Predation by Female Chimpanzees: Toward an Understanding of Sex Differences in Meat Acquisition in the Last Common Ancestor of Pan and Homo

Citation

Gilby, IC, ZP Machanda, RC O'Malley, CM Murray, EV Lonsdorf, K Walker, DC Mjungu, E Otali, MN Muller, M Emery Thompson, AE Pusey, and RW Wrangham. Predation by Female Chimpanzees: Toward an Understanding of Sex Differences in Meat Acquisition in the Last Common Ancestor of Pan and Homo. Journal of Human Evolution 110 (2017): 82-94.

Permanent link

http://nrs.harvard.edu/urn-3:HUL.InstRepos:42656569

Terms of Use

Share Your Story

1   **Title**

2   Predation by female chimpanzees: toward an understanding of sex differences in meat acquisition

3   among early hominins

4

5   **Authors**

6   Ian C. Gilby[1] (ian.gilby@asu.edu) ***Corresponding Author***

7   Zarin P. Machanda[2,3] (zarin.machanda@tufts.edu)

8   Robert C. O'Malley[4] (omalleyrc@gmail.com)

9   Carson M. Murray[4] (cmmurray@gwu.edu)

10   Elizabeth V. Lonsdorf[5] (elonsdor@fandm.edu)

11   Kara Walker[6] (k.schroepfer@duke.edu)

12   Deus C. Mjungu[7] (dmjungu@janegoodall.or.tz)

13   Emily Otali[8] (eotali@yahoo.co.uk)

14   Martin N. Muller[9] (muller@unm.edu)

15   Melissa Emery Thompson[9] (memery@unm.edu)

16   Anne E. Pusey[6] (anne.pusey@duke.edu)

17   Richard W. Wrangham[2] (wrangham@fas.harvard.edu)

18 [1]School of Human Evolution and Social Change, and Institute of Human Origins, Arizona State University,

19 Tempe, AZ 85287, USA

20 [2]Department of Human Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA

21 [3]Department of Anthropology, Tufts University, Medford, MA 02155, USA

22 [4]Center for the Advanced Study of Human Paleobiology, the George Washington University,

23 Washington, D.C. 20052, USA

24 [5]Department of Psychology and Biological Foundations of Behavior Program, Franklin & Marshall

25 College, Lancaster, PA 17603, USA

26 [6]Department of Evolutionary Anthropology, Duke University, Durham, NC 27708, USA

27 [7]Gombe Stream Research Centre, The Jane Goodall Institute, Kigoma, Tanzania

28 [8]Kibale Chimpanzee Project, Kibale National Park, Uganda

29 [9]Department of Anthropology, University of New Mexico, Albuquerque, NM 87131

30

Abstract

Among modern foraging societies, men hunt more than women, who mostly target low-quality, yet reliable resources (i.e. plants). This sex difference has long been assumed to reflect female reproductive constraints, particularly caring for, and provisioning offspring. Chimpanzees (*Pan troglodytes*) enable tests of hypotheses about the origins of human sex differences in predation, prior to the appearance of pair-bonding and regular provisioning. We studied two chimpanzee communities (Kasekela, Mitumba) in Gombe, Tanzania and one (Kanyawara) in Kibale, Uganda. Female chimpanzees consistently hunted less often than males did. In Kasekela and Kanyawara, this was partly because females encountered red colobus monkeys (chimpanzees' primary prey) less often than males did. However, when present at a red colobus hunt attempt, females in all three communities were less likely than males to participate, indicating additional constraints. Consistent with the hypothesis that females should be more risk-averse than males, Gombe females specialized in terrestrial/sedentary prey (e.g. young ungulates, fledglings) which seem less risky or costly to acquire than red colobus. Kanyawara chimpanzees (both sexes) preyed almost exclusively on arboreal monkeys. Female dominance rank was positively correlated with red colobus hunting probability at Kasekela, suggesting that those in good physical condition are less sensitive to the potential costs of a failed hunt attempt. There was no evidence that clinging offspring hampered female hunting of red colobus. Finally, the potential for carcass appropriation deterred Kasekela females from hunting in parties containing many adult males. Together, these results enable us to make inferences about the biological bases of sex differences in predation among early hominins. We suggest that before the advent of social obligations regarding sharing and provisioning, hominin females faced similar constraints as chimpanzees. An inherent sex difference in hunting behavior would have provided the basis for the evolution of the sexual division of labor among modern humans.

54   **Key words**

55   Pan troglodytes; Hunting; Meat eating; Diet; Foraging

56

57   **Introduction**

58   Across modern foraging societies, men consistently hunt more often and contribute more meat to their

59   group's diet than women do (Marlowe, 2007). For example, Hadza women acquired only 3.2% (by mass)

60   of the prey brought back to camp (Wood and Marlowe, 2013). On average, Aché men spent 110 minutes

61   per day in active pursuit of game, not including search time (Hill et al., 1985), in contrast with women's 3

62   minutes (Hurtado et al., 1985). Even in societies such as the Aka, in which women frequently participate

63   in cooperative net hunts of small ungulates (Noss and Hewlett, 2001), they did so on only 20% of

64   observation days, compared to 65% for men (Kitanishi, 1995). Also, unlike men, women rarely hunt

65   alone or with projectiles, nor do they target large game (reviewed in Wood and Gilby, in revision). For

66   example, Hadza, /Gui and //Gana women typically target small, relatively immobile prey such as

67   tortoises, young ungulates, hyrax, and nesting birds (Tanaka, 1980; Wood and Marlowe, 2013). Aché

68   women often capture burrowing animals, but tend to call men when they locate more mobile

69   vertebrate game (Gurven and Hill, 2009).

70   This ubiquitous sex difference in rates of meat acquisition among modern human foraging

71   societies has long been assumed to be a result of the constraints that women face in carrying, caring for,

72   and provisioning offspring (reviewed in Bliege Bird and Codding, 2015). Women focus on reliable, yet

73   relatively low-quality, resources (i.e. plants) that ensure a regular supply of food for their children

74   (Marlowe, 2007; Bliege Bird and Codding, 2015). Free from these constraints, males pursue higher-

75   quality but less reliable resources (i.e. meat), either to complement women's contributions to the

76   family's diet (the 'economy of scale' model, reviewed in Bliege Bird and Bird, 2008) or to elevate their

77   status by sharing widely with the larger social group (the 'show off' hypothesis, Hawkes, 1991).

78   Women's foraging efforts ensure that families will not go hungry when males fail to obtain meat. This

79   scenario relies upon regular offspring provisioning, and in the case of the economy of scale model, food

80   exchange within the pair bond. Among the great apes, these behaviors are unique to humans. Although

81   4-8 million years of evolution separate modern humans from their last common ancestor with

82   chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) (Patterson et al., 2006; Langergraber et al.,

83   2012), morphological and behavioral data indicate that the chimpanzee is a valuable point of

84   comparison for identifying the possible range of behavior exhibited by early hominins (Muller et al., in

85   revision; Wrangham and Pilbeam, 2001; Stanford, 2012). As such, chimpanzees allow for tests

86   ofhypotheses about the biological origins of sex differences in meat acquisition prior to the appearance

87   of pair bonds and the sexual division of labor. Some documented sex differences in the foraging and

88   feeding patterns of wild chimpanzees include the frequency and duration of tool-assisted insectivory

89   (multiple sites, female biased; McGrew, 1979, 1992; Nishida and Hiraiwa, 1982), the frequency and

90   efficiency of nut-cracking behavior with stones (one site, female biased; Boesch and Boesch, 1981,

91   1984), the use of sticks to acquire bushbabies (one site, female biased; Pruetz and Bertolani, 2007;

92   Pruetz et al., 2015), and the frequency and duration of meat consumption (multiple sites, male biased;

93   Stanford et al., 1994a; Uehara, 1997; Mitani and Watts, 2001).

94   The hunting behavior of chimpanzees has been studied extensively, but the vast majority of this

95   work is devoted to male predation upon red colobus monkeys (*Procolobus spp*) (Taï National Forest,

96   Côte d'Ivoire: Boesch, 1994; Gombe National Park, Tanzania: Stanford et al., 1994b, Gilby et al. 2006,

97   2015; Mahale Mountains National Park, Tanzania: Uehara, 1997, Ngogo, Kibale National Park, Uganda:

98   Mitani and Watts, 2001; Kanyawara, Kibale: Gilby et al., 2008). Relatively little attention has been given

99   to predation on these or other vertebrates by female chimpanzees (but see Pruetz et al., 2015). Some of

100   this bias is likely due to the fact that hunts of red colobus monkeys ('red colobus' hereafter), which are

101   chimpanzees' most frequent prey (Uehara, 1997; Newton-Fisher, 2014), are most likely to occur in

102   parties containing many male chimpanzees (Stanford et al., 1994b; Mitani and Watts, 2001; Gilby et al.,

103   2006), which non-estrous females tend to avoid (Wrangham, 2000). Since large parties are easier to find

104   and follow, female predation rates may be underestimated if they hunt alone and/or specialize in cryptic

105   prey that require stealth or an element of surprise to capture. In the few studies that report kills of all

106   mammalian prey species by hunter age/sex class, female representation varies considerably across sites.

107   Nearly 1/3 of all predation events at Fongoli, Senegal (30% of 99 captures or possessions; Pruetz et al.,

108   2015) and Mahale (31% of 54 hunts or first observed possessions; Takahata et al., 1984) were made by

109   females, compared to only 3% of 128 kills at Ngogo (Mitani and Watts, 1999). Females contributed 18%

110   of kills at Taï (Boesch and Boesch, 1989) and 23% at Gombe (Goodall, 1986). At Gombe, males killed 26

111   animals during 7,098 hours of observation, while one female participated (jointly with a male) in a single

112   kill in 7,485 hours (Wrangham and Bergmann-Riss, 1990). The variation among study sites is noteworthy,

113   and is likely due to a combination of social and ecological factors, as well as research focus and effort.

