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4 1 Correlates of individual participation in boundary patrols by male chimpanzees

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51 18 Key words: intergroup aggression; territorial behaviour; collection action problems; boundary

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54 19 patrols; hunting; *Pan troglodytes*

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3 20 Group territory defense poses a collective action problem: individuals can free-ride, benefiting
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5 21 without paying the costs. Individual heterogeneity has been proposed to solve such problems, as
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8 22 individuals high in reproductive success, rank, fighting ability, or motivation may benefit from
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10 23 defending territories even if others free-ride. To test this hypothesis, we analyzed 30 years of
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12 24 data from chimpanzees (*Pan troglodytes*) in the Kasekela community, Gombe National Park,
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14 25 Tanzania (1978-2007). We examined the extent to which individual participation in patrols
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16 26 varied according to correlates of reproductive success (mating rate, rank, age), fighting ability
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18 27 (hunting), motivation (scores from personality ratings), costs of defecting (the number of adult
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20 28 males in the community), and gregariousness (sighting frequency). In contrast to expectations
21
22 29 from collective action theory, males participated in patrols at consistently high rates (mean \pm
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24 30 S.D. = $74.5 \pm 11.1\%$ of patrols, $n=23$ males). The best predictors of patrol participation were
25
26 31 sighting frequency, age, and hunting participation. Current and former alpha males did not
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28 32 participate at a higher rate than males that never achieved alpha status. These findings suggest
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30 33 that the temptation to free-ride is low, and that a mutualistic mechanism such as group
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32 34 augmentation may better explain individual participation in group territorial behavior.
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3 35 Many group-living mammals defend group territories (e.g., meerkats, *Suricata suricatta* [1]; free-
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5 36 ranging dogs, *Canis lupus familiaris* [2]; lions, *Panthera leo* [3]; ring-tailed lemurs, *Lemur catta*
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7 [4]; white-faced capuchins, *Cebus capucinus* [5]; chimpanzees, *Pan troglodytes* [6]; primates in
8
9 general [7,8]). These territories provide benefits to group members, including resources such as
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11 38 food, water, and shelter [9–12], and safety from intergroup attacks [13]. These benefits are public
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13 39 goods, because group members can obtain these benefits regardless of whether they have paid
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15 40 the costs of production [14]. This poses a collective action problem [15]: insofar as territorial
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17 41 effort is costly, individuals will be tempted to free-ride, benefiting from the public goods without
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19 42 paying the costs. But if all individuals free-ride, the good will not be produced. A group
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21 43 composed entirely of free-riders eventually will have no territory to defend. What motivates
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23 44 individuals to participate in territorial behavior, despite the temptation to defect?
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34 47 Heterogeneity among individuals has been proposed as a solution to this collective action
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36 48 problem [16]. Although assuming homogeneity among group members can make mathematical
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38 49 models of behavior easier to construct, in the real world, individuals are unlikely to be identical
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40 50 to one another [17]. Individuals may vary in their fighting ability or tolerance of risk, and thus
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42 51 experience differing costs from participation in territorial behavior. Additionally, despite
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44 52 assumptions of earlier models, public goods are not necessarily shared equally. Individuals with
45
46 53 high dominance rank may produce a disproportionate share of offspring, which then benefit from
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48 54 the food resources and safety provided by their parent's territorial effort. Thus, apparently
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50 55 altruistic territorial behavior could instead result from heterogeneity in individual costs,
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52 56 propensities, or benefits of participation in collective action [16,17].
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3 58 Findings from field studies of chimpanzees (*Pan troglodytes*) have supported this theoretical
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5 59 expectation. In the Ngogo community of Kibale National Park, Uganda, individual participation
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7 60 in boundary patrols by male chimpanzees correlated with measures of reproductive success,
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10 61 rank, and hunting success [18]. These findings have since been partially supported by a follow-
11
12 62 up study examining 20 years of data from Ngogo [19], which found that males participated more
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14 63 in patrolling if they had more offspring and were high in dominance rank. Additionally, they
15
16 64 found that males patrolled more when the group had fewer males, suggesting that males
17
18 65 increased participation when the costs of defecting were higher [19]. However, this study also
19
20 66 found results contrary to some predictions of collective action theory. In particular, males had
21
22 67 generally high rates of participation, with each male participating in a mean of 33% of patrols.
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24 68 Additionally, despite the expectation that patrolling should be based on reproductive success,
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26 69 some males that had no offspring in the group participated frequently in patrols. Based on these
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28 70 and other considerations, Langergraber and colleagues [19] proposed that a group augmentation
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30 71 model was a better predictor of individual participation in patrols.
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39 73 Group augmentation theory was developed to explain why helpers in cooperatively breeding
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41 74 species delay or even forgo their own reproduction to help others raise young [20]. If individuals
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43 75 survive or reproduce better in larger groups, then they may benefit from the increased production
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45 76 of new group members, even if they are unrelated. Applying this logic to chimpanzees,
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47 77 Langergraber and colleagues [19] argued that because reproductive skew is generally low among
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49 78 male chimpanzees, and all males depend on successful defense of a territory to ensure safety and
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51 79 sufficient food for themselves, their mates and their offspring, individuals have lower incentives
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53 80 for free-riding than predicted by a collective action framework.
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6 82 To provide an additional test of factors affecting individual participation in territorial behavior,
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8 83 we examined data from the Kasekela community of chimpanzees in Gombe National Park,
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10 84 Tanzania. The Ngogo community is exceptionally large, with up to 206 members [19].
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12 85 Additionally, this community fissioned into two mutually hostile communities in 2017 [21].
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14 86 Given the expectation that larger group size exacerbates collective action problems, and the
15
16 87 possibility that substructuring within Ngogo affected patterns of cooperation in that community,
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18 88 we sought to test whether similar patterns held in a community that is more typical in size, and
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20 89 not undergoing a fission. With a median population of 50 individuals (range 39–61, 1978–2007,
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22 90 the Kasekela community is close to the median size for chimpanzee communities in long-term
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24 91 studies (median = 42.3 members; range: 6.7–144; including a median 8.2 males (range: 1.9–37)
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26 92 and 14.4 females (range: 2.1–51) at least 12 years old; N = 18 communities [22]), Additionally,
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28 93 by using 30 years of data, we sought to explore how individual participation in boundary patrols
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30 94 varies across the male lifespan.
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41 96 Chimpanzees have been studied intensively at multiple long-term field sites [23–26].
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43 97 Chimpanzees live in groups (‘communities’ [6] or ‘unit-groups’ [27]) that exhibit fission-fusion
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45 98 dynamics, in which individuals travel in subgroups (‘parties’) that vary in size and composition
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47 99 [6,28]. Male chimpanzees defend group territories and maintain hostile relations with neighbors
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49 100 [6,29,30], sometimes killing members of other groups [22,31]. Chimpanzees conduct boundary
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51 101 patrols, during which parties, often mainly of males, travel to the periphery of their range,
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53 102 behaving as if they are searching for signs of chimpanzees from other communities [6,18,29].
