territorial behavior, despite the temptation to defect?

46

47   Heterogeneity among individuals has been proposed as a solution to this collective action

48   problem [16]. Although assuming homogeneity among group members can make mathematical

49   models of behavior easier to construct, in the real world, individuals are unlikely to be identical

50   to one another [17]. Individuals may vary in their fighting ability or tolerance of risk, and thus

51   experience differing costs from participation in territorial behavior. Additionally, despite

52   assumptions of earlier models, public goods are not necessarily shared equally. Individuals with

53   high dominance rank may produce a disproportionate share of offspring, which then benefit from

54   the food resources and safety provided by their parent's territorial effort. Thus, apparently

55   altruistic territorial behavior could instead result from heterogeneity in individual costs,

56   propensities, or benefits of participation in collective action [16,17].

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58 Findings from field studies of chimpanzees (*Pan troglodytes*) have supported this theoretical

59 expectation. In the Ngogo community of Kibale National Park, Uganda, individual participation

60 in boundary patrols by male chimpanzees correlated with measures of reproductive success,

61 rank, and hunting success [18]. These findings have since been partially supported by a follow-

62 up study examining 20 years of data from Ngogo [19], which found that males participated more

63 in patrolling if they had more offspring and were high in dominance rank. Additionally, they

64 found that males patrolled more when the group had fewer males, suggesting that males

65 increased participation when the costs of defecting were higher [19]. However, this study also

66 found results contrary to some predictions of collective action theory. In particular, males had

67 generally high rates of participation, with each male participating in a mean of 33% of patrols.

68 Additionally, despite the expectation that patrolling should be based on reproductive success,

69 some males that had no offspring in the group participated frequently in patrols. Based on these

70 and other considerations, Langergraber and colleagues [19] proposed that a group augmentation

71 model was a better predictor of individual participation in patrols.

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73 Group augmentation theory was developed to explain why helpers in cooperatively breeding

74 species delay or even forgo their own reproduction to help others raise young [20]. If individuals

75 survive or reproduce better in larger groups, then they may benefit from the increased production

76 of new group members, even if they are unrelated. Applying this logic to chimpanzees,

77 Langergraber and colleagues [19] argued that because reproductive skew is generally low among

78 male chimpanzees, and all males depend on successful defense of a territory to ensure safety and

79 sufficient food for themselves, their mates and their offspring, individuals have lower incentives

80 for free-riding than predicted by a collective action framework.

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82   To provide an additional test of factors affecting individual participation in territorial behavior,

83   we examined data from the Kasekela community of chimpanzees in Gombe National Park,

84   Tanzania. The Ngogo community is exceptionally large, with up to 206 members [19].

85   Additionally, this community fissioned into two mutually hostile communities in 2017 [21].

86   Given the expectation that larger group size exacerbates collective action problems, and the

87   possibility that substructuring within Ngogo affected patterns of cooperation in that community,

88   we sought to test whether similar patterns held in a community that is more typical in size, and

89   not undergoing a fission. With a median population of 50 individuals (range 39–61, 1978–2007,

90   the Kasekela community is close to the median size for chimpanzee communities in long-term

91   studies (median = 42.3 members; range: 6.7–144; including a median 8.2 males (range: 1.9–37)

92   and 14.4 females (range: 2.1-51) at least 12 years old; N = 18 communities [22]), Additionally,

93   by using 30 years of data, we sought to explore how individual participation in boundary patrols

94   varies across the male lifespan.

95

96   Chimpanzees have been studied intensively at multiple long-term field sites [23–26].

97   Chimpanzees live in groups ('communities' [6] or 'unit-groups' [27]) that exhibit fission-fusion

98   dynamics, in which individuals travel in subgroups ('parties') that vary in size and composition

99   [6,28]. Male chimpanzees defend group territories and maintain hostile relations with neighbors

100   [6,29,30], sometimes killing members of other groups [22,31]. Chimpanzees conduct boundary

101   patrols, during which parties, often mainly of males, travel to the periphery of their range,

102   behaving as if they are searching for signs of chimpanzees from other communities [6,18,29].

103   Males can adjust their participation in boundary patrols by associating with or avoiding parties

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104 with many males, which are more likely to visit boundaries [32], or by going with or staying

105 behind if a party travels towards the periphery [19,33]. Intergroup encounters occur most

106 frequently when seasonally abundant fruit attracts members of rival communities to borderlands

107 [33]. Participating in a patrol also likely increases the chances of encountering neighbors. Most

108 intergroup encounters involve only auditory contact, in which individuals hear vocalizations

109 from distant chimpanzees, and may respond with vocalizations of their own [33,34], and/or

110 approach or retreat, depending on their apparent relative numerical strength [33,35,36]. If

111 chimpanzees come within visual range, they may chase, attack, and sometimes kill members of

112 rival groups [30,34,37]. Intergroup killings occur mainly when attackers greatly outnumber

113 victims (median ratio of attackers to victims = 8:1 [22]).

114

115 Winners of intergroup contests may increase their territory size [6,37], which can result in

116 community-wide benefits, particularly increased access to food resources, as indicated by

117 heavier body mass [10] and larger parties [9] in years with larger territory size. Increased food

118 provides fitness benefits: in years with larger territory size, females have shorter interbirth

119 intervals [9,12]. Thus, group territorial effort creates the public good of increased food supply.