114   Here we use long-term data from three communities of eastern chimpanzees

115   (*P.t.schweinfurthii*) to test three hypotheses explaining differences in vertebrate hunting frequency.

116   While hunting and foraging for invertebrates occurs in many primates, chimpanzees are one of the only

117   species, other than humans, white-faced capuchins (Rose et al., 2003; Perry and Ordoñez Jiménez, 2006)

118   and baboons (Butynski, 1982), to consume a significant amount of vertebrate prey, suggesting that a

119   specific focus on hunting of vertebrates is warranted. We do not address cannibalism, which is

120   complicated by selection pressure favoring infanticide in the context of intrasexual competition (Pusey

121   and Schroepfer-Walker, 2013). While bonobos also hunt vertebrates, including arboreal monkeys (e.g.

122   Hohmann and Fruth, 2007; Surbeck and Hohmann, 2008; Surbeck et al., 2009), they do so very rarely,

123   prohibiting hypothesis-driven analyses.

124

Hypotheses

<u>Opportunity hypothesis</u>

Due to the costs of feeding competition, non-sexually receptive adult female chimpanzees at some sites

(e.g. Kanyawara (Wrangham et al., 1992) and Gombe (Wrangham and Smuts, 1980; Murray et al.,

2007)), spend more time alone compared to adult males. Because the probability of hunting (and

capturing) red colobus is strongly positively correlated with male chimpanzee party size (Mitani and

Watts, 2001; Gilby et al., 2006, 2008), females in these communities may simply have fewer

opportunities to hunt red colobus because they travel in large parties less frequently than males do.

Large parties also travel greater distances relative to small parties, increasing the probability of

encountering red colobus (Gilby et al., 2013). Since red colobus make up a high percentage of the prey

at most long-term chimpanzee research sites (53% - 92% (Newton-Fisher, 2014)), the relatively low

gregariousness of females compared to males is a simple explanation for lower female predation rates.

However, females may have more opportunities than males to hunt prey types that require some

element of stealth or surprise to capture (e.g., bushbuck fawns; *Tragelaphus scriptus*).

The opportunity hypothesis predicts (Table 1) that 1) chimpanzee parties will be smaller at kills

of terrestrial and/or sedentary prey species (that require surprise or stealth to capture) compared to

kills of arboreal monkeys; 2) females will encounter red colobus less often than males will; 3) female

hunting rates of red colobus will be positively correlated with overall gregariousness; and 4) when

present at a hunt attempt of red colobus, male and female chimpanzees will be equally likely to hunt.

<u>Risk-sensitivity hypothesis</u>

Female chimpanzees are expected to be less risk-prone than males. First, variation in female

reproductive success is determined more by calorie intake than by access to mates (Trivers, 1972).

148   Therefore, females should be more sensitive than males to the costs and benefits associated with

149   hunting, including energy expenditure, individual condition, and the net energetic and nutritional value

150   of the prey. Second, females are often carrying young offspring that could be injured during a hunt.

151   Predation upon red colobus appears risky (in terms of energy and injury) relative to other forms of

152   predation (e.g. snatching an infant bushbuck or duiker). It can be time consuming - the average red

153   colobus hunt at Gombe lasts 28 minutes (Stanford, 1998), although there is considerable variation

154   (Gilby, personal observation). Also, climbing through the canopy in pursuit of monkeys is likely to be

155   energetically expensive (Gilby and Wrangham, 2007), and hunters may be mobbed and bitten, or fall

156   from considerable heights (Goodall, 1986; Stanford, 1998). Together, these observations suggest that

157   risk-averse individuals should avoid hunting red colobus. Prior studies suggest that terrestrial or

158   sedentary animals make up a substantial fraction of the prey captured by female chimpanzees (Takahata

159   et al., 1984; Goodall, 1986; Pruetz et al., 2015), although the relative acquisition of different prey types

160   by males and females has not been systematically examined.

161   The risk-sensitivity hypothesis predicts sex differences in both the types of prey captured and

162   the factors affecting the decision to pursue risky prey. It predicts that 1) females will specialize in

163   terrestrial or sedentary prey (as these don't involve extensive pursuit, and/or involve a lower risk of

164   injury to the hunter). When present at a red colobus hunt attempt, the probability that a given female

165   hunts is expected to be 2) *lower* if she is has a clinging infant, and 3) *greater* if she is high-ranking (as a

166   proxy for physical condition (Pusey et al., 2005)).

167

168   *Male appropriation hypothesis*

169   When females capture a prey item, it is often immediately stolen by an adult male. For example, seven

170   of 19 prey captured by females in mixed-sex parties at Gombe were immediately appropriated (Goodall

171 1986, p. 307). Ten of the 12 that were not stolen had been captured (and were retained) by Gigi, a large

172 (probably sterile) female who was able to resist male attempts to steal the carcass. To our knowledge,

173 appropriation by adult females has not been reported from any long-term site. The potential for carcass

174 appropriation by males may therefore deter females from hunting in parties containing many adult

175 males, as long as the likelihood of losing the carcass outweighs any net benefit to individual hunters in

176 large groups (via by-product mutualism; West-Eberhard, 1975; Brown, 1983; Connor, 1995), as is the

177 case for male chimpanzees (Gilby et al., 2008, 2015).

178   The male appropriation hypothesis predicts that 1) the likelihood of having one's carcass stolen

179 will be higher for females than for males; 2) when a female makes a kill, the probability that the carcass

180 is stolen from her will be positively associated with the number of adult males present; and 3) at a hunt,

181 the probability that a given female participates will be negatively correlated with the number of adult

182 male chimpanzees present.

183

184 **Methods**

185 *Research sites*

186 We tested these predictions using data collected over a total of 71 community-years from three

187 chimpanzee (*P. t. schweinfurthii*) communities at 2 East African study sites.

188   Gombe National Park comprises 35 km^2 of riverine forest, woodland and grassland (Clutton-

189 Brock and Gillett, 1979) on the shore of Lake Tanganyika, in Western Tanzania. It contains 3

190 communities of chimpanzees: Mitumba in the north, Kasekela in the center and Kalande in the south.

191 Research at Gombe began in 1960 (Goodall, 1986), and daily follows (see below) of adult chimpanzees

192 have been conducted in Kasekela and Mitumba since the early 1970s and mid-1990s, respectively

193 (Goodall, 1986; Wilson, 2012). The Kalande group remains relatively unhabituated. During our study

194 period (1976-2013), the Kasekela community consisted of an average of 11 (range: 7-14) adult males

195 and 17 (range: 11-25) adult females. Following previous hunting studies from Gombe (Gilby et al., 2006,

196 2013, 2015) and Kanyawara (Gilby and Wrangham, 2007; Gilby et al., 2008), we considered males that

197 were at least 12 years old as adults. We defined females as adult at ≥13 years of age, by which time they

198 have settled and the earliest pregnancies have been reported (Emery Thompson et al., 2007; Emery

199 Thompson, 2013). Mean yearly community range size (90% MCP) for Kasekela (± 1 SD) was 8.42 (± 2.99)

200 km^2. The Mitumba community is much smaller than Kasekela. During our study period (2000-2015),

201 there was an average of 3 (range: 2-6) adult males and 8 (range: 6-9) adult females in Mitumba, ranging

202 in an area of 3.01 (± 0.47) km^2.

203   The Kanyawara chimpanzee community inhabits an area of 16.4 km^2 (Wilson et al., 2012) in the

204 northwest quadrant of Kibale National Park, Uganda. Their range consists of approximately 60% moist

205 deciduous forest, with small areas of swamp, grassland and colonizing forest (Chapman & Wrangham

206 1993). The community has been continuously studied since 1987, and all individuals were habituated to

207 human observers by 1993. During our study period (1996-2015), there was an average of 12 (range: 9-

208 15) adult males and 16 (range: 12-19) adult females in Kanyawara.

209

210 *Data collection*

211 <u>Gombe (Kasekela and Mitumba)</u>

212   For the present study, we analyzed data collected on chimpanzees in Kasekela between 1976

213 and 2013, and in Mitumba between 2000 and 2014. Each day, field assistants follow a focal adult

214 chimpanzee in each community from night-nest to night-nest, when possible (Goodall, 1986; Wilson,

215   2012). Observers locate focal animals by utilizing ranging and party composition data from the previous

216   day, listening for vocalizations and/or checking recent feeding trees, and attempt to follow each adult

217   once per month. One observer uses a checksheet to continuously record party composition, the identity

218   of any females with full sexual swellings (indicating sexual receptivity), all feeding by the focal individual

219   and the presence of other species (regardless of any interest in hunting). The second observer uses all-

220   occurrence sampling (Altmann, 1974) to record the behavior of the focal chimpanzee, as well as

221   conspicuous group-level activities, including aggression, hunting, scavenging and piracy (theft of prey

222   from baboons). When hunting occurs, he records the identity of all chimps observed to pursue prey.

223   When possible, he records the identity of each chimpanzee to make a kill (or initially obtain the carcass

224   in the case of piracy or scavenging), and those that subsequently acquire and eat parts of the carcass.

225   Family follows (of mothers and dependent offspring) began in 1970 in Kasekela, and

226   complement the individual focal data described above. Observers collect data on a target mother, her

227   youngest dependent offspring, and next oldest offspring, when present. They record behaviors such as

228   traveling, resting, feeding, and grooming at 1-minute point samples, as well as collecting data on group

229   composition. Events such as hunts, aggression and vocalizations are recorded *ad libitum*.