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55 103 Males can adjust their participation in boundary patrols by associating with or avoiding parties
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3 104 with many males, which are more likely to visit boundaries [32], or by going with or staying
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5 105 behind if a party travels towards the periphery [19,33]. Intergroup encounters occur most
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7 106 frequently when seasonally abundant fruit attracts members of rival communities to borderlands
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9
10 107 [33]. Participating in a patrol also likely increases the chances of encountering neighbors. Most
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12 108 intergroup encounters involve only auditory contact, in which individuals hear vocalizations
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14 109 from distant chimpanzees, and may respond with vocalizations of their own [33,34], and/or
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16 110 approach or retreat, depending on their apparent relative numerical strength [33,35,36]. If
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18 111 chimpanzees come within visual range, they may chase, attack, and sometimes kill members of
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20 112 rival groups [30,34,37]. Intergroup killings occur mainly when attackers greatly outnumber
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22 113 victims (median ratio of attackers to victims = 8:1 [22]).
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30 115 Winners of intergroup contests may increase their territory size [6,37], which can result in
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32 116 community-wide benefits, particularly increased access to food resources, as indicated by
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34 117 heavier body mass [10] and larger parties [9] in years with larger territory size. Increased food
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36 118 provides fitness benefits: in years with larger territory size, females have shorter interbirth
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38 119 intervals [9,12]. Thus, group territorial effort creates the public good of increased food supply.
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40 120 Additionally, communities with larger territories suffer lower rates of intergroup mortality,
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42 121 perhaps as a consequence of reduction in the relative size of the periphery as the territory
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44 122 increases in area [13].
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52 124 Participating in patrols appears to be costly for individuals, as traveling further incurs energetic
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54 125 [38] and physiological costs from higher levels of cortisol [39] and testosterone [40]. Insofar as
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3 126 patrolling borders increases the likelihood of meeting and fighting with members of rival
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5 127 communities, participating in patrols potentially increases risks of injury or death.
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11 129 While the collective action framework focuses on how these costs may promote free-riding, two
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13 130 factors may mitigate these costs. First, as Langergraber et al. [19] argue, the benefits of territorial
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15 131 effort may be distributed more evenly than would appear from a focus on individual differences.
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17 132 In a world divided among competing social groups, individual survival and reproduction may
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19 133 depend so critically on intergroup effort that all individuals or all individuals of a particular sex
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21 134 are motivated to participate, such that participation in territorial behavior evolves through
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23 135 mutualistic benefits, as in lions [41]. Second, while patrolling incurs energetic and physiological
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25 136 costs, these may be offset by various direct benefits to patrollers. Traveling with many males
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27 137 reduces the risks of being injured or killed [30,42,43], and traveling to the periphery may provide
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29 138 opportunities to find and exploit new food resources [33], monitor females with peripheral home
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31 139 ranges [44], recruit new females [45], and participate in other activities that benefit from larger
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33 140 numbers of males, such as hunting [46].
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43 142 In the present study, we tested four sets of variables predicted to promote individual participation
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45 143 in boundary patrols. First, according to the collective action problem framework, individuals
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47 144 should participate according to their expected returns [15,16]. Insofar as males defend a feeding
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49 145 territory for themselves, their mates and offspring, males with more mating opportunities and
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51 146 more existing offspring stand to benefit more. Because we do not have genetic paternity data for
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53 147 the early decades of the study, we considered three main proxies of reproductive success: mating
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3 148 rate, age, and dominance rank. In the short term, males that mate more frequently with fertile
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5 149 females should have a higher chance of siring offspring. In the long-term, if males continue to
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8 150 sire offspring, older males should have more offspring. High-ranking males sire more offspring
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10 151 [47], although recent analysis indicates that only the highest-ranking males (“alphas”) sire a
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12 152 disproportionate share [48].
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18 154 Second, collective action theory predicts that individuals may contribute territorial effort if the
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20 155 costs of doing so are low, because they are strong fighters and/or highly motivated [16]. In male
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22 156 chimpanzees, dominance rank typically peaks in early adulthood [49], and thus likely reflects
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24 157 peak physical condition and competitive ability, in addition to being correlated with reproductive
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26 158 success as discussed above. We considered two additional factors associated with individual
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28 159 fighting ability and motivation: hunting and personality ratings. Chimpanzees engage in group-
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30 160 level hunts of monkeys, which like intergroup contests involve collective efforts to attack and
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32 161 kill victims [46]. Watts and Mitani [18] found that at Ngogo, male participation rates in hunting
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34 162 correlated with patrolling frequency. For measures of motivation, we considered scores derived
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36 163 from ratings of chimpanzee personality by long-term researchers [50]. We considered scores for
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38 164 two dimensions expected to correlate with willingness to patrol boundaries: Dominance and
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40 165 Conscientiousness. These personality dimensions are derived differently and independently from
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42 166 behavioral measures such as dominance rank. Based on studies of personality in captive
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44 167 chimpanzees [51,52], we predict that individuals with high Dominance scores should patrol more
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46 168 often, due to being bolder, and that individuals with low Conscientiousness scores should patrol
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48 169 more often, due to reduced concern for the associated risks.
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3 171 Third, the “group size paradox” contends that collective action should break down more readily
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5 172 in larger groups due to increased opportunity for free-riders and decreased benefits for
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7 173 individuals [15]. Studies of individual species [2,5,19] and comparative analysis [8] indicate that
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9 174 cooperative investment decreases with increase in group size. Because chimpanzees are more
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11 175 likely to initiate boundary patrols when traveling in larger parties [43], in communities with
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13 176 fewer males, a larger proportion of males may be required to mount an effective patrol.
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15 177 Furthermore, individuals may be more sensitive to the costs of defecting when in smaller groups,
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17 178 because each individual’s contribution matters more to the success of the collective effort. In this
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19 179 case, individual participation in boundary patrols should increase when the number of males in
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21 180 the community is low.
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31 182 Fourth, variation in patrolling frequency potentially reflects differences in gregariousness, or an
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33 183 individual's propensity to travel in larger groups. Because patrols typically involve parties with
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35 184 many males, an individual who rarely spends time traveling in large parties will likely participate
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37 185 in patrols less frequently. To control for this possibility, we included a measure of sighting
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39 186 frequency, the proportion of days on which an individual was observed.
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45 188 **Methods**