120 Additionally, communities with larger territories suffer lower rates of intergroup mortality,

121 perhaps as a consequence of reduction in the relative size of the periphery as the territory

122 increases in area [13].

123

124 Participating in patrols appears to be costly for individuals, as traveling further incurs energetic

125 [38] and physiological costs from higher levels of cortisol [39] and testosterone [40]. Insofar as

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126   patrolling borders increases the likelihood of meeting and fighting with members of rival

127   communities, participating in patrols potentially increases risks of injury or death.

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129   While the collective action framework focuses on how these costs may promote free-riding, two

130   factors may mitigate these costs. First, as Langergraber et al. [19] argue, the benefits of territorial

131   effort may be distributed more evenly than would appear from a focus on individual differences.

132   In a world divided among competing social groups, individual survival and reproduction may

133   depend so critically on intergroup effort that all individuals or all individuals of a particular sex

134   are motivated to participate, such that participation in territorial behavior evolves through

135   mutualistic benefits, as in lions [41]. Second, while patrolling incurs energetic and physiological

136   costs, these may be offset by various direct benefits to patrollers. Traveling with many males

137   reduces the risks of being injured or killed [30,42,43], and traveling to the periphery may provide

138   opportunities to find and exploit new food resources [33], monitor females with peripheral home

139   ranges [44], recruit new females [45], and participate in other activities that benefit from larger

140   numbers of males, such as hunting [46].

141

142   In the present study, we tested four sets of variables predicted to promote individual participation

143   in boundary patrols. First, according to the collective action problem framework, individuals

144   should participate according to their expected returns [15,16]. Insofar as males defend a feeding

145   territory for themselves, their mates and offspring, males with more mating opportunities and

146   more existing offspring stand to benefit more. Because we do not have genetic paternity data for

147   the early decades of the study, we considered three main proxies of reproductive success: mating

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148　rate, age, and dominance rank. In the short term, males that mate more frequently with fertile

149　females should have a higher chance of siring offspring. In the long-term, if males continue to

150　sire offspring, older males should have more offspring. High-ranking males sire more offspring

151　[47], although recent analysis indicates that only the highest-ranking males ("alphas") sire a

152　disproportionate share [48].

153

154　Second, collective action theory predicts that individuals may contribute territorial effort if the

155　costs of doing so are low, because they are strong fighters and/or highly motivated [16]. In male

156　chimpanzees, dominance rank typically peaks in early adulthood [49], and thus likely reflects

157　peak physical condition and competitive ability, in addition to being correlated with reproductive

158　success as discussed above. We considered two additional factors associated with individual

159　fighting ability and motivation: hunting and personality ratings. Chimpanzees engage in group-

160　level hunts of monkeys, which like intergroup contests involve collective efforts to attack and

161　kill victims [46]. Watts and Mitani [18] found that at Ngogo, male participation rates in hunting

162　correlated with patrolling frequency. For measures of motivation, we considered scores derived

163　from ratings of chimpanzee personality by long-term researchers [50]. We considered scores for

164　two dimensions expected to correlate with willingness to patrol boundaries: Dominance and

165　Conscientiousness. These personality dimensions are derived differently and independently from

166　behavioral measures such as dominance rank. Based on studies of personality in captive

167　chimpanzees [51,52], we predict that individuals with high Dominance scores should patrol more

168　often, due to being bolder, and that individuals with low Conscientiousness scores should patrol

169　more often, due to reduced concern for the associated risks.

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171 Third, the "group size paradox" contends that collective action should break down more readily

172 in larger groups due to increased opportunity for free-riders and decreased benefits for

173 individuals [15]. Studies of individual species [2,5,19] and comparative analysis [8] indicate that

174 cooperative investment decreases with increase in group size. Because chimpanzees are more

175 likely to initiate boundary patrols when traveling in larger parties [43], in communities with

176 fewer males, a larger proportion of males may be required to mount an effective patrol.

177 Furthermore, individuals may be more sensitive to the costs of defecting when in smaller groups,

178 because each individual's contribution matters more to the success of the collective effort. In this

179 case, individual participation in boundary patrols should increase when the number of males in

180 the community is low.

181

182 Fourth, variation in patrolling frequency potentially reflects differences in gregariousness, or an

183 individual's propensity to travel in larger groups. Because patrols typically involve parties with

184 many males, an individual who rarely spends time traveling in large parties will likely participate

185 in patrols less frequently. To control for this possibility, we included a measure of sighting

186 frequency, the proportion of days on which an individual was observed.

187

188 **Methods**

189 *Study site*: The site of long-term chimpanzee research since 1960 [6], Gombe National Park

190 (4°40′S 29°38′E) covers a rugged landscape with a land area of 35.69 km^2 along the shore of

191 Lake Tanganyika as well as 20.72 km^2 of the lake itself [53]. During our study period, three

192 chimpanzee communities lived in Gombe. We analyze data from the Kasekela community,

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193   which occupied a large range at the center of Gombe during our study period (1978-2007;

194   median=12.17 km^2, range 5.30–19.16 km^2), with a median population of 50 individuals (1978-

195   2007, range 39–61, n=30 years). To the north, the Mitumba community (1994-2007;

196   median=4.63 km^2, range 3.19–5.91 km^2) had a median population of 22 individuals (range 20–

197   25, 1996–2007). To the south, the Kalande community [54], remained unhabituated for most of

198   this study period. Observational monitoring and non-invasive genetic sampling indicated that

199   Kalande had a median population of 14.5 individuals (range 12–19, 2001–2007). Both

200   communities were likely larger and more formidable earlier in the study period [54,55].