230

231   Kanyawara

232   Field assistants at Kanyawara work in teams of two and enter the forest before dawn to locate

233   chimpanzees by returning to the nesting site from the previous night. If no nesting location is known,

234   then the assistants will listen for calls or wait at known fruiting trees. Once they locate a party of

235   chimpanzees, at 15 minute intervals, one observer records party composition (including female sexual

236   swellings), feeding, and (since 1996) the presence of any potential prey species within 100 m of the

237   chimpanzees. Prior to 2009, the second field assistant took detailed narrative notes on all occurrences of

238   conspicuous behavior, including aggression and hunting. Since 2009, these observations have targeted a

239   focal individual from the start of the follow to the end, usually all day. He records the behavior of the

240   focal individual at 1 minute intervals, as well as all occurrences of aggression, submissive behavior,

241   hunting, etc. When the chimpanzees begin hunting or are seen holding a prey item, both field assistants

242   spread out to ensure that they have clear observations of as many party members as possible. They

243   confer after the hunt and record all details on an additional predation-specific checksheet. This includes

244   the timing and identity of any chimpanzees who hunt, kill, possess a carcass and/or eat meat.

245

246   *Data extraction*

247   From the data collected at all three sites, we extracted the start times of all 'encounters' with

248   red colobus from the checksheets and notes. At Kasekela and Mitumba, an encounter began when red

249   colobus were first observed within approximately 50 meters of the focal chimpanzee. At Kanyawara, we

250   identified encounters as any 15 minute scan when the chimpanzees were within 100m of red colobus

251   that was not immediately preceded by another scan of red colobus. For each encounter, we calculated

252   the number of adult males and females who were present within 15 minutes of the start of the

253   encounter (Kasekela and Mitumba) or at the 15 minute scan at the start of an encounter (Kanyawara). In

254   all three communities, we matched each encounter with hunt observations to identify all 'hunt

255   attempts'. We defined these as encounters at which there was at least one 'hunter' (any chimpanzee

256   observed to climb in pursuit of red colobus) of either sex (Gilby et al., 2006, 2008, 2015). We excluded all

257   encounters for which there was insufficient detail in the notes to determine whether or not at least one

258   chimpanzee actually climbed (Gilby et al., 2006, 2008, 2015). A 'successful hunt' was any hunt attempt

259   at which at least one monkey was killed. Whenever possible, we recorded the identity of the

260   chimpanzee(s) that made the kill(s). On the rare occasion when two chimpanzees simultaneously

261   captured the same prey item, we credited each captor with half of the kill.

262   In most cases, opportunities to acquire prey other than arboreal monkeys are difficult to identify

263   unless the attempt is successful. For example, it is unlikely that researchers will notice the presence of

264   nestlings in a tree hole, or a bushbuck fawn hidden in undergrowth unless the chimpanzees make an

265   attempt to acquire them. Usually, with these types of prey, the success rate is high, as the prey is

266   defenseless. Also, while the observers note encounters with all species, it is not always clear whether a

267   catchable prey item (e.g. an infant) is available. Therefore, we began all analyses of non-red colobus

268   prey items at acquisition. At Kanyawara, we identified non-red colobus acquisition events using the

269   predation checksheets. At Gombe, we used several methods. First, for the whole study period in each

270   community (Kasekela: 1976-2013, Mitumba: 2000-2014), we used the focal feeding records to identify

271   all cases when the focal chimpanzee ate non-colobus meat. We then extracted acquisition details from

272   the narrative notes. Second, for Kasekela between 1994 and 2013 (for which the narrative notes had

273   been digitally transcribed), we used keyword searches to find all instances when non-colobus animal

274   species were mentioned. Finally, we supplemented this dataset with successful hunts and meat eating

275   recorded during family follows (Kasekela) and by one of us (KW), who conducted 226 focal follows of

276   adolescent and young adult female chimpanzees (ages 8 – 16 years) between June 2011 and May 2014

277   in Kasekela and Mitumba (Walker, 2015).

278   When meat was acquired, we recorded 1) whether a prey item was eaten (at least partially) by

279   any member of the party, 2) the identity of the acquirer (if known), 3) chimpanzee party composition,

280   and 4) the mode of acquisition (kill, piracy, scavenging). At Gombe, 'piracy' occurred when the

281   chimpanzees were seen (or strongly suspected) to take a carcass from baboons. Piracy has not been

282   observed at Kanyawara. 'Scavenging' occurred when chimpanzees encountered and ate a prey item that

283 was already dead, and there were no predators in the area. Finally, at Kasekela and Kanyawara, for

284 every case when a chimpanzee possessed a prey item, and it was clear from the notes that the

285 observation was complete (i.e. the possessor was the focal chimpanzee or there was sufficient detail to

286 indicate that the entire possession was observed), we recorded whether another chimpanzee stole the

287 carcass from him/her. We defined such 'theft' as carcass appropriation that evoked a negative reaction

288 from the possessor (e.g. scream, retaliate). Theft data had not yet been extracted from the Swahili notes

289 from Mitumba.

290   For all three communities, we used submissive pant-grunt data to calculate female Elo

291 dominance scores (Neumann et al., 2011) using the method developed by Foerster et al. (in revision)

292 which uses maximum likelihood to determine the initial score for each individual and the weight (k) of

293 each dominance interaction. In order to be able to compare Elo-ratings across periods and communities,

294 we re-scaled them to fall between 0 and 1, preserving gaps among individuals. One Kanyawara female

295 (LP) never pant-grunted to another female during the study period, which made it impossible to

296 calculate an Elo-rating for her. Therefore, we gave her a score of 1 in the re-scaled hierarchy.

297

298 *Statistical Analyses*

299   We used R version 3.2.3 (R Development Core Team, 2015) with the lme4 (Bates et al., 2014),

300 multcomp (Hothorn et al., 2008) packages for statistical analyses. For simplicity, we describe the

301 specifics of each analysis in the Results section.

302

303 **Results**

304 *Summary statistics*

305   Kasekela

306   Kasekela chimpanzees were observed to feed upon 2206 vertebrate prey items between 1976 and 2013

307   (Table 2). Females accounted for 14.5% of the 1819 cases in which the sex of the initial acquirer was

308   clear, although females acquired a greater percentage of non-colobus prey (33.6% of 297). Notably,

309   females acquired 45.9% of the 49 bushbuck fawns and 69.2% of the 39 birds. By contrast, females

310   captured only 10.7% of the 1523 red colobus. Of the 360 non-colobus prey items for which the mode of

311   acquisition could be ascertained, there were 38 cases of piracy, in which chimpanzees stole meat (37

312   bushbuck and 1 bushpig) from baboons. In 44.4% (12/27) of the piracy cases in which the sex of the

313   acquirer was known, it was a female. There were three cases of scavenging – a blue monkey, a

314   bushbuck, and a redtail monkey. The observers estimated that the bushbuck (mainly ribs and skin) had

315   been dead for about 2 days based on the presence of maggots. In one case, chimpanzees retrieved a

316   rodent that was dropped by an eagle. There were no observed cases of piracy or scavenging of red

317   colobus.

318

319   Mitumba

320   Mitumba chimpanzees were observed to feed upon 254 prey items between 2000 and 2014 (Table 2).

321   208 of these were red colobus. As in Kasekela, females acquired a larger percentage of non-colobus

322   (33.3% (12/36)) than colobus prey, and 45% (5/11) of the bushbuck. However, females were responsible

323   for a greater percentage (19.1%) of the red colobus kills (35.5/186) in Mitumba than in Kasekela (10.7%).

324   There were 10 cases of piracy, all of which were bushbuck fawns stolen from baboons. In 3

325   (37.5%) of the 8 cases in which the sex of the acquirer was known, it was a female. No scavenging events

326   were observed.

327

Kanyawara

329   At Kanyawara, chimpanzees were observed to feed upon 349 prey items between 1996 and 2015 (Table

330   2). All but one of these (a red duiker, which was scavenged, see below) was an arboreal monkey. As at

331   Gombe, the majority (N = 288, 82.5%) were red colobus. The second-most frequent prey (N = 44) were

332   black and white colobus monkeys, which are not present at Gombe. When the killer could be identified,

333   females at Kanyawara were responsible for 5.1% and 16.7% of the 214 red colobus and 36 black and

334   white colobus kills, respectively. As at Gombe, females at Kanyawara were responsible for a higher

335   proportion of the kills of redtail monkeys (3/4, 75%) and blue monkeys (3/5, 60%) than of red colobus.

336   There was one case in which chimpanzees caught a red duiker which they then used in

337   dominance displays for over an hour. The duiker eventually died and was not consumed, and is

338   therefore not included in the above totals. In a separate incident, an adult female found a dead duiker in

339   a tree and fed on part of the head. On 12 March, 1997, adult male KK emerged from the undergrowth

340   with an infant red colobus that the observers noted was decomposing, emitting a strong odor. KK fed on

341   the carcass for 120 minutes before relinquishing it to adult female LP, who was still eating it 15 minutes

342   later when the chimpanzee party was lost. There were no cases of piracy at Kanyawara.

343

344   *Opportunity hypothesis: Prey type and chimpanzee party size*

345   In Kasekela, a mean of 39.7% (S.E. = 0.7) of community adults were present at kills of arboreal

346   monkeys, compared to 32.4% (S.E. = 1.8) of kills of terrestrial or sedentary prey. To test whether this

347   difference was statistically significant, we ran a Generalized Linear Model (GLM) with the number of

348   adult chimpanzees present as the (continuous) dependent variable, and prey type (arboreal monkey,

349   other) as a categorical independent variable. To control for changes in community size over time, we

350   included the number of adult chimpanzees alive in the community on that date as a second factor in the

351   model. As expected, the association between adult party size and adult community size was positive

352   (parameter estimate: 0.50, t = 12.8, P < 0.0001). With this controlled for, chimpanzee party size at kills of

353   arboreal monkeys was significantly greater than at kills of other prey: (estimate = 1.94, t = 3.66, P =

354   0.0003), supporting the opportunity hypothesis (Table 1).

355   In Mitumba, a mean of 61.5% (S.E. = 2.1), of community adults were present at kills of arboreal

356   monkeys (N = 145) compared to 58.5% (S.E. = 6.5) of terrestrial or sedentary prey. This difference was

357   not statistically significant (GLM, estimate = 0.46, t =0.65, P = 0.52) whether or not we controlled for the

358   number of adults in the community (which was not significant at P = 0.42). Therefore, in Mitumba, there

359   was no evidence that fewer community members were present at hunts of prey that may require stealth

360   or an element of surprise to capture, a finding that does not support the Opportunity hypothesis.