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48 189 *Study site:* The site of long-term chimpanzee research since 1960 [6], Gombe National Park
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50 190 (4°40'S 29°38'E) covers a rugged landscape with a land area of 35.69 km² along the shore of
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52 191 Lake Tanganyika as well as 20.72 km² of the lake itself [53]. During our study period, three
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54 192 chimpanzee communities lived in Gombe. We analyze data from the Kasekela community,
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3 193 which occupied a large range at the center of Gombe during our study period (1978-2007;
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5 194 median=12.17 km², range 5.30–19.16 km²), with a median population of 50 individuals (1978-
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8 195 2007, range 39–61, n=30 years). To the north, the Mitumba community (1994-2007;
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10 196 median=4.63 km², range 3.19–5.91 km²) had a median population of 22 individuals (range 20–
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12 197 25, 1996–2007). To the south, the Kalande community [54], remained unhabituated for most of
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14
15 198 this study period. Observational monitoring and non-invasive genetic sampling indicated that
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17 199 Kalande had a median population of 14.5 individuals (range 12–19, 2001–2007). Both
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19 200 communities were likely larger and more formidable earlier in the study period [54,55].
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25 202 In Kasekela, researchers conducted all-day focal follows of individual chimpanzees on a nearly
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27 203 daily basis [56]. Chimpanzees use branches to make simple sleeping platforms in trees each
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29 204 night. Ideally, follows started at the focal target's sleeping site before dawn, and continued until
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31 205 the target nested that night. Observers recorded party location at 15-minute intervals while
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33 206 maintaining a continuous record of party composition and focal feeding behavior. While
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35 207 following the focal subject, one researcher wrote an *ad libitum* narrative of the day's events,
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37 208 noting the time and individuals involved in all observed occurrences of selected behaviors,
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39 209 including aggression, mating, boundary patrols, and intercommunity interactions. Observers
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41 210 documented the reproductive state of all adult females seen each day, based on the size of
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43 211 anogenital sexual swellings [57], and recorded the dates of births, deaths, and changes in
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45 212 community membership.
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3 214 *Study Subjects:* We analyzed 30 years of behavioral observations of male chimpanzees of the
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5 215 Kasekela community, starting with the first year for which daily dominance hierarchy data have
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7 216 been calculated (1978 [49]) and ending with the most recent year for which boundary patrol data
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9 217 have been extracted (2007 [46]). To include all potential sires, we included males starting from
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11 218 12 years old, the age of the youngest known sire from Gombe [47]. We refer to these males as
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13 219 “adult males,” though we recognize that most males do not reach full adult size and behavior
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15 220 until later. Our sample included 23 males that were ≥ 12 years old during the study period,
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17 221 excluding from analysis one male (*PX*) who was effectively castrated by a scrotal injury at a
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19 222 young age [6]. We calculated annual records for each male, which resulted in 283 male-years
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21 223 with complete data, with a median of 12 years per male (range = 2–22 years), during which
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23 224 males had a median age of 22.8 years (range = 12.1–40.6 years). Because some males reached 12
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25 225 years of age and/or died part way through the year, observation days per year ranged from 20 to
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27 226 366 days (median=365 days). We calculated the mean number of adult males present in the
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29 227 community each year based on the number of days each male was known to be alive and ≥ 12
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31 228 years old. Over these years, Kasekela had a median of 11.1 males (range = 7.6–13.0 males).
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41 230 *Boundary Patrols:* We extracted boundary patrols from long-term records, based on explicit
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43 231 statements that chimpanzees were patrolling, and descriptions of cautious travel where
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45 232 individuals appeared to be looking and/or listening for chimpanzees from neighboring
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47 233 communities [46]. We considered all adult males present in the party at the start of the boundary
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49 234 patrol to be participants. We used records of party composition to calculate the proportion of
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51 235 time each participant stayed for each patrol.
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3 237 Periphery Visits: To capture any visits to the far periphery missed by our method of extracting
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5 238 boundary patrols, we used map location data to identify all occasions on which parties traveled \geq
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7 239 3 standard deviations north or south of the annual north-south range center. We chose this
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9 240 benchmark as it identified periphery visits on approximately the same order as boundary patrols.
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11 241 Kasekela faced intergroup threats to the north (Mitumba) and south (Kalande), but not from Lake
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13 242 Tanganyika to the west, or the human-dominated village lands to the east. Any boundary patrols
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15 243 that also met the criteria for periphery visits were considered solely as boundary patrols for
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17 244 purposes of analysis. We identified all adult Kasekela males present during a periphery visit as
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19 245 participants. We considered all adult Kasekela males alive at the time, but absent from the visit,
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21 246 to be non-participants.
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29 248 *Comparison of boundary patrols and periphery visits:* Visits to the periphery could serve other
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31 249 purposes, such as searching for food or females. We therefore compared party composition and
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33 250 feeding behavior during each of these two categories of event, using a set of boundary patrols
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35 251 (N=180) and periphery visits (N=147) for which we had complete party composition and feeding
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37 252 data. We used Mann-Whitney U-tests with corrections for the false discovery rate [58] to test for
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39 253 differences in party size, number of adult males, and number of adult females. We used Poisson
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41 254 regression to compare time spent feeding during boundary patrols and periphery visits. We
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43 255 modeled minutes spent feeding, including the individual as a random intercept, and log(duration
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45 256 of patrol or periphery visit) as an offset.
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3 258 *Mating Frequency*: To obtain unbiased estimates of mating frequency, we estimated each male's
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5 259 rate of mating on days when he was the focal follow target. We limited analysis to matings with
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7 260 females that had given birth (parous females) because they are more likely to conceive than
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10 261 females who had not given birth (nulliparous females), and males compete more intensively over
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12 262 access to parous females [59,60]. Researchers observed each male as a focal target for a median