201

202   In Kasekela, researchers conducted all-day focal follows of individual chimpanzees on a nearly

203   daily basis [56]. Chimpanzees use branches to make simple sleeping platforms in trees each

204   night. Ideally, follows started at the focal target's sleeping site before dawn, and continued until

205   the target nested that night. Observers recorded party location at 15-minute intervals while

206   maintaining a continuous record of party composition and focal feeding behavior. While

207   following the focal subject, one researcher wrote an *ad libitum* narrative of the day's events,

208   noting the time and individuals involved in all observed occurrences of selected behaviors,

209   including aggression, mating, boundary patrols, and intercommunity interactions. Observers

210   documented the reproductive state of all adult females seen each day, based on the size of

211   anogenital sexual swellings [57], and recorded the dates of births, deaths, and changes in

212   community membership.

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214 *Study Subjects*: We analyzed 30 years of behavioral observations of male chimpanzees of the

215 Kasekela community, starting with the first year for which daily dominance hierarchy data have

216 been calculated (1978 [49]) and ending with the most recent year for which boundary patrol data

217 have been extracted (2007 [46]). To include all potential sires, we included males starting from

218 12 years old, the age of the youngest known sire from Gombe [47]. We refer to these males as

219 "adult males," though we recognize that most males do not reach full adult size and behavior

220 until later. Our sample included 23 males that were ≥12 years old during the study period,

221 excluding from analysis one male (*PX*) who was effectively castrated by a scrotal injury at a

222 young age [6]. We calculated annual records for each male, which resulted in 283 male-years

223 with complete data, with a median of 12 years per male (range = 2–22 years), during which

224 males had a median age of 22.8 years (range = 12.1–40.6 years). Because some males reached 12

225 years of age and/or died part way through the year, observation days per year ranged from 20 to

226 366 days (median=365 days). We calculated the mean number of adult males present in the

227 community each year based on the number of days each male was known to be alive and ≥12

228 years old. Over these years, Kasekela had a median of 11.1 males (range = 7.6–13.0 males).

229

230 *Boundary Patrols*: We extracted boundary patrols from long-term records, based on explicit

231 statements that chimpanzees were patrolling, and descriptions of cautious travel where

232 individuals appeared to be looking and/or listening for chimpanzees from neighboring

233 communities [46]. We considered all adult males present in the party at the start of the boundary

234 patrol to be participants. We used records of party composition to calculate the proportion of

235 time each participant stayed for each patrol.

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237 Periphery Visits: To capture any visits to the far periphery missed by our method of extracting

238 boundary patrols, we used map location data to identify all occasions on which parties traveled ≥

239 3 standard deviations north or south of the annual north-south range center. We chose this

240 benchmark as it identified periphery visits on approximately the same order as boundary patrols.

241 Kasekela faced intergroup threats to the north (Mitumba) and south (Kalande), but not from Lake

242 Tanganyika to the west, or the human-dominated village lands to the east. Any boundary patrols

243 that also met the criteria for periphery visits were considered solely as boundary patrols for

244 purposes of analysis. We identified all adult Kasekela males present during a periphery visit as

245 participants. We considered all adult Kasekela males alive at the time, but absent from the visit,

246 to be non-participants.

247

248 *Comparison of boundary patrols and periphery visits:* Visits to the periphery could serve other

249 purposes, such as searching for food or females. We therefore compared party composition and

250 feeding behavior during each of these two categories of event, using a set of boundary patrols

251 (N=180) and periphery visits (N=147) for which we had complete party composition and feeding

252 data. We used Mann-Whitney U-tests with corrections for the false discovery rate [58] to test for

253 differences in party size, number of adult males, and number of adult females. We used Poisson

254 regression to compare time spent feeding during boundary patrols and periphery visits. We

255 modeled minutes spent feeding, including the individual as a random intercept, and log(duration

256 of patrol or periphery visit) as an offset.

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258 *Mating Frequency*: To obtain unbiased estimates of mating frequency, we estimated each male's

259 rate of mating on days when he was the focal follow target. We limited analysis to matings with

260 females that had given birth (parous females) because they are more likely to conceive than

261 females who had not given birth (nulliparous females), and males compete more intensively over

262 access to parous females [59,60]. Researchers observed each male as a focal target for a median

263 of 137.8 hours annually (range 1.57–941.9 hours per male per year). Males mated with parous

264 females a median of 2 times during focal follows per year (range: 0–60 mating events per year).

265

266 *Dominance Rank*: Chimpanzees give pant-grunt vocalizations to indicate submission towards

267 higher-ranking individuals [6,61,62]. To determine relative dominance rank for each individual

268 in each year of observation, we used rank data from Foerster et al. [49], who calculated mean

269 daily Elo scores based on pant-grunt records, using a modified method that employed maximum

270 likelihood fitting to optimize starting parameters, using the EloOptimized package in R [63].