361   We were unable test this prediction at Kanyawara, where all but one of the 346 identifiable prey

362   items were arboreal monkeys.

363

364   *Opportunity hypothesis: Sex differences in red colobus encounter rate*

365   To test the prediction that females encounter red colobus less often than males do, we ran one

366   Generalized Linear Mixed Model (GLMM) for each community with focal follow as the unit of analysis

367   and red colobus encounter (Y/N) as the response variable. Note that full-day focal data collection began

368   at Kanyawara in 2009, yielding only 7 years of data. We included focal chimpanzee sex and follow

369   duration as main effects, with a binomial error structure, logit link function, and focal chimpanzee ID as

370   a random effect.

371   At all three sites, there was a significant, positive association between follow duration and the

372   probability of encountering red colobus (Kasekela: estimate = 0.19, Z = 21.2, P < 0.0001; Mitumba:

373   estimate = 0.15, Z = 10.0, P <0.0001; Kanyawara: estimate = 0.08, Z = 2.9, P = 0.004). With follow

374   duration statistically controlled for, the models indicated that the probability of encountering red

375   colobus was significantly lower if the focal chimpanzee was female at Kasekela (estimate = -0.66, Z = -

376   5.1, P <0.0001) and at Kanyawara (estimate = -0.31, Z = -2.1, P = 0.04), supporting the opportunity

377   hypothesis. This was not the case at Mitumba, however (Z = 0.1, P = 0.9).

378

379   *Opportunity hypothesis: Female gregariousness and red colobus hunting frequency*

380   For each adult female in each community, we determined the number of adults present at each 15

381   minute interval that she was observed in a party, and then calculated the mean for each year she was an

382   adult. We used this measure of gregariousness as a main effect in one GLMM per community, with red

383   colobus hunting frequency (number of red colobus hunt attempts in a given year at which the female

384   hunted) as the dependent variable. The models used a Poisson link function and included observation

385   time of each female as an offset, with year and chimpanzee ID as random effects.

386   There was a strong positive association between a female's gregariousness and her participation

387   in red colobus hunting in all three communities (Kasekela: estimate = 0.34, z = 6.17, P < 0.0001;

388   Mitumba: estimate = 1.54, z = 6.31, P < 0.0001, Kanyawara: estimate = 0.63, z = 5.11, P < 0.0001),

389   supporting the opportunity hypothesis.

390

391   *Opportunity hypothesis: Hunting probability by sex*

392   Next, we asked whether, when present at a red colobus hunt attempt, focal females were less likely to

393   hunt than focal males were. For each community, we ran a GLMM (error structure: binomial, link

394   function: logit, random effect: focal ID) with focal hunt (Y/N) as the dependent variable and sex of the

395   focal as the main effect. The focal chimpanzee was less likely to participate in a hunt if female than if

396   male at Kasekela (N=1498 hunts, 432 focal females, estimate = -1.22, Z = -6.9, P < 0.0001) and Mitumba

397   (N = 303 hunts, 166 focal females, estimate = -1.01, Z = -4.08, P < 0.0001), but not at Kanyawara (35

398   hunts, 9 focal females, estimate = -2.31, Z = -1.50, P = 0.13) (Figure 1). The lack of statistical significance

399   at Kanyawara was likely due to the relatively small sample size (7 years of focal data, 35 hunt attempts).

400   Therefore, we ran one more GLM, this time on the full Kanyawara dataset (1996-2015), with each adult

401   chimpanzee present at a hunt attempt (rather than the focal individual) as the sampling unit. We

402   modelled the probability that a given individual hunted (Y/N) as a function of sex, with chimpanzee ID

403   and hunt ID as random factors. When analyzed in this way, female chimpanzees were significantly less

404   likely to participate than males were (estimate = -2.27, Z = -5.72, P < 0.0001).

405   Together with the previous analyses of red colobus encounter rates, these results indicate that

406   the opportunity hypothesis does not account for all the variance in female hunting frequency. While

407   females in Kasekela and Kanyawara were less likely to encounter red colobus than males were, and

408   female gregariousness was correlated with hunting frequency at all three sites, females were still less

409   likely than males to participate in a hunt when given the opportunity.

410

411   *Risk-sensitivity hypothesis: Prey type vs sex of acquirer*

412   Given the relatively limited prey profile at Kanyawara, we conducted the following analysis for Kasekela

413   and Mitumba only. For each prey item acquired, we used a Generalized Linear Model (GLM) to

414   determine whether the sex of the acquirer was associated with prey type. The GLM modeled the

415   probability that the acquirer was female (Y/N), using a binomial error structure and logit link function.

416   We included prey type (arboreal monkey, bushpig/baboon, bushbuck/other) as a main effect in the

417   model. In order to account for chance, we also included the number of adult male and adult female

418   chimpanzees present at the acquisition as main effects.

419   At Kasekela, as expected by chance, the likelihood that a prey acquirer was female correlated

420   negatively with the number of adult male chimpanzees (estimate = -0.21, z = -7.7, P < 0.0001) and

421   positively with the number of adult females (estimate= 0.14, z = 6.89, P < 0.0001) present at a prey

422   acquisition event. With these factors controlled for, the probability that a given prey item was acquired

423   by a female was higher if the prey was a bushpig or baboon than if it was an arboreal monkey (estimate=

424   0.56, z = 2.3, P = 0.02) (Figure 2). If the prey was a bushbuck (or egg, rodent, etc.) the odds that the

425   acquirer was female was even higher (estimate = 2.2, Z = 8.99, P < 0.0001).

426   In Mitumba, there was no effect of the number of adult male (Z = -0.28, P = 0.07) or female (Z = -

427   0.06, P = 0.41) chimpanzees on the probability that a prey acquirer was female. However, as in Kasekela,

428   when the prey was bushbuck/other, the probability that the acquirer was female was significantly higher

429   than if the prey was an arboreal monkey (estimate = 1.77, Z = 3.09, P = 0.002), or a baboon or bushpig

430   (estimate = 3.17, Z = 2.70, P = 0.007, Figure 2). There was no sex difference in the acquisition of

431   baboon/bushpig and arboreal monkeys (Z = -1.32, P = 0.19).

432

433   *Risk-sensitivity and male appropriation hypotheses: female participation in red colobus hunts*

434   Given the potential confounding effects of dominance rank, clinging offspring and adult male party size,

435   we ran separate GLMMs for each community that incorporated these variables, thus simultaneously

436   testing the risk sensitivity and male appropriation hypotheses. For Kasekela and Mitumba, we modeled

437   the probability that a focal female hunted red colobus (when present at a hunt attempt), with her scaled

438   Elo-rating on that day, dependent offspring (≤2yr old, Y/N) and adult male party size as main effects. We

439   used a binomial error structure, logit link function, and included focal ID as a random effect. Because

440   there was only 1 red colobus hunt by a focal female at Kanyawara, we ran a similar GLMM on the entire

441   dataset (1996-2015), with each female present at a hunt attempt (rather than the focal) as the unit of

442   analysis and hunt ID as an additional random effect.

443   There was a significant positive association between dominance rank and focal female hunting

444   probability at Kasekela (N = 384 hunt attempts attended, 35 females), (Table 3), supporting the risk

445   sensitivity hypothesis. However, this was not the case at Mitumba (N = 123 hunt attempts attended, 9

446   females) or Kanyawara (N = 135 hunt attempts attended, 18 females, mean 3.9 females per hunt)

447   Focal females at both Kasekela and Mitumba were equally likely to hunt red colobus whether or

448   not they had an offspring under two years of age (Table 3), a result that does not support the Risk

449   Sensitivity hypothesis. At Kanyawara, females with offspring under two years old were actually more

450   likely to hunt than those with older (or no) offspring (Table 3). To investigate this result more fully, we

451   conducted a pair-wise test on the 8 adult females that were present for at least 15 red colobus hunt

452   attempts with an offspring under 2 years of age, and 15 hunt attempts without. For each female, we

453   calculated the proportion of hunt attempts in which she hunted with and without young offspring. Five

454   females exhibited higher rates when they had young offspring, and three had lower rates, a difference

455   that was not statistically significant (Wilcoxon Signed Ranks Test, V = 33, p = 0.23).

456   Focal females at Kasekela were less likely to hunt as the number of adult males present

457   increased (Table 3), supporting the male appropriation hypothesis. However, this was not the case at

458   Mitumba or with female hunt attendees at Kanyawara (Table 3).

459

460   *Male appropriation: Carcass theft vs. sex and # adult males*

461   For each carcass possession by an adult chimpanzee, we recorded whether or not the possessor had the

462   carcass stolen. At Kasekela, there were 220 cases for which we could be absolutely sure whether or not

463   theft took place – e.g. the possessor was the focal individual, a theft was explicitly described, or there

464   were multiple descriptions of a non-focal individual continually possessing meat from beginning to end.

465   If a non-focal meat possessor was simply seen later without meat, and there was no description of a

466   theft, we did not include the possession in the following analysis. Carcasses were stolen from adult

467   males in 3.8% (5/131) possessions, compared to 28.1% (25/89) for females. This difference was

468   statistically significant – females were more likely to have their carcass stolen than males were: (GLMM

469   of steal (Y/N) vs. female possessor (Y/N): Estimate: 2.29, Z = 4.45, P < 0.0001, error = binomial, link =

470   logit, random effect = chimpanzee ID). We then ran another GLMM, including the number of adult males

471   present and the female possessor*adult males interaction term. The interaction term was significant,

472   indicating that the probability that a female had the carcass stolen from her increased with the number

473   of males present (Table 4, Figure 3). These results support the male appropriation hypothesis.