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14 263 of 137.8 hours annually (range 1.57–941.9 hours per male per year). Males mated with parous
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16 264 females a median of 2 times during focal follows per year (range: 0–60 mating events per year).
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23 266 *Dominance Rank*: Chimpanzees give pant-grunt vocalizations to indicate submission towards
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25 267 higher-ranking individuals [6,61,62]. To determine relative dominance rank for each individual
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27 268 in each year of observation, we used rank data from Foerster et al. [49], who calculated mean
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29 269 daily Elo scores based on pant-grunt records, using a modified method that employed maximum
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31 270 likelihood fitting to optimize starting parameters, using the EloOptimized package in R [63].
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33 271 From these daily scores, they calculated cardinalized Elo scores, which take into account the Elo
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35 272 scores of all males in the community and specify the probability that an individual will succeed
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37 273 in a given contest [49,63]. Males had a median annual cardinalized daily Elo score of 0.536
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39 274 (range 0.014–1.000).
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47 276 *Hunts*: We extracted hunts from narrative notes of focal follows [46], counting hunts only if at
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49 277 least one individual climbed in pursuit of prey. For each hunt, we extracted the identities of all
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51 278 individuals that observers named as participants. Each male had the opportunity to join a median
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3 279 of 38 hunts (range: 2–64 hunts) annually and participated in a median of 8 hunts (range: 0–39
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5 280 hunts) annually.
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11 282 *Personality*: For measures of personality traits, we use scores from Weiss et al. [50]. For this
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13 283 study, long-term Tanzanian field researchers rated chimpanzees using a 24-item version of the
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15 284 Hominoid Personality Questionnaire [50]. For each item, raters scored each individual on a 7-
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17 285 point scale, based on the extent to which that individual’s behavior and interactions with others
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19 286 corresponded to a particular adjective (e.g., “Fearful,” “Dominant,” “Persistent”). Each adjective
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21 287 was followed by a brief explanation of how that trait may be manifested in chimpanzees. For
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23 288 example, researchers scored the personality dimension Dominance according to their assessment
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25 289 that the individual “is able to displace, threaten, or take food from other chimpanzees” or that the
26
27 290 subject “may express high status by decisively intervening in social interactions” [50]. These
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29 291 ratings were then used to estimate each chimpanzee’s standing on six personality factors
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31 292 identified in captive studies of chimpanzees [51]: Dominance, Extraversion, Agreeableness,
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33 293 Conscientiousness, Neuroticism, and Openness. For this study, we used scores for two
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35 294 dimensions that had high inter-observer reliability: Dominance and Conscientiousness.
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37 295 Dominance is similar to, but not synonymous with, dominance rank. Conscientiousness can best
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39 296 be described as the degree to which individuals are predictable and careful. Multiple researchers
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41 297 rated each chimpanzee. Males from our sample had median scores of 4.2 for Dominance (range:
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43 298 2.8–5.7, N=23 males) and 4.0 for Conscientiousness (range: 2.4–5.2, N=23 males).
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3 300 *Sighting Frequency*: To control for variation in observation time for each individual, we
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5 301 calculated the proportion of days on which each male was recorded as present during a focal
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7 302 follow within each observation period.
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13 304 *Causal Inference*: To minimize the chances of discovering spurious or misleading relationships
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15 305 among the variables of interest, we employed a causal inference framework to inform our
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17 306 modeling [64,65]. We incorporated our prior understanding of causal relationships among the
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19 307 variables using a directed acyclic graph (DAG; Figure S1). DAGs facilitate causal inference by
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21 308 allowing researchers to identify causal relationships that result in (i) spurious statistical
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23 309 correlations between variables and (ii) masking of real statistical correlations between variables.
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25 310 This knowledge allows researchers to make causally informed decisions about which variables
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27 311 should and should not be controlled for in the statistical analysis. Using the R-package DAGitty
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29 312 [66], we specified the DAG and identified the minimally sufficient adjustment sets of
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31 313 confounding variables to be controlled for when testing for relationships of interest in our
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33 314 multiple regressions using the *adjustmentSets* function. A minimally sufficient adjustment set is
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35 315 a set of variables that is sufficient to control for to obtain an unbiased estimate of the effect of an
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37 316 independent variable on a dependent variable [65]. We summarize these sets for the relationships
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39 317 of interest in Table 1.
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49 319 *Model fitting and model selection*: We used binomial Generalized Linear Mixed Models to
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51 320 model the relationships in Table 1. The dependent variable in each model was a binary variable
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53 321 for either patrols, representing whether an individual participated in a given boundary patrol
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3 322 (N=1945 opportunities to patrol), or periphery visits, representing whether an individual
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5 323 participated in a given periphery visit (N=1511 opportunities to participate in a periphery visit).
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8 324 These models examined the effect of variables associated with reproductive success (mating rate,
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10 325 age, dominance rank), costs of participation (hunting), motivation (personality scores), costs of
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12 326 defecting (number of males ≥ 12 years old), and a measure of gregariousness (sighting frequency)
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14 327 on patrolling and periphery visit behaviors. All models included individual identity as a random
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16 328 intercept to control for individual variation. Models 2, 3, and 5 (Table 1) included additional
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18 329 independent variables to account for their confounding effects.
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25 331 We used information-theoretic model selection [67] to assess the relative importance of different
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27 332 variables hypothesized to predict participation in patrols and other periphery visits. We used the
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29 333 *AICcmodavg* package [68] in R to calculate each model's weight (w). Model weight represents
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31 334 the probability that each model is the best model of a set of models. We used these model
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33 335 weights to identify the best predictors of patrolling and periphery visits. Furthermore, we report
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35 336 the unbiased estimates of the causal effects of each independent variable on patrolling and
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37 337 periphery visits and its 95% confidence interval.
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43 44 45 339 **Results**