271 From these daily scores, they calculated cardinalized Elo scores, which take into account the Elo

272 scores of all males in the community and specify the probability that an individual will succeed

273 in a given contest [49,63]. Males had a median annual cardinalized daily Elo score of 0.536

274 (range 0.014–1.000).

275

276 *Hunts*: We extracted hunts from narrative notes of focal follows [46], counting hunts only if at

277 least one individual climbed in pursuit of prey. For each hunt, we extracted the identities of all

278 individuals that observers named as participants. Each male had the opportunity to join a median

13

279　of 38 hunts (range: 2–64 hunts) annually and participated in a median of 8 hunts (range: 0–39

280　hunts) annually.

281

282　*Personality*: For measures of personality traits, we use scores from Weiss et al. [50]. For this

283　study, long-term Tanzanian field researchers rated chimpanzees using a 24-item version of the

284　Hominoid Personality Questionnaire [50]. For each item, raters scored each individual on a 7-

285　point scale, based on the extent to which that individual's behavior and interactions with others

286　corresponded to a particular adjective (e.g., "Fearful," "Dominant," "Persistent"). Each adjective

287　was followed by a brief explanation of how that trait may be manifested in chimpanzees. For

288　example, researchers scored the personality dimension Dominance according to their assessment

289　that the individual "is able to displace, threaten, or take food from other chimpanzees" or that the

290　subject "may express high status by decisively intervening in social interactions" [50]. These

291　ratings were then used to estimate each chimpanzee's standing on six personality factors

292　identified in captive studies of chimpanzees [51]: Dominance, Extraversion, Agreeableness,

293　Conscientiousness, Neuroticism, and Openness. For this study, we used scores for two

294　dimensions that had high inter-observer reliability: Dominance and Conscientiousness.

295　Dominance is similar to, but not synonymous with, dominance rank. Conscientiousness can best

296　be described as the degree to which individuals are predictable and careful. Multiple researchers

297　rated each chimpanzee. Males from our sample had median scores of 4.2 for Dominance (range:

298　2.8–5.7, N=23 males) and 4.0 for Conscientiousness (range: 2.4–5.2, N=23 males).

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300   *Sighting Frequency*: To control for variation in observation time for each individual, we

301   calculated the proportion of days on which each male was recorded as present during a focal

302   follow within each observation period.

303

304   *Causal Inference:* To minimize the chances of discovering spurious or misleading relationships

305   among the variables of interest, we employed a causal inference framework to inform our

306   modeling [64,65]. We incorporated our prior understanding of causal relationships among the

307   variables using a directed acyclic graph (DAG; Figure S1). DAGs facilitate causal inference by

308   allowing researchers to identify causal relationships that result in (i) spurious statistical

309   correlations between variables and (ii) masking of real statistical correlations between variables.

310   This knowledge allows researchers to make causally informed decisions about which variables

311   should and should not be controlled for in the statistical analysis. Using the R-package DAGitty

312   [66], we specified the DAG and identified the minimally sufficient adjustment sets of

313   confounding variables to be controlled for when testing for relationships of interest in our

314   multiple regressions using the *adjustmentSets* function. A minimally sufficient adjustment set is

315   a set of variables that is sufficient to control for to obtain an unbiased estimate of the effect of an

316   independent variable on a dependent variable [65]. We summarize these sets for the relationships

317   of interest in Table 1.

318

319   *Model fitting and model selection:* We used binomial Generalized Linear Mixed Models to

320   model the relationships in Table 1. The dependent variable in each model was a binary variable

321   for either patrols, representing whether an individual participated in a given boundary patrol

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322   (N=1945 opportunities to patrol), or periphery visits, representing whether an individual

323   participated in a given periphery visit (N=1511 opportunities to participate in a periphery visit).

324   These models examined the effect of variables associated with reproductive success (mating rate,

325   age, dominance rank), costs of participation (hunting), motivation (personality scores), costs of

326   defecting (number of males ≥12 years old), and a measure of gregariousness (sighting frequency)

327   on patrolling and periphery visit behaviors. All models included individual identity as a random

328   intercept to control for individual variation. Models 2, 3, and 5 (Table 1) included additional

329   independent variables to account for their confounding effects.

330

331   We used information-theoretic model selection [67] to assess the relative importance of different

332   variables hypothesized to predict participation in patrols and other periphery visits. We used the

333   *AICcmodavg* package [68] in R to calculate each model's weight (*w*). Model weight represents

334   the probability that each model is the best model of a set of models. We used these model

335   weights to identify the best predictors of patrolling and periphery visits. Furthermore, we report

336   the unbiased estimates of the causal effects of each independent variable on patrolling and

337   periphery visits and its 95% confidence interval.