474   At Kanyawara, there were 207 initial carcass possessions by adult chimpanzees for which it

475   could be determined conclusively whether or not theft occurred. Carcasses were stolen from adult

476   females in 21.4 % (3/14) of possessions, compared to 8.3% (16/193) for males. However, this difference

477   was not statistically significant (GLMM: estimate = 1.46, Z = 1.36, P = 0.17, error = binomial, link = logit,

478   random effect = chimpanzee ID), probably due to the relative rarity of possessions by adult females.

479   Similarly, with the small sample, we were unable to test whether theft from females increased with

480   adult male party size. However, of the 3 thefts from adult females, 2 occurred in relatively large groups

481   (10 and 11 adult males).

482

Discussion

484   We analyzed long-term data from three eastern chimpanzee communities in order to test hypotheses

485   explaining sex differences in predation in one of human's closest relatives. Genetic, morphological and

486   behavioral data indicate that the chimpanzee is a valuable point of comparison for identifying the

487   possible range of behavior exhibited by the last common ancestor of apes and humans (Muller et al., in

488   revision.; Wrangham and Pilbeam, 2001; Stanford, 2012). Our results provide insight into the biological

489   constraints faced by early hominin females before the development of regular offspring provisioning

490   and food sharing within the pair bond. As is ubiquitous among modern human societies, female

491   chimpanzees in all three study communities hunted less often than males did. At Kasekela and

492   Kanyawara, which were of similar mean size (28 adults) and female:male sex ratio (Kasekela: 1.5:1;

493   Kanyawara: 1.3:1), females were responsible for only 14.5% and 8.8% of all kills, respectively. At

494   Mitumba, which had fewer adults (11) and a more female-biased sex ratio (2.6:1), females accounted for

495   21.4% of kills.

496

497   *Females had fewer hunting opportunities*

498   Part of the reason for the relatively low female hunting rates at Kasekela and Kanyawara was

499   that females there had fewer opportunities to capture red colobus, chimpanzees' most frequent prey.

500   Females, which are less gregarious than males, encountered red colobus less often than males did,

501   because large parties travel greater distances and are therefore more likely to encounter a monkey

502   troop (Gilby et al., 2013). Also, party sizes at Kasekela were larger at kills of red colobus than other of

503   prey types, suggesting that relatively gregarious females more quality chances to hunt (because larger

504   parties are more likely to hunt red colobus (reviewed in Newton-Fisher, 2014)). Indeed, in all three

505   communities, the total number of kills a female made was positively correlated with her gregariousness.

506   In Mitumba, however, females and males were equally likely to encounter red colobus, and there was

507   no difference in the average party size at hunts of arboreal monkeys versus other prey. It may be that

508   parties are more stable (in size and composition) in this smaller community, explaining this lack of sex

509   difference. Previous work showed that Mitumba is unusual in that hunting probability was positively

510   associated with female, as well as male, party size (Gilby et al., 2015), suggesting that females play a

511   more active role in hunts. This is possible, however at all three sites in the current study, when present

512   at a red colobus hunt attempt, the odds that a given female participated were 64-90% lower than they

513   were for a male. Therefore, the opportunity hypothesis only partly explains the sex difference in

514   predation rates at Kasekela and Kanyawara, indicating that there are other constraints on female

515   hunting in all three communities.

516   Among human foragers, women travel shorter distances than men (e.g. the Hadza (Marlowe,

517   2010; Pontzer et al., 2015)), but we are not aware of any studies that explicitly address sex differences in

518   prey encounter rates. This is complicated by the fact that men typically travel farther farther *because*

519   they seeking prey. By contrast, both male and female chimpanzees at Gombe and Kanyawara make

520   hunting decisions only when they encounter prey. (At Ngogo and Taï, however, male chimpanzees do

521   appear to deliberately search for prey (Boesch and Boesch-Achermann, 2000; Watts and Mitani,

522   2002a)). Additionally, when specialized tools (e.g. poisoned arrows) are needed to kill certain species

523   that men typically target, women foraging for plant material might not be equipped to hunt upon

524   chance encounter with prey.

525

526   *Risk-aversion – females targeted terrestrial/sedentary prey*

527   Relative to males, variation in female reproductive success is determined more by calorie intake than by

528   access to mates. Females are therefore more constrained by the need to acquire enough food to satisfy

529   their daily nutritional requirements. Human females also forage for, and share with, their dependents.

530   Hence, women follow a risk-averse foraging strategy, in which they seek low-variance, but often low-

531   quality, foods (Marlowe, 2007; Bliege Bird and Codding, 2015). When they do hunt, they typically target

532   small, sedentary prey. We found that female chimpanzees follow a similar hunting strategy. While

533   females participated successfully in hunts of arboreal monkeys in both Gombe communities (accounting

534   for 11.2% and 19.5% of kills at Kasekela and Mitumba, respectively), the probability that a killer (or

535   acquirer, in the case of piracy) was female was greater when the prey was terrestrial. Hunts of arboreal

536   monkeys at Gombe are lengthy, energetically costly, and involve conflict with formidable males

537   equipped with large canines. By contrast, while hunts of infant bushpigs and baboons involve

538   confrontations with adults, they do not appear to entail the same energetic costs, and there is no risk of

539   falling. Capturing sedentary or concealed prey appears to involve even fewer costs, and indeed,

540   bushbuck fawns, nestlings, eggs and rodents were captured more often by females than by males at

541   Kasekela and Mitumba. It is important to note, however, that in 42.9% (15/35) of the cases of bushbuck

542   piracy at Gombe, the thief was female, indicating that they frequently risk confrontation with baboons.

543   This suggests that females at Gombe are most sensitive to the costs of arboreal pursuit, rather than risk

544   of injury from prey.

545   At Kanyawara, where the prey profile is almost exclusively arboreal monkeys, females captured

546   16.7% (6/36 for which the sex of the killer was known) of the black and white colobus monkeys,

547   compared to only 5.1% (11/ 214) of the red colobus. Red colobus at Kanyawara actively and aggressively

548   defend themselves, sometimes preemptively attacking chimpanzees that show no interest in hunting

549   (Kibale Chimpanzee Project, unpublished data). By contrast, black and white colobus appear more

550   passive and slow, are less defensive in the presence of chimpanzees, and therefore seem to be less

551 costly to pursue. Given the rarity of terrestrial/sedentary prey at Kanyawara, perhaps black and white

552 colobus present a valuable low-cost option for females. However, if this is the case, why don't

553 chimpanzees hunt them more frequently? One possibility is that their meat is somehow less desirable, a

554 notion that is supported by observations of lower levels of excitement and conflict at kills of black and

555 white colobus relative to red colobus (Kibale Chimpanzee Project, unpublished data).

556

557 *Risk-aversion – clinging offspring did not deter females from hunting red colobus*

558 The foraging strategies of human females must also allow for the transport and care of dependent

559 offspring. Often this involves travelling shorter distances than men, and targeting resources that allow

560 them to forage while carrying children while avoiding contact with dangerous prey. We expected that

561 female chimpanzees would be constrained in similar ways. However, female chimpanzees with young

562 offspring (≤2 yrs) did not avoid hunting red colobus. There are several possible explanations for this

563 result. Perhaps females temporarily leave young offspring behind while hunting. Or, the benefits of

564 meat for lactating females may offset the added costs of hunting with offspring. That is, lactating

565 females may take on the added costs of hunting with offspring because they benefit disproportionately

566 (relative to other females) by obtaining food rich in fat and micronutrients. However, O'Malley et al.

567 (2016) found that among lower-ranking females at Kasekela, pregnancy was associated with greater

568 meat consumption than lactation was (although this could result from differences in begging rather than

569 hunting). Finally, in our study, 'hunt' was a binary variable, based on whether or not a chimpanzee

570 climbed in active pursuit of prey. It is possible that females with young offspring may hunt just as often

571 as other females, but they do so with less 'intensity', or they give up more easily.

572

573   *Risk-aversion – high-ranking females hunted more*

574   The risk-sensitivity hypothesis predicts that individuals in good physical condition (indicative of a

575   positive energy balance), should be more willing than individuals in poor condition to target resources

576   with some risk of failure. We are not aware of any studies in humans that examine within-sex variation

577   in risk-prone foraging. Among chimpanzees, however, the probability that a Kasekela female hunted red

578   colobus was positively correlated with dominance rank. In that community, high ranking females weigh

579   more, and their mass fluctuates less than that of low-ranking females (Pusey et al. 2005), suggesting that

580   they have access to higher quality and/or less variable resources. As such, high-ranking females may be

581   more likely to have sufficient energetic reserves required to hunt, or they are able to absorb the costs of

582   failure more easily. A low-ranking female may forego hunting in favor of more predictably-acquired

583   plant foods. There are, of course, many other factors associated with dominance rank that are likely to

584   affect female hunting decisions, such as age, experience and gregariousness. This may explain why there

585   was no statistical relationship between female rank and hunting at Kanyawara or Mitumba, although

586   small sample sizes cannot be ruled out.

587

588   *Male appropriation – males stole carcasses from females*

589   Among human foragers, sharing norms ensure that food is distributed among group members, and it

590   therefore seems unlikely that women avoid hunting because of the fear of losing the quarry to

591   aggressive males. However, this appears to be a real cost among chimpanzees, at least at Kasekela.

592   There, the probability that a given female hunted red colobus was negatively correlated with the

593   number of adult males present in the party. By contrast, previous work at several sites has shown that

594   the likelihood of hunting by males increased with male party size (reviewed by Newton-Fisher, 2014).