46 47 48 340 **Boundary patrols and periphery visits**

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51 341 During the study period, we documented 180 patrols and 147 other periphery visits. Thirty of the
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53 342 180 identified boundary patrols also met the criteria to be considered periphery visits. The
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55 343 number of such events varied from year to year (patrols, median = 4.5, range = 0–19; periphery

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3 344 visits, median = 4, range = 0–11). Boundary patrols (median = 88.5 minutes, range = 3–595) and
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5 345 periphery visits (median = 90 minutes, range = 15–735) did not differ significantly in duration
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7 346 (Mann-Whitney U test, $U=13080$, $p=0.86$, BH correction $p=0.86$). Boundary patrols contained
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9 347 more individuals (patrols: median = 14 independently traveling individuals, range = 1–32;
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11 348 periphery visits: median = 12 individuals, range = 1–47; Mann-Whitney U test, $U=14922$,
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13 349 $p=0.05$, BH correction $p=0.06$), and also contained more adult males than other periphery visits
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15 350 (patrols: median = 8 males, range = 1–13; periphery visits: median = 7 males, range = 0–13;
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17 351 Mann-Whitney U, $U=16214$, $p<0.01$, BH correction $p<0.01$). After correction for multiple
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19 352 testing, boundary patrols and periphery visits did not differ significantly in the number of adult
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21 353 females present (patrols: median = 3 females, range = 0–20; other periphery visits: median = 2
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23 354 females, range = 0–15; Mann-Whitney U, $U=15022$, $p=0.03$, BH correction $p=0.06$) or the
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25 355 number of adult females with sexual swellings (patrols: median = 1 swollen female, range = 0–6;
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27 356 other periphery visits: median = 1 swollen female, range = 0–4; Mann-Whitney U, $U=14956$,
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29 357 $p=0.03$, BH correction $p=0.06$). Chimpanzees on boundary patrols spent less time feeding than
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31 358 those on other periphery visits (patrols: median = 6.51 minutes per hour, range = 0–60; other
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33 359 periphery visits: median = 17.2 minutes per hour, range = 0–60; Poisson regression, $\beta=0.29$, 95%
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35 360 CI = [0.26–0.33], $n_1=180$ patrols, $n_2=147$ periphery visits, $z=18.3$, $p<0.01$).
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362 **Individual variation in participation**

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49 363 Over the entire study period, individuals participated in a mean of $74.5\pm 11\%$ of boundary patrols
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51 364 (Figure 1). The few males with extremely low or high rates of participation were young males
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53 365 who reached age 12 only during the last years of the study, and therefore had small sample sizes
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55 366 (50%: *ZS*, b. 1993, $N=4$ patrols; 100%: *TN*, b. 1994, $N=5$ patrols; 95%: *FE*, b. 1992, $N=18$
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3 367 patrols). All other males exhibited strikingly similar patrol participation rates, between 58 and
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5 368 85%. Moreover, males identified to be present at the start of the patrol stayed for a median 96%
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8 369 of the duration of the patrol (range = 92%–100%, N=23 males). We therefore considered each
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10 370 male present at the start of a patrol to have participated in that patrol.