338

339   **Results**

340   **Boundary patrols and periphery visits**

341   During the study period, we documented 180 patrols and 147 other periphery visits. Thirty of the

342   180 identified boundary patrols also met the criteria to be considered periphery visits. The

343   number of such events varied from year to year (patrols, median = 4.5, range = 0–19; periphery

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344 visits, median = 4, range = 0–11). Boundary patrols (median = 88.5 minutes, range = 3–595) and

345 periphery visits (median = 90 minutes, range = 15–735) did not differ significantly in duration

346 (Mann-Whitney U test, U=13080, p=0.86, BH correction p=0.86). Boundary patrols contained

347 more individuals (patrols: median = 14 independently traveling individuals, range = 1–32;

348 periphery visits: median = 12 individuals, range = 1–47; Mann-Whitney U test, U=14922,

349 p=0.05, BH correction p=0.06), and also contained more adult males than other periphery visits

350 (patrols: median = 8 males, range = 1–13; periphery visits: median = 7 males, range = 0–13;

351 Mann-Whitney U, U=16214, p<0.01, BH correction p<0.01). After correction for multiple

352 testing, boundary patrols and periphery visits did not differ significantly in the number of adult

353 females present (patrols: median = 3 females, range = 0–20; other periphery visits: median = 2

354 females, range = 0–15; Mann-Whitney U, U=15022, p=0.03, BH correction p=0.06) or the

355 number of adult females with sexual swellings (patrols: median = 1 swollen female, range = 0–6;

356 other periphery visits: median = 1 swollen female, range = 0–4; Mann-Whitney U, U=14956,

357 p=0.03, BH correction p=0.06). Chimpanzees on boundary patrols spent less time feeding than

358 those on other periphery visits (patrols: median = 6.51 minutes per hour, range =0–60; other

359 periphery visits: median = 17.2 minutes per hour, range =0–60; Poisson regression, β=0.29, 95%

360 CI = [0.26–0.33], n_1=180 patrols, n_2=147 periphery visits, z=18.3, p<0.01).

361

Individual variation in participation

363 Over the entire study period, individuals participated in a mean of 74.5±11% of boundary patrols

364 (Figure 1). The few males with extremely low or high rates of participation were young males

365 who reached age 12 only during the last years of the study, and therefore had small sample sizes

366 (50%: *ZS*, b. 1993, N=4 patrols; 100%: *TN*, b. 1994, N = 5 patrols; 95%: *FE*, b. 1992, N = 18

367   patrols). All other males exhibited strikingly similar patrol participation rates, between 58 and

368   85%. Moreover, males identified to be present at the start of the patrol stayed for a median 96%

369   of the duration of the patrol (range = 92%–100%, N=23 males). We therefore considered each

370   male present at the start of a patrol to have participated in that patrol.

371

372   For both boundary patrols and periphery visits, information-theoretic model selection identified

373   the hunting model, which also controlled for sighting frequency and personality dimensions, to

374   be the most-likely candidate model (boundary patrols, Table 2: w=0.99, periphery visits, Table 3:

375   w=0.80), followed by the model with sighting frequency alone. Males varied considerably in the

376   percentage of days they were recorded by observers (mean = $0.52 \pm 0.13\%$ of days per year;

377   N=283 male-years). Males who were observed more frequently participated in more patrols

378   (Figure 2, β = 3.37, 95% CI = [2.42–4.35]), as did males who participated in more hunts (Figure

379   3, β = 1.83, 95% CI = [0.79–2.92]).

380

381   For the remaining variables tested, the 95% confidence interval of the parameter estimate

382   included zero. Though we therefore lack confidence in the effect of these parameters, some

383   variables had effects in the direction predicted by collective action theory: higher rank, greater

384   mating success, high scores for Dominance, and low scores for Conscientiousness correlated

385   with higher patrol participation. The estimates for periphery visits closely resembled those for

386   boundary patrols (Table 3), with the exception that males who mated more often during focal

387   follows were more likely to participate in periphery visits (β = 9.16, 95% CI = [3.90–14.69]).

388

18

389   Mating frequency is admittedly an imperfect measure of reproductive success, given that

390   chimpanzees mate promiscuously. Given that only alpha males obtain a disproportionate share of

391   paternities [48], we compared patrol participation rates for current and former alpha males with

392   those of males that never reached top rank. However, the patrol participation rate for current and

393   former alpha males (mean = 75±3%, N=8) did not differ significantly from that of males who

394   had never reached alpha status (70±3%, N=15; binomial regression, β=0.11, z=1.00, p=0.32).

395

Discussion

397   Collective action theory predicts that individuals in group-territorial species should be strongly

398   tempted to free-ride [8,14,15]. As a result, territorial effort should be undertaken

399   disproportionately by individuals that expect to gain a greater share of the spoils, or that can

400   afford the costs because they are high-ranking, strong, or highly motivated [14,16]. In contrast to

401   these expectations, we found that male chimpanzees in the Kasekela community participated in

402   patrols at an exceptionally high rate (mean = 74.5%). Kasekela males participated at more than

403   double the rate of Ngogo males (mean = 33%), which Langergraber et al. [19] considered to be

404   higher than expected from collective action theory. Moreover, we found little evidence that

405   individual traits, such as rank, mating rate, or age explained variation in patrolling. Instead, all

406   Kasekela males participated in at least half of all boundary patrols. Recent paternity analysis at

407   Gombe indicate that the alpha male obtains a disproportionate share of paternities in Kasekela

408   [48]. Despite these reproductive benefits, current and former alpha males did not patrol at

409   significantly higher rates than other males. Indeed, one male that we excluded from our analysis

410   because he was not a potential father (*PX*) nonetheless participated in patrols at a high rate

19

411   (78.4%; Figure 1; Supplementary Figure 1D); higher, indeed, than some males (e.g., *FR, SL*) that

412   attained alpha status and sired many offspring.

413

414   Why did Kasekela males join patrols at such high rates, regardless of their rank or mating rate?

415   Potential motivating factors include (1) a broader than expected distribution of benefits; (2)

416   lower than expected costs of participation; (3) effects of group size; and (4) benefits of

417   gregariousness.