595   Gilby et al. (2008, 2015) argued that this pattern is the result of a by-product mutualism in which the

596   independent actions of individual hunters incidentally decrease the costs for other hunters, thus

597   providing an incentive to join a hunt. Why does this not appear to apply to females at Kasekela? We

598   suggest that any decrease in hunting costs associated with the presence of more male hunters is offset

599   by a greater likelihood that a successful female hunter will immediately have the carcass stolen. Indeed,

600   females at Kasekela were much more likely to have carcasses stolen from them than males were, and

601   the probability of theft from a female increased with male party size. At Kanyawara and Mitumba,

602   however, there was no association between adult male party size and female hunting probability. At

603   Mitumba, we suspect that this was due to the small number of males; either there was not enough

604   variation in the number of males that could be present, or theft may be less of a threat. Unfortunately,

605   theft data from Mitumba are not currently available. The small sample of female carcass possessions at

606   Kanyawara prevented statistical tests of theft versus male party size.

607

608   *Overall predation rates differed among sites*

609   Given that humans inhabit a wide range of habitats, it is not surprising that diets vary considerably. By

610   comparison, chimpanzees have a relatively limited range, restricted to forests and woodlands across

611   central Africa. Nevertheless, both chimpanzee prey profiles and meat-eating frequency vary greatly,

612   even among East African sites (Newton-Fisher, 2014). Our study suggests that both ecological and

613   demographic factors help to explain this variation. Although they were of similar size (~28 adults), meat

614   eating was 3 times more frequent at Kasekela (~58 prey/year) than at Kanyawara (~18 prey/year), a

615   difference that could not be explained by either red colobus encounter rate or research effort. At

616   Mitumba, although much smaller (~11 adults), chimpanzees captured prey at a similar rate (17

617   prey/year) as at Kanyawara. For a community of its size that regularly encounters its most common

618   prey, why do the Kanyawara chimpanzees hunt so rarely? Forest structure, grouping and travel patterns,

619   and prey distribution are all likely factors. For example, chimpanzees are more likely to hunt red colobus

620   in areas with broken canopy at Ngogo (Mitani and Watts, 2001) and in woodland (where trees are

621   sparsely distributed) at Kasekela (Gilby et al., 2006). Perhaps there are relatively few low-cost options to

622   hunt arboreal monkeys at Kanyawara. At all sites where chimpanzees hunt red colobus, larger

623   chimpanzee parties are more likely to hunt and to succeed (reviewed by Newton-Fisher, 2014). The

624   same is true at Kanyawara (Gilby et al., 2008), but it may be that large parties form relatively rarely in

625   comparison to Kasekela. Strikingly, Kanyawara chimpanzees focused almost exclusively on arboreal

626   monkeys. The most parsimonious explanation for this result is that alternative prey species are relatively

627   rare within their range. While many of the types of prey targeted at Gombe (e.g. small ungulates) are

628   present at Kanyawara, and eaten by chimpanzees elsewhere within the same forest (Ngogo: Watts and

629   Mitani, 2002), their distribution and abundance is not well documented.

630

631   *Conclusions*

632   There was mixed support for 3 hypotheses addressing the relatively low rates of predation by

633   female chimpanzees. In the two larger communities, females had fewer opportunities to hunt red

634   colobus than males did. In the smaller Mitumba community, though, males and females were equally

635   likely to encounter red colobus. In support of the notion that females are less risk-prone than males,

636   females were more likely to hunt terrestrial and/or sedentary prey at Gombe. However, this was not the

637   case at Kanyawara, where they preyed upon arboreal monkeys almost exclusively. Furthermore, clinging

638   offspring did not hamper female participation in hunts, and only Kasekela females hunted more often if

639   they were high-ranking. Finally, female hunting probability was negatively affected by the threat of

640   losing the carcass to a male at Kasekela, but not Mitumba or Kanyawara.

641   This study highlights the variability in female hunting that exists between communities, and

642   raises many questions about the sources of these differences. Why don't the Kanyawara chimpanzees

643   hunt terrestrial or sedentary prey? Why did females at Mitumba encounter red colobus at the same rate

644   as males did? Future studies must examine ecological variation, community composition, range size and

645   prey dynamics to explain these inter-community differences. Additionally, females also varied in their

646   hunting decisions *within* communities. For example, dominance rank was an important determinant of

647   female hunting at Kasekela. Future studies will likely identify other factors affecting individual variation,

648   such as demography and kinship.

649   It is important to acknowledge the possibility that small sample sizes might be affecting our

650   results. Despite being the most comprehensive study of chimpanzee hunting to date, spanning 71 years

651   and 3 communities, we were unable to test all of our predictions at Mitumba or Kanyawara. For

652   example, over 20 years of Kanyawara data collection observers recorded over 200 initial monkey

653   possessions by adult chimpanzees. However, only 14 of those were by females and in only 3 cases did a

654   female have the carcass stolen. While it is possible that Kanyawara females are not hunting because of

655   the fear of theft by males, at the current rate, many more years of data are needed to test this

656   prediction. This substantiates the necessity of long-term data when studying a rare behavior performed

657   by a long-lived species and also highlights the need for comparable datasets collected from multiple

658   sites where animals experience different social and ecological environments.

659   Ultimately, however, we have shown that despite variation within and between communities,

660   female chimpanzees hunt significantly less often than adult males and that this difference is due to a

661   number of factors that constrain females. This has important implications for understanding the

662   evolution of human hunting patterns. We suggest that before the advent of social obligations regarding

663   sharing and provisioning, hominin females faced similar constraints as chimpanzees. An inherent sex

664   difference in hunting behavior would have provided the basis for the evolution of the sexual division of

665   labor among modern humans. Finally, our study identifies the need to more fully understand the

666   constraints that modem humans face. What factors other than the prospect of sharing and provisioning

667   affect what (and when) women hunt? For example, we are not aware of data from human populations

668   on sex differences in prey encounter rate. We suggest that the current study can be used as a model for

669   future research on human hunting patterns.

670

686

694

695   **References**

696   Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour. 49, 227–267.

697   Bartoń, K., 2014. MuMIn: Multi-model inference.

698   Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., 2014. lme4:

699   Linear mixed-effects models using Eigen and S4.

700   http://cran.rproject.org/web/packages/lme4/index. html.

701   Bliege Bird, R., Codding, B.F., 2015. The Sexual Division of Labor. In: Emerging Trends in the Social and

702   Behavioral Sciences. John Wiley & Sons, Inc., Hoboken, NJ, USA, pp. 1–16.

703   Bliege Bird, R.L., Bird, D.W., 2008. Why Women Hunt. Current Anthropology. 39, 655–683.

704   Boesch, C., 1994. Cooperative hunting in wild chimpanzees. Animal Behaviour. 48, 653–667.

705   Boesch, C., Boesch, H., 1981. Sex differences in the use of natural hammers by wild chimpanzees: A

706   preliminary report. Journal of Human Evolution. 10, 585–593.

707   Boesch, C., Boesch, H., 1984. Possible causes of sex differences in the use of natural hammers by wild

708   chimpanzees. Journal of Human Evolution. 13, 415–440.

709   Boesch, C., Boesch, H., 1989. Hunting behavior of wild chimpanzees in the Taï National Park. American

710   Journal of Physical Anthropology. 78, 547–573.

711   Boesch, C., Boesch-Achermann, H., 2000. The Chimpanzees of the Taï Forest: behavioural ecology and

712   evolution. Oxford University Press, Oxford.

713   Brown, J.L., 1983. Cooperation - a biologist's dilemma. In: Rosenblatt, J.S. (Ed.), Advances in Behaviour.

714   Academic Press, New York, pp. 1–37.

715   Clutton-Brock, T.H., Gillett, J.B., 1979. A survey of forest composition in the Gombe National Park,

716   Tanzania. African Journal of Ecology. 17, 131–158.

717   Connor, R.C., 1995. The benefits of mutualism: a conceptual framework. Biological Reviews of the

718   Cambridge philosophical society. 70, 427–457.

719   Emery Thompson, M., 2013. Reproductive Ecology of Female Chimpanzees. American Journal of

720   Primatology. 75, 222–237.

721   Emery Thompson, M., Jones, J.H., Pusey, A.E., Brewer-Marsden, S., Goodall, J., Marsden, D., Matsuzawa,

722   T., Nishida, T., Reynolds, V., Sugiyama, Y., Wrangham, R.W., 2007. Aging and fertility patterns in

723   wild chimpanzees provide insights into the evolution of menopause. Current Biology. 17, 2150–6.

724   Foerster, S., Franz, M., Murray, C.M., Gilby, I.C., Feldblum, J.T., Schroepfer-Walker, K., Pusey, A.E., in

725   revision. Chimpanzee females queue but males strive for social status.

726   Gilby, I.C., Eberly, L.E., Pintea, L., Pusey, A.E., 2006. Ecological and social influences on the hunting

727   behaviour of wild chimpanzees (*Pan troglodytes schweinfurthii*). Animal Behaviour. 72, 169–180.

728   Gilby, I.C., Eberly, L.E., Wrangham, R.W., 2008. Economic profitability of social predation among wild

729   chimpanzees: individual variation promotes cooperation. Animal Behaviour. 75, 351–360.

730   Gilby, I.C., Machanda, Z.P., Mjungu, D.C., Rosen, J., Muller, M.N., Pusey, A.E., Wrangham, R.W., 2015.

731   "Impact hunters" catalyse cooperative hunting in two wild chimpanzee communities. Philosophical

732   Transactions of the Royal Society B: Biological Sciences. 370, 20150005.

733   Gilby, I.C., Wilson, M.L., Pusey, A.E., 2013. Ecology rather than psychology explains co-occurrence of

734   predation and border patrols in male chimpanzees. Animal Behaviour. 86, 61–74.

735   Gilby, I.C., Wrangham, R.W., 2007. Risk-prone hunting by chimpanzees (*Pan troglodytes schweinfurthii*)

736   increases during periods of high diet quality. Behavioral Ecology and Sociobiology. 61, 1771–1779.

737   Goodall, J., 1986. The chimpanzees of Gombe: patterns of behavior. Harvard University Press,

738   Cambridge, MA.

739   Gurven, M., Hill, K., 2009. Why Do Men Hunt? A Reevaluation of "Man the Hunter" and the Sexual

740   Division of Labor. Current Anthropology. 50, 51–74.

741   Hawkes, K., 1991. Showing off: tests of a hypothesis about men's foraging goals. Ethology and

742   Sociobiology. 12, 29–54.

743   Hill, K.R., Kaplan, H.S., Hawkes, K., Hurtado, A.M., 1985. Men's time allocation to subsistence work

744   among the Ache of eastern Paraguay. Human Ecology. 13, 29–47.