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16 372 For both boundary patrols and periphery visits, information-theoretic model selection identified
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18 373 the hunting model, which also controlled for sighting frequency and personality dimensions, to
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20 374 be the most-likely candidate model (boundary patrols, Table 2: $w=0.99$, periphery visits, Table 3:
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22 375 $w=0.80$), followed by the model with sighting frequency alone. Males varied considerably in the
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24 376 percentage of days they were recorded by observers (mean = $0.52 \pm 0.13\%$ of days per year;
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26 377 N=283 male-years). Males who were observed more frequently participated in more patrols
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28 378 (Figure 2, $\beta = 3.37$, 95% CI = [2.42–4.35]), as did males who participated in more hunts (Figure
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30 379 3, $\beta = 1.83$, 95% CI = [0.79–2.92]).
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38 381 For the remaining variables tested, the 95% confidence interval of the parameter estimate
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40 382 included zero. Though we therefore lack confidence in the effect of these parameters, some
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42 383 variables had effects in the direction predicted by collective action theory: higher rank, greater
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44 384 mating success, high scores for Dominance, and low scores for Conscientiousness correlated
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46 385 with higher patrol participation. The estimates for periphery visits closely resembled those for
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48 386 boundary patrols (Table 3), with the exception that males who mated more often during focal
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50 387 follows were more likely to participate in periphery visits ($\beta = 9.16$, 95% CI = [3.90–14.69]).
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3 389 Mating frequency is admittedly an imperfect measure of reproductive success, given that
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5 390 chimpanzees mate promiscuously. Given that only alpha males obtain a disproportionate share of
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7 391 paternities [48], we compared patrol participation rates for current and former alpha males with
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10 392 those of males that never reached top rank. However, the patrol participation rate for current and
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12 393 former alpha males (mean = $75\pm 3\%$, $N=8$) did not differ significantly from that of males who
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14 394 had never reached alpha status ($70\pm 3\%$, $N=15$; binomial regression, $\beta=0.11$, $z=1.00$, $p=0.32$).
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20 396 **Discussion**

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23 397 Collective action theory predicts that individuals in group-territorial species should be strongly
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25 398 tempted to free-ride [8,14,15]. As a result, territorial effort should be undertaken
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28 399 disproportionately by individuals that expect to gain a greater share of the spoils, or that can
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30 400 afford the costs because they are high-ranking, strong, or highly motivated [14,16]. In contrast to
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32 401 these expectations, we found that male chimpanzees in the Kasekela community participated in
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34 402 patrols at an exceptionally high rate (mean = 74.5%). Kasekela males participated at more than
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36 403 double the rate of Ngogo males (mean = 33%), which Langergraber et al. [19] considered to be
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38 404 higher than expected from collective action theory. Moreover, we found little evidence that
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40 405 individual traits, such as rank, mating rate, or age explained variation in patrolling. Instead, all
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42 406 Kasekela males participated in at least half of all boundary patrols. Recent paternity analysis at
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44 407 Gombe indicate that the alpha male obtains a disproportionate share of paternities in Kasekela
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46 408 [48]. Despite these reproductive benefits, current and former alpha males did not patrol at
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48 409 significantly higher rates than other males. Indeed, one male that we excluded from our analysis
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50 410 because he was not a potential father (*PX*) nonetheless participated in patrols at a high rate
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3 411 (78.4%; Figure 1; Supplementary Figure 1D); higher, indeed, than some males (e.g., *FR*, *SL*) that
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5 412 attained alpha status and sired many offspring.
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11 414 Why did Kasekela males join patrols at such high rates, regardless of their rank or mating rate?
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13 415 Potential motivating factors include (1) a broader than expected distribution of benefits; (2)
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15 416 lower than expected costs of participation; (3) effects of group size; and (4) benefits of
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17 417 gregariousness.
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24 419 ***Distribution of benefits***

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26 420 If males participate in patrols mainly to benefit their own current or future offspring, then
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28 421 correlates of reproductive success, such as rank, mating rate, and age, should predict patrol
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30 422 participation. However, we did not find strong effects of rank, mating rate, or age on patrol
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32 423 participation. One possible explanation for this is that the benefits of territorial behavior are
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34 424 distributed broadly enough that each male has a strong incentive to participate. This is the
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36 425 perspective of group augmentation theory: if individual survival and reproduction depend
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38 426 strongly on group size, then each individual can be motivated to invest in increasing group size,
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40 427 even if reproductive skew is high [19,20]. All males participate because they all benefit from
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42 428 raising more future fighters to defend their community.
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51 430 ***Costs of participation***