418

Distribution of benefits

419   ***Distribution of benefits***

420   If males participate in patrols mainly to benefit their own current or future offspring, then

421   correlates of reproductive success, such as rank, mating rate, and age, should predict patrol

422   participation. However, we did not find strong effects of rank, mating rate, or age on patrol

423   participation. One possible explanation for this is that the benefits of territorial behavior are

424   distributed broadly enough that each male has a strong incentive to participate. This is the

425   perspective of group augmentation theory: if individual survival and reproduction depend

426   strongly on group size, then each individual can be motivated to invest in increasing group size,

427   even if reproductive skew is high [19,20]. All males participate because they all benefit from

428   raising more future fighters to defend their community.

429

430   ***Costs of participation***

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431   Based on collective action theory, we expected to find evidence that males with individual traits

432   that made patrolling less costly for them would patrol more often. Males that hunt frequently

433   might also be expected to be good fighters; and individuals with certain behavioral tendencies or

434   personality traits might be more strongly motivated to patrol. Males that hunted more did patrol

435   more as well — though the possibility exists that this correlation results, at least to some extent,

436   from the fact that both patrols and hunting occur more often when males group together and

437   travel long distances [46]. Personality scores correlated in the expected directions with

438   patrolling, but the model including personality scores received weak support. This may partially

439   result from the temporal scale of these measures. The personality questionnaire produced a single

440   value for each personality dimension for each individual whereas hunting observations reflected

441   the behavior of each individual in a given year. Yet, we found substantial variation in patrol

442   participation rates both between individuals and within individuals over their lifetime

443   (Supplemental Figure 1). Thus, the personality questionnaire may not be capturing this variation

444   fully.

445

446   While patrols entail energetic and physiological costs [38–40], they may also provide direct

447   benefits to patrollers, such as providing opportunities to find food and females in areas that

448   would otherwise be unsafe to visit. While chimpanzees spent less time feeding during patrols

449   than other visits to the far periphery, patrols nonetheless may provide opportunities to find

450   remote food resources and assess the safety of visiting them. Traveling in large groups may also

451   provide increased opportunities to eat meat. Hunting and patrolling are temporally correlated,

452   because both are more likely to occur when parties contain many males and travel long distances

453   [46]. In our dataset, 26% of patrols (N=47) took place on the same day that a hunt occurred.

21

454   With all of these direct benefits from patrol participation, the temptations to free-ride may in fact

455   be low.

456

457   Additionally, while we might expect patrols to be costly because of the increased risk of

458   encountering neighbors, the costs of such encounters might in fact be low, provided chimpanzees

459   travel in sufficiently large parties. Because chimpanzees prefer to attack when they greatly

460   outnumber their opponents [22,42], attackers rarely suffer injuries in intergroup fights. Indeed, if

461   traveling with many males in the periphery, staying with those males is likely safer than

462   attempting to defect by dropping away. Both chimpanzees [35] and another group territorial

463   species, lions [41] exhibit low rates of defection in response to simulated intruders.

464

465   *Group size effects*

466   Following Olson's [15] argument that collective action is more effective in smaller groups, Watts

467   and Mitani [18] predicted that participation in boundary patrols would be more consistent

468   amongst males living in smaller communities. We found mixed support for this prediction. As

469   noted above, Kasekela males participated in a much larger percentage of patrols than males in

470   the much larger Ngogo community. Nonetheless, in our analysis, the model including the

471   number of males received weak support, and the parameter estimate was positive instead of

472   negative. Perhaps the number of males in Kasekela during our study period (7–13 males)

473   remained within a range conductive to collective action in chimpanzees.

474

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475   The mean participation rate in patrols is mathematically a function of the mean number of males

476   patrolling and the mean total number of males in the community. For Kasekela, these numbers

477   yield an expected participation rate of 8/11 = 0.73, close to the observed mean of 74.5%. If

478   safety requires an average of 8 males to patrol, then either 73% of males will need to participate

479   100% of the time, or each male must participate on average 73% of the time. Similarly, at

480   Ngogo, patrols contained a mean 37.5% of the group's males, similar to the mean rate of

481   participation (33%) [19]. Kasekela differs strikingly from Ngogo both in the higher overall rate

482   of participation, the much narrower range of participation among males (Kasekela: range = 50-

483   100%; Ngogo: range = 2–74%)

484

Benefits of gregariousness

486   The factor that best predicted participation in patrols by Kasekela males was sighting frequency,

487   which likely reflects gregariousness. Males that spend more time with other chimpanzees are

488   more likely to be observed by researchers, and also more likely to be present when a patrol starts.

489   Males likely gain many benefits from gregariousness, including opportunities for mating,

490   grooming, coalition building, and hunting. The costs of patrolling may thus be negligible

491   compared to these benefits of socializing.

492

493   In summary, our study provides further insight into how collective action problems are solved in

494   nature. In contrast to expectations that group territorial effort would be undertaken primarily by

495   those males with more to gain, we found that males consistently participated in patrols at a high

496   rate. Participation may be encouraged by an even distribution of the benefits accrued to

23

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497   individuals, an increased cost of defection in smaller groups, and/or direct benefits from

498   travelling in large parties.