745   Hohmann, G., Fruth, B., 2007. New records on prey capture and meat eating by bonobos at Lui Kotale,

746   Salonga National Park, Democratic Republic of Congo. Folia Primatologica. 79, 103–110.

747   Hothorn, T., Frank, B., Westfall, P., 2008. Simultaneous Inference in General Parametric Models.

748   Biometrical Journal. 50, 346–363.

749   Hurtado, A.M., Hawkes, K., Hill, K.R., Kaplan, H.S., 1985. Female subsistence strategies among the Ache

750   hunter-gatherers of eastern Paraguay. Human Ecology. 13, 1–28.

751   Kitanishi, K., 1995. Seasonal changes in the subsistence activities and food intake of the aka hunter-

752   gatherers in northeastern Congo. African Study Monographs. 16, 73–118.

753   Langergraber, K.E., Prufer, K., Rowney, C., Boesch, C., Crockford, C., Fawcett, K., Inoue, E., Inoue-

754   Muruyama, M., Mitani, J.C., Muller, M.N., Robbins, M.M., Schubert, G., Stoinski, T.S., Viola, B.,

755   Watts, D., Wittig, R.M., Wrangham, R.W., Zuberbuhler, K., Paabo, S., Vigilant, L., 2012. Generation

756   times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human

757   evolution. Proceedings of the National Academy of Sciences. 109, 15716–15721.

758   Marlowe, F.W., 2007. Hunting and Gathering: The Human Sexual Division of Foraging Labor. Cross-

759   Cultural Research. 41, 170–195.

760   Marlowe, F.W., 2010. The Hadza: Hunter-gatherers of Tanzania. University of California Press, Berkeley,

761   California.

762   McGrew, W.C., 1979. Evolutionary implications of sex differences in chimpanzee predation and tool use.

763   In: Hamburg, D.A., McCown, E.R. (Eds.), The Great Apes. Benjamin Cummings, London, pp. 441–

764   463.

765   McGrew, W.C., 1992. Chimpanzee material culture. Cambridge University Press, Cambridge.

766   Mitani, J.C., Watts, D.P., 1999. Demographic influences on the hunting behavior of chimpanzees.

767   American Journal of Physical Anthropology. 109, 439–454.

768   Mitani, J.C., Watts, D.P., 2001. Why do chimpanzees hunt and share meat? Animal Behaviour. 61, 915–

769   924.

770   Muller, M.N., Wrangham, R.W., Pilbeam, D., in revision. Chimpanzees and human evolution. Harvard

771   University Press, Cambridge MA.

772   Murray, C.M., Mane, S., Pusey, A.E., 2007. Dominance rank influences female space use in wild

773   chimpanzees, *Pan troglodytes*: towards an ideal despotic distribution. Animal Behaviour. 74, 1795–

774   1804.

775   Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A.M., Agil, M., Widdig, A., Engelhardt, A., 2011.

776   Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-

777   rating. Animal Behaviour. 82, 911–921.

778   Newton-Fisher, N.E., 2014. The hunting behavior and carnivory of wild chimpanzees. In: Henke, W.,

779   Tattersall, I. (Eds.), Handbook of Paleoanthropology, Vol. II. Springer-Verlag, Berlin, pp. 1–19.

780   Nishida, T., Hiraiwa, M., 1982. Natural history of a tool-using behavior by wild chimpanzees in feeding

781   upon wood-boring ants. Journal of Human Evolution. 11, 73–99.

782   Noss, A.J., Hewlett, B.S., 2001. The contexts of female hunting in central africa. American

783   Anthropologist. 103, 1024–1040.

784   O'Malley, R.C., Stanton, M.A., Gilby, I.C., Lonsdorf, E. V, Pusey, A.E., Markham, A.C., Murray, C.M., 2016.

785   Reproductive state and rank influence patterns of meat consumption in wild female chimpanzees

786   (*Pan troglodytes schweinfurthii*). Journal of Human Evolution. 90, 16–28.

787   Patterson, N., Richter, D.J., Gnerre, S., Lander, E.S., Reich, D., 2006. Genetic evidence for complex

788   speciation of humans and chimpanzees. Nature. 441, 1103–1108.

789   Perry, S., Ordoñez Jiménez, J.C., 2006. The effects of food size, rarity, and processing complexity on

790   white-faced capuchins' visual attention to foraging conspecifics. In: Hohmann, G., Robbins, M.M.,

791   Boesch, C. (Eds.), Feeding Ecology in Apes and Other Primates: Ecological, Physical and Behavioral

792   Aspects. Cambridge University Press, Cambridge, pp. 203–234.

793   Pontzer, H., Raichlen, D.A., Wood, B.M., Emery Thompson, M., Racette, S.B., Mabulla, A.Z.P., Marlowe,

794   F.W., 2015. Energy expenditure and activity among Hadza hunter-gatherers. American Journal of

795   Human Biology. 27, 628–637.

796   Pruetz, J.D., Bertolani, P., 2007. Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. Current

797   Biology. 17, 412–417.

798   Pruetz, J.D., Bertolani, P., Ontl, K.B., Lindshield, S., Shelley, M., Wessling, E.G., 2015. New evidence on

799   the tool-assisted hunting exhibited by chimpanzees (*Pan troglodytes verus*) in a savannah habitat

800   at Fongoli, Sénégal. Royal Society Open Science. 2, 140507.

801   Pusey, A.E., Oehlert, G.W., Williams, J.M., Goodall, J., 2005. Influence of Ecological and Social Factors on

802   Body Mass of Wild Chimpanzees. International Journal of Primatology. 26, 3–31.

803   Pusey, A.E., Schroepfer-Walker, K., 2013. Female competition in chimpanzees. Philosophical

804   Transactions of the Royal Society of London. Series B, Biological sciences. 368, 20130077.

805   R Development Core Team, 2015. R: A language and environment for statistical computing. R

806   Foundation for Statistical Computing, Vienna, Austria.

807   Rose, L.M., Perry, S., Panger, M. a, Jack, K., Manson, J.H., Gros-Louis, J., Mackinnon, K.C., Vogel, E., 2003.

808   Interspecific interactions between *Cebus capucinus* and other species: data from three Costa Rican

809   sites. International Journal of Primatology. 24, 759–796.

810   Stanford, C.B., 1998. Chimpanzee and red colobus. Harvard University Press, Cambridge, MA.

811   Stanford, C.B., 2012. Chimpanzees and the behavior of *Ardipithecus ramidus*. Annual Review of

812   Anthropology. 41, 139–149.

813   Stanford, C.B., Wallis, J., Matama, H., Goodall, J., 1994a. Patterns of predation by chimpanzees on red

814   colobus monkeys in Gombe National Park, 1982-1991. American Journal of Physical Anthropology.

815   94, 213–228.

816   Stanford, C.B., Wallis, J., Mpongo, E., Goodall, J., 1994b. Hunting decisions in wild chimpanzees.

817   Behaviour. 131, 1–18.

818   Surbeck, M., Fowler, A., Deimel, C., Hohmann, G., 2009. Evidence for the Consumption of Arboreal,

819   Diurnal Primates by Bonobos (*Pan paniscus*). American Journal of Primatology. 71, 171–174.

820   Surbeck, M., Hohmann, G., 2008. Primate hunting by bonobos at LuiKotale, Salonga National Park.

821   Current Biology. 18, R906–R907.

822   Takahata, Y., Hasegawa, T., Nishida, T., 1984. Chimpanzee predation in the Mahale Mountains from

823   August 1979 to May 1982. International Journal of Primatology. 5, 213–233.

824   Tanaka, J., 1980. The San, hunter-gatherers of the Kalahari: A study in ecological anthropology.

825   University of Tokyo Press, Tokyo.

826   Trivers, R.L., 1972. Parental investment and sexual selection. In: Campbell, B. (Ed.), Sexual Selection and

827   the Descent of Man. Aldine, Chicago, pp. 136–179.

828   Uehara, S., 1997. Predation on mammals by the chimpanzee (*Pan troglodytes*). Primates. 38, 193–214.

829   Walker, K.K., 2015. Dispersal and integration in female chimpanzees. Ph.D. Dissertation, Duke University.

830   Watts, D.P., Mitani, J.C., 2002a. Hunting behavior of chimpanzees at Ngogo, Kibale National Park,

831   Uganda. International Journal of Primatology. 23, 1–28.

832   Watts, D.P., Mitani, J.C., 2002b. Hunting and meat sharing by chimpanzees at Ngogo, Kibale National

833   Park, Uganda. In: Boesch, C., Hohmann, G., Marchant, L. (Eds.), Behavioural Diversity in

834   Chimpanzees and Bonobos. Cambridge University Press, Cambridge, pp. 244–255.

835   West-Eberhard, M.J., 1975. The evolution of social behavior by kin selection. Quarterly Review of

836   Biology. 50, 1–33.

837   Wilson, M.L., 2012. Long-term studies of the chimpanzees of Gombe National Park, Tanzania. In:

838   Kappeler, P.M., Watts, D.P. (Eds.), Long-Term Field Studies of Primates. Springer-Verlag, Berlin

839   Heidelberg, pp. 357–384.

840   Wilson, M.L., Kahlenberg, S.M., Wells, M., Wrangham, R.W., 2012. Ecological and social factors affect

841   the occurrence and outcomes of intergroup encounters in chimpanzees. Animal Behaviour. 83,

842   277–291.

843   Wood, B., Gilby, I.C., in revision. Pan the hunter. In: Muller, M.N., Wrangham, R.W. (Eds.), Pancestor:

844   Chimpanzees and Human Evolution. Harvard University Press

845   Wood, B.M., Marlowe, F.W., 2013. Household and kin provisioning by hadza men. Human Nature. 24,

846   280–317.