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3 431 Based on collective action theory, we expected to find evidence that males with individual traits
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5 432 that made patrolling less costly for them would patrol more often. Males that hunt frequently
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7 433 might also be expected to be good fighters; and individuals with certain behavioral tendencies or
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9 434 personality traits might be more strongly motivated to patrol. Males that hunted more did patrol
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11 435 more as well — though the possibility exists that this correlation results, at least to some extent,
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13 436 from the fact that both patrols and hunting occur more often when males group together and
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15 437 travel long distances [46]. Personality scores correlated in the expected directions with
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17 438 patrolling, but the model including personality scores received weak support. This may partially
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19 439 result from the temporal scale of these measures. The personality questionnaire produced a single
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21 440 value for each personality dimension for each individual whereas hunting observations reflected
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23 441 the behavior of each individual in a given year. Yet, we found substantial variation in patrol
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25 442 participation rates both between individuals and within individuals over their lifetime
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27 443 (Supplemental Figure 1). Thus, the personality questionnaire may not be capturing this variation
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29 444 fully.
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39 446 While patrols entail energetic and physiological costs [38–40], they may also provide direct
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41 447 benefits to patrollers, such as providing opportunities to find food and females in areas that
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43 448 would otherwise be unsafe to visit. While chimpanzees spent less time feeding during patrols
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45 449 than other visits to the far periphery, patrols nonetheless may provide opportunities to find
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47 450 remote food resources and assess the safety of visiting them. Traveling in large groups may also
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49 451 provide increased opportunities to eat meat. Hunting and patrolling are temporally correlated,
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51 452 because both are more likely to occur when parties contain many males and travel long distances
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53 453 [46]. In our dataset, 26% of patrols (N=47) took place on the same day that a hunt occurred.
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3 454 With all of these direct benefits from patrol participation, the temptations to free-ride may in fact
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11 457 Additionally, while we might expect patrols to be costly because of the increased risk of
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13 458 encountering neighbors, the costs of such encounters might in fact be low, provided chimpanzees
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15 459 travel in sufficiently large parties. Because chimpanzees prefer to attack when they greatly
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17 460 outnumber their opponents [22,42], attackers rarely suffer injuries in intergroup fights. Indeed, if
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19 461 traveling with many males in the periphery, staying with those males is likely safer than
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21 462 attempting to defect by dropping away. Both chimpanzees [35] and another group territorial
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23 463 species, lions [41] exhibit low rates of defection in response to simulated intruders.
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31 465 ***Group size effects***
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34 466 Following Olson's [15] argument that collective action is more effective in smaller groups, Watts
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36 467 and Mitani [18] predicted that participation in boundary patrols would be more consistent
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38 468 amongst males living in smaller communities. We found mixed support for this prediction. As
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40 469 noted above, Kasekela males participated in a much larger percentage of patrols than males in
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42 470 the much larger Ngogo community. Nonetheless, in our analysis, the model including the
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44 471 number of males received weak support, and the parameter estimate was positive instead of
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46 472 negative. Perhaps the number of males in Kasekela during our study period (7–13 males)
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48 473 remained within a range conducive to collective action in chimpanzees.
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3 475 The mean participation rate in patrols is mathematically a function of the mean number of males
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5 476 patrolling and the mean total number of males in the community. For Kasekela, these numbers
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7 477 yield an expected participation rate of $8/11 = 0.73$, close to the observed mean of 74.5%. If
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9 478 safety requires an average of 8 males to patrol, then either 73% of males will need to participate
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11 479 100% of the time, or each male must participate on average 73% of the time. Similarly, at
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13 480 Ngogo, patrols contained a mean 37.5% of the group's males, similar to the mean rate of
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15 481 participation (33%) [19]. Kasekela differs strikingly from Ngogo both in the higher overall rate
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17 482 of participation, the much narrower range of participation among males (Kasekela: range = 50-
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19 483 100%; Ngogo: range = 2–74%)
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26 27 485 *Benefits of gregariousness*

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30 486 The factor that best predicted participation in patrols by Kasekela males was sighting frequency,
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32 487 which likely reflects gregariousness. Males that spend more time with other chimpanzees are
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34 488 more likely to be observed by researchers, and also more likely to be present when a patrol starts.
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36 489 Males likely gain many benefits from gregariousness, including opportunities for mating,
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38 490 grooming, coalition building, and hunting. The costs of patrolling may thus be negligible
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40 491 compared to these benefits of socializing.
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48 493 In summary, our study provides further insight into how collective action problems are solved in
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50 494 nature. In contrast to expectations that group territorial effort would be undertaken primarily by
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52 495 those males with more to gain, we found that males consistently participated in patrols at a high
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54 496 rate. Participation may be encouraged by an even distribution of the benefits accrued to
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497 individuals, an increased cost of defection in smaller groups, and/or direct benefits from
498 travelling in large parties.

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 \leftarrow Age	DV: Patrolling or Periphery Visits IV: Age	None
2	Patrolling/Periphery Visits \leftarrow 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 \leftarrow 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 \leftarrow No. of Adult males	DV: Patrolling or Periphery Visits IV: No. of Adult males	None
5	Patrolling/Periphery Visits \leftarrow Hunting	DV: Patrolling or Periphery Visits IV: Hunting	Personality & Sighting Frequency
6	Patrolling/Periphery Visits \leftarrow Personality	DV: Patrolling or Periphery Visits IV: Personality	None
7	Patrolling/Periphery Visits \leftarrow Sighting Frequency	DV: Patrolling or Periphery Visits IV: Sighting Frequency	None

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; age²; patrol participation, periphery visit participation, hunting participation; Dominance, Conscientiousness; the number of free parameters (K); the difference in Akaike information criterion between the *i*th model and the best model (Δ_i); and model weight (w_i). Models are arranged in order from best (lowest $\Delta AICc$) to worst (highest $\Delta AICc$). 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