24

499   Table 1: Minimally sufficient adjustment sets (i.e. confounding variables to control for) for the

500   tests of relationships of interest.

Model ID	Relationship of interest	Dependent variable (DV) Independent variable (IV)	Confounding variables to control for
1	Patrolling/Periphery Visits <— Age	DV: Patrolling or Periphery Visits IV: Age	None
2	Patrolling/Periphery Visits <— Rank	DV: Patrolling or Periphery Visits IV: Rank	1) Personality, if model 1 relationship does not hold 2) Personality & Age, if model 1 relationship holds
3	Patrolling/Periphery Visits <— Mating	DV: Patrolling or Periphery Visits IV: Mating	1) Personality, if neither model 1 or 2 relationships hold 2) Personality & Age, if model 1 relationship holds AND model 2 relationship does not hold 3) Personality & Rank, if model 2 relationship holds
4	Patrolling/Periphery Visits <— No. of Adult males	DV: Patrolling or Periphery Visits IV: No. of Adult males	None
5	Patrolling/Periphery Visits <— Hunting	DV: Patrolling or Periphery Visits IV: Hunting	Personality & Sighting Frequency
6	Patrolling/Periphery Visits <— Personality	DV: Patrolling or Periphery Visits IV: Personality	None
7	Patrolling/Periphery Visits <— Sighting Frequency	DV: Patrolling or Periphery Visits IV: Sighting Frequency	None

25

Table 2. Information-Theoretic Model Selection Results: Boundary Patrols

Model	Intercept	Age	Mating	Rank	Adult males in the community	Hunting Participation	Dominance	Conscientious-ness	Sighting Frequency	K	Δ_i	w_i
Hunting	-1.52					1.83	0.21	-0.08	2.82	6	0.00	0.99
Observation Frequency	-0.73								3.37	3	9.18	0.01
Total Males	0.20				0.08					3	54.97	0.00
Rank	0.97			0.38			0.13	-0.18		5	56.76	0.00
Personality	1.28						0.14	-0.22		4	56.93	0.00
Mating Frequency	1.26		2.45				0.13	-0.22		5	58.31	0.00
Age	1.03	0.00								3	58.69	0.00
Model-Averaged Parameter	-1.51	0.00	2.45	0.38	0.08	**1.83**	0.21	-0.08	**2.82**			
2.5%	-3.51	-0.02	-3.34	-0.11	0.00	**0.77**	-0.08	-0.38	**1.81**			
97.5%	0.5	0.02	8.23	0.86	0.16	**2.89**	0.50	0.23	**3.84**			

Bolded values indicate variables with non-zero model averaged parameter estimates. Parameters include the intercept; Elo rank; operational sex ratio; age; age^2; patrol participation, periphery visit participation, hunting participation; Dominance, Conscientiousness; the number of free parameters (K); the difference in Akaike information criterion between the ith model and the best model (Δ_i); and model weight (w_i). Models are arranged in order from best (lowest ΔAICc) to worst (highest ΔAICc). The weight of the model (w_i) is the probability that a given model is the best model in a given set of models. Model-averaged parameter estimates (MAP) with upper (97.5%) and lower (2.5%) bounds of the 95% confidence intervals are given in the bottom rows.

Table 3. Information-Theoretic Model Selection Results: Periphery Visits

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Model	Intercept	Age	Mating	Rank	Adult males in the community	Hunting Participation	Dominance	Conscientious-ness	Sighting Frequency	K	Δ_i	w_i
Hunting	-1.82					1.27	0.02	0.00	3.73	6	0.00	0.80
Sighting Frequency	-1.74								4.41	3	0.73	0.20
Mating Frequency	0.78		9.16				0.01	-0.11		5	64.63	0.00
Age	0.97	-0.02								3	69.55	0.00
Total Males	0.41				0.01					3	72.89	0.00
Personality	0.98			-0.28			-0.01	-0.10		4	74.61	0.00
Rank	1.17			-0.30			0.00	-0.12		5	75.61	0.00
Model-Averaged Parameter	**-1.80**	-0.02	**9.16**	-0.30	0.01	**1.27**	0.00	-0.10	**3.87**			
2.5%	**-3.06**	-0.04	**3.77**	-0.87	-0.06	**0.39**	-0.21	-0.38	**2.65**			
97.5%	**-0.54**	0.00	**14.55**	0.27	0.09	**2.14**	0.20	0.18	**5.09**			

Bolded values indicate variables with non-zero model averaged parameter estimates. Parameters include the intercept; Elo rank; operational sex ratio; age; age^2; patrol participation, periphery visit participation, hunting participation; Dominance, Conscientiousness; the number of free parameters (K); the difference in Akaike information criterion between the ith model and the best model (Δ_i); and model weight (w_i). Models are arranged in order from best (lowest ΔAICc) to worst (highest ΔAICc). The weight of the model (w_i) is the probability that a given model is the best model in a given set of models. Model-averaged parameter estimates (MAP) with upper (97.5%) and lower (2.5%) bounds of the 95% confidence intervals are given in the bottom row.