847   Wrangham, R.W., 2000. Why are male chimpanzees more gregarious than mothers? A scramble

848   competition hypothesis. In: Kappeler, P.M. (Ed.), Primate Males: Causes and Consequences of

849   Variation in Group Composition. Cambridge University Press, Cambridge, pp. 248–258.

850   Wrangham, R.W., Bergmann-Riss, E., 1990. Rates of predation on mammals by Gombe chimpanzees,

851   1972-1975. Primates. 31, 157–170.

852   Wrangham, R.W., Clark, A.P., Isabirye-Basuta, G., 1992. Female social relationships and social

853   organization of Kibale forest chimpanzees. In: Nishida, T., McGrew, W.C., Marler, P., Pickford, M.,

854   de Waal, F.B.M. (Eds.), Topics in Primatology. Vol. 1. Human Origins. Tokyo University Press, Tokyo,

855   pp. 81–98.

856 Wrangham, R.W., Pilbeam, D., 2001. African apes as time machines. In: Galdikas, B., Briggs, N., Sheeran,

857   L., Shapiro, G., Goodall, J. (Eds.), All Apes Great and Small, Volume I: African Apes. Kluwer

858   Academics / Plenum Publishers, New York, pp. 5–17.

859 Wrangham, R.W., Smuts, B., 1980. Sex differences in the behavioral ecology of chimpanzees in the

860   Gombe National Park, Tanzania. Journal of Reproduction and Fertility, Supplement. 28, 13–31.

861

862

863 **Figure legends**

864 Figure 1. Relationship between the probability of hunting by a focal chimpanzee (when present at a red

865 colobus hunt attempt) and sex of the focal. These predicted values were calculated from the GLMM

866 described in the text, with error bars representing 1 standard error. Study period, and the number of

867 hunts and focal chimpanzees are reported for each community. ***P < 0.0001.

868

869 Figure 2. Prey type by sex of acquirer, Kasekela. Numbers indicate the total prey items for which the

870 identity of the killer was known. * P<0.05; ** P<0.005. P-values based on GLMs described in the text,

871 which controlled for the number of male and female chimpanzees present at a kill.

872

873 Figure 3. Likelihood of carcass theft vs. sex of possessor and number of adult male chimpanzees present,

874 Kasekela. Number of adult males was divided into categories for illustration only. In parties with more

875 males, females were more likely to have the carcass stolen than in parties with fewer males. Males

876 rarely had carcasses stolen, and were not affected by adult male party size. Numbers indicate sample

877 sizes.

878

879 **Tables and table legends**

Hypothesis	Predictions	Supported?		
		Kasekela	Mitumba	Kanyawara
Opportunity	1) Chimp parties smaller for terrestrial/sedentary prey	Y	N	
	2) Females encounter red colobus less often than males do	Y	N	Y
	3) Frequency of red colobus hunting correlates positively with female gregariousness	Y	Y	Y
	4) When present at a red colobus hunt, males and females equally likely to participate.	N	N	N
Risk-sensitivity	1) Females will specialize in terrestrial or sedentary prey	Y	Y	
	2) At a red colobus hunt, a female will be :			
	a) less likely to participate with clinging offspring	N	N	N
	b) more likely to participate if high-ranking	Y	N	N
Male appropriation	1) Likelihood of carcass theft higher for females	Y	N	
	2) Stealing from females will occur more often in parties with many adult males	Y		N
	3) At a hunt, the probability that a female participates will be negatively correlated with # males present	Y	N	N

880

881 **Table 1**: Summary of hypotheses, predictions and results. Grey cells indicate that a prediction could not

882 be tested in a particular community. See text for explanation.

Community	Sex of Killer	All Prey	Red colobus	Black & white colobus	Red-tailed monkey	Blue monkey	Grey-cheeked mangabey	Total	Bushpig	Baboon	Vervet monkey	Total	Bushbuck	Bird	Red duiker	Rodent	Egg	Galago	Lizard	Bat	Unknown	Total
			Arboreal Monkeys						Terrestrial/Active				Concealed/sedentary/other									
Kasekela 1976-2013	M	1556	1359.5		10.5	3		1373	84.5	55	1	140.5	26.5	12		2	1			1		42.5
	F	263	163.5		5.5	4		173	23.5	7		30.5	22.5	27		2	7	1	1			60.5
	U	387	290		6	3		299	31	22		53	34	1								35
	Total	2206	1813		22	10		1845	139	84	1	224	83	40		4	8	1	1	1		138
	% by F†	14.5	10.7		34.4	57.1		11.2	21.8	11.3	0	17.8	45.9	69.2			87.5					58.7
Mitumba 2000-2014	M	174.5	150.5		3	1		154.5	11	3		14	6									6
	F	47.5	35.5		1	1		37.5	1			1	5	2		1	1					9
	U	32	22		2			24	2			2	6									6
	Total	254	208		6	2		216	14	3		17	17	2		1	1					21
	% by F†	21.4	19.1		25	50		19.5	8.3	0		6.7	45.5	100		100	100					60
Kanyawara 1996-2015	M	238	203	30	1	2	2	238														0
	F	23	11	6	3	3		23														0
	U	88	74	8	1	1		84								1					3	4
	Total	349	288	44	5	6	2	345								1					3	4
	% by F†	8.8	5.1	16.7	75	60	0	8.8														

†Only cases when sex of acquirer is known

Table 2: Predation totals by community, sex of killer and prey type. Sex of killer: M = Male, F = Female, U = Unknown. Decimals arise when one prey item is captured jointly by a male and a female - each was credited with half of the kill. Shaded cells indicate absence of that species at that site.

Community	Fixed Effect	Estimate	Z	P-value
Kasekela	Intercept	-4.29	-1.28	0.2
	Scaled Elo-rating	**0.93**	**2.01**	**0.04**
	Offspring <= 2yr	0.18	0.76	0.45
	Adult males	**-0.06**	**-2**	**0.04**
Mitumba	Intercept	-0.25	-0.39	0.7
	Scaled Elo-rating	-0.61	-0.96	0.34
	Offspring <= 2yr	0.08	0.18	0.86
	Adult males	-0.26	-1.25	0.21
Kanyawara	**Intercept**	**-6.4**	**-2.76**	**0.006**
	Scaled Elo-rating	-0.17	-0.19	0.85
	Offspring <= 2yr	**0.82**	**1.93**	**0.050**
	Adult males	0.18	1.15	0.25

888

889 **Table 3:** Summary of GLMMs of female hunting probability (Y/N) vs. dominance rank, clinging offspring

890 and adult male party size. Bold indicates statistical significance.

891

Fixed Effect	Estimate	Z	P-value
Intercept	**-2.66**	**-2.99**	**0.003**
Female possessor (Y)	0.25	0.238	0.81
# Adult Males	-0.08	-0.69	0.49
Female Possessor (Y)* #Adult Males	**0.29**	**2.2**	**0.03**

892

893 **Table 4.** Output of GLMM of the probability of having a carcass stolen vs. sex of the possessor and the
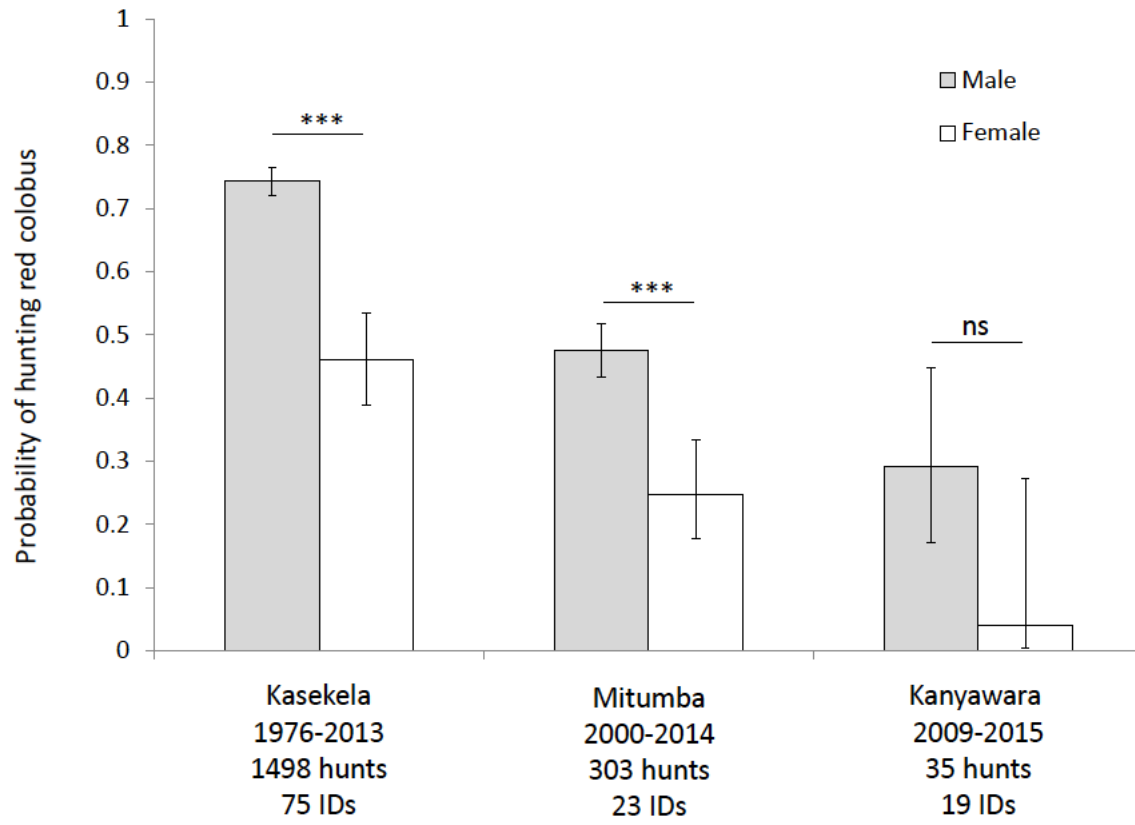
894 number of adult males present, Kasekela. Bold indicates statistical significance