Model	Intercept	Age	Mating	Rank	Adult males in the community	Hunting Participation	Dominance	Conscientiousness	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; age²; patrol participation, periphery visit participation, hunting participation; Dominance, Conscientiousness; the number of free parameters (K); the difference in Akaike information criterion between the *i*th model and the best model (Δ_i); and model weight (w_i). Models are arranged in order from best (lowest $\Delta AICc$) to worst (highest $\Delta AICc$). 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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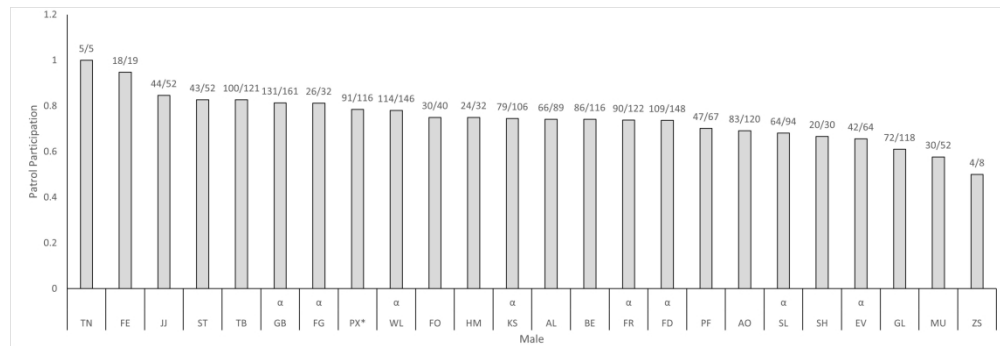
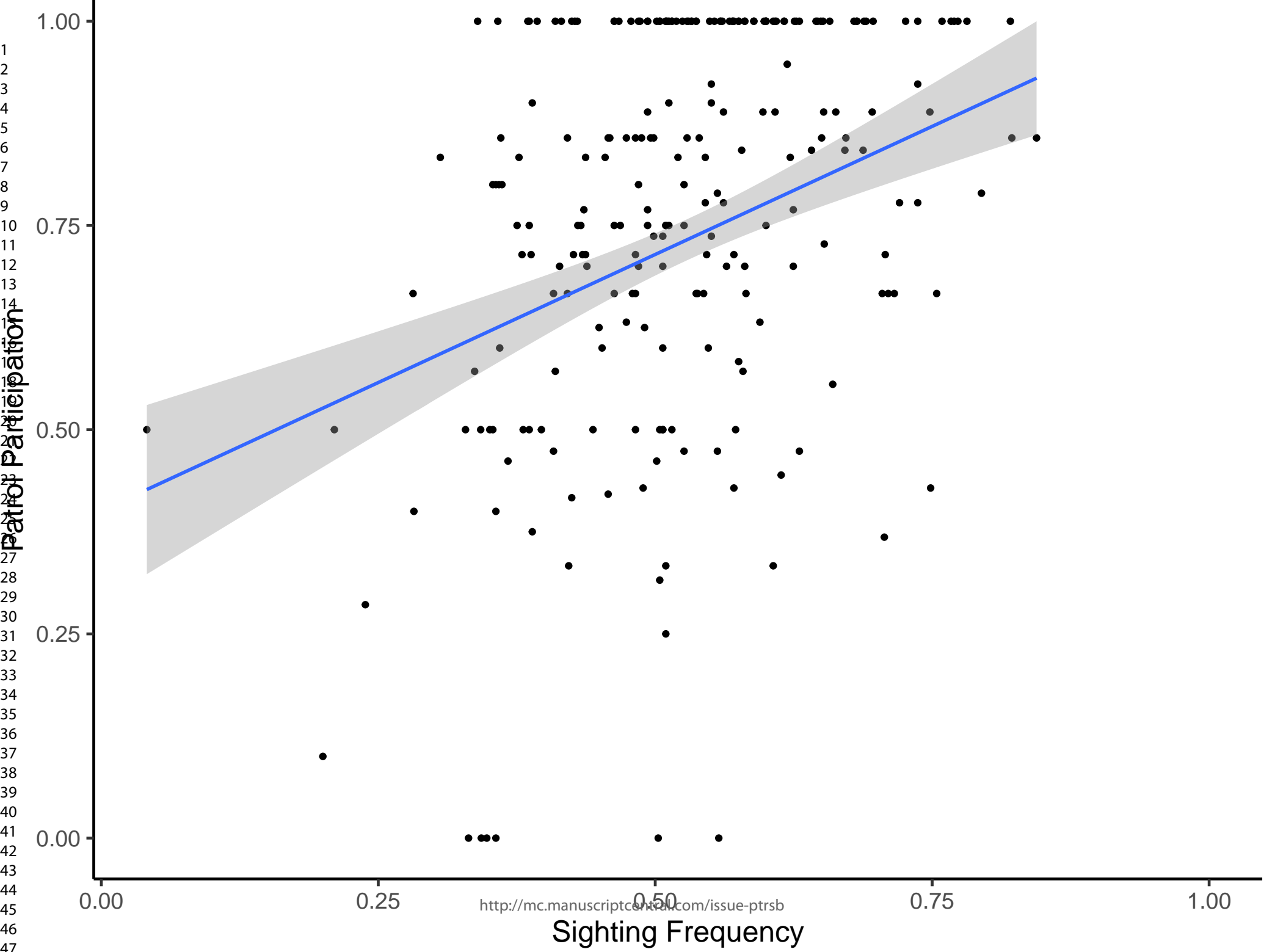


Figure 1. Boundary patrol participation for 24 Kasekela males. Column height indicates the percentage of patrols that each individual participated in while >12 years old. Numbers above the columns indicate the total number of patrols that each individual joined (numerator), and the number of patrols 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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