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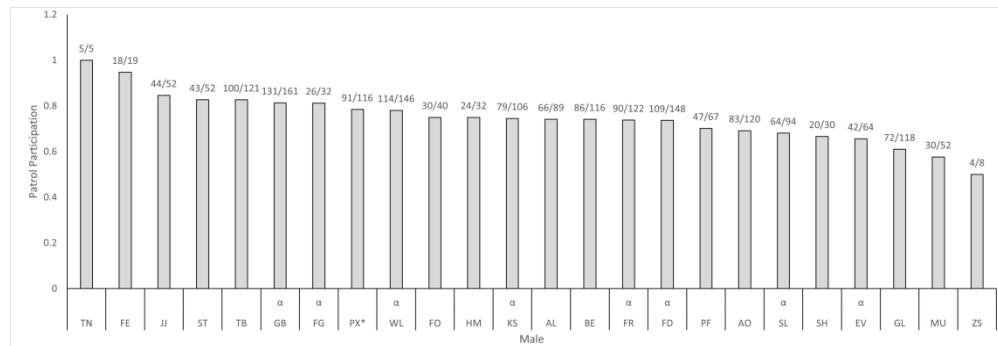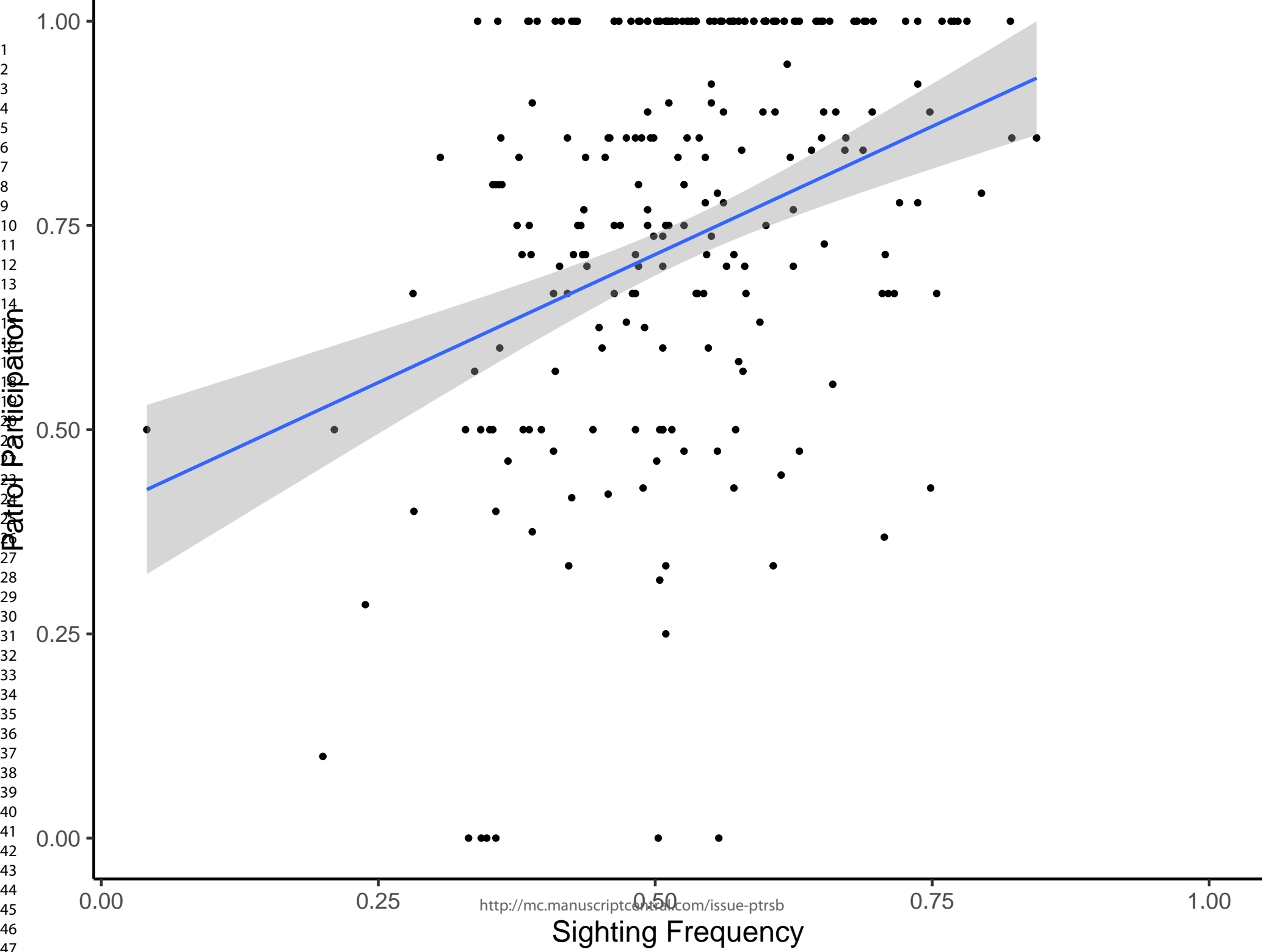45
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Figure 1. Boundary patrol participation for 24 Kasekela males. Column height indicates the percentage of patrols that each individual participated in while >12 years old. Numbers above the columns indicate the total number of patrols that each individual joined (numerator), and the number of patrols recorded while that individual was alive and ≥12 years old (denominator). All current and former alpha males are labeled with an alpha (α). Here, we include PX, who suffered a scrotal wound at a young age and was effectively castrated. We excluded PX from analyses.

295x100mm (300 x 300 DPI)

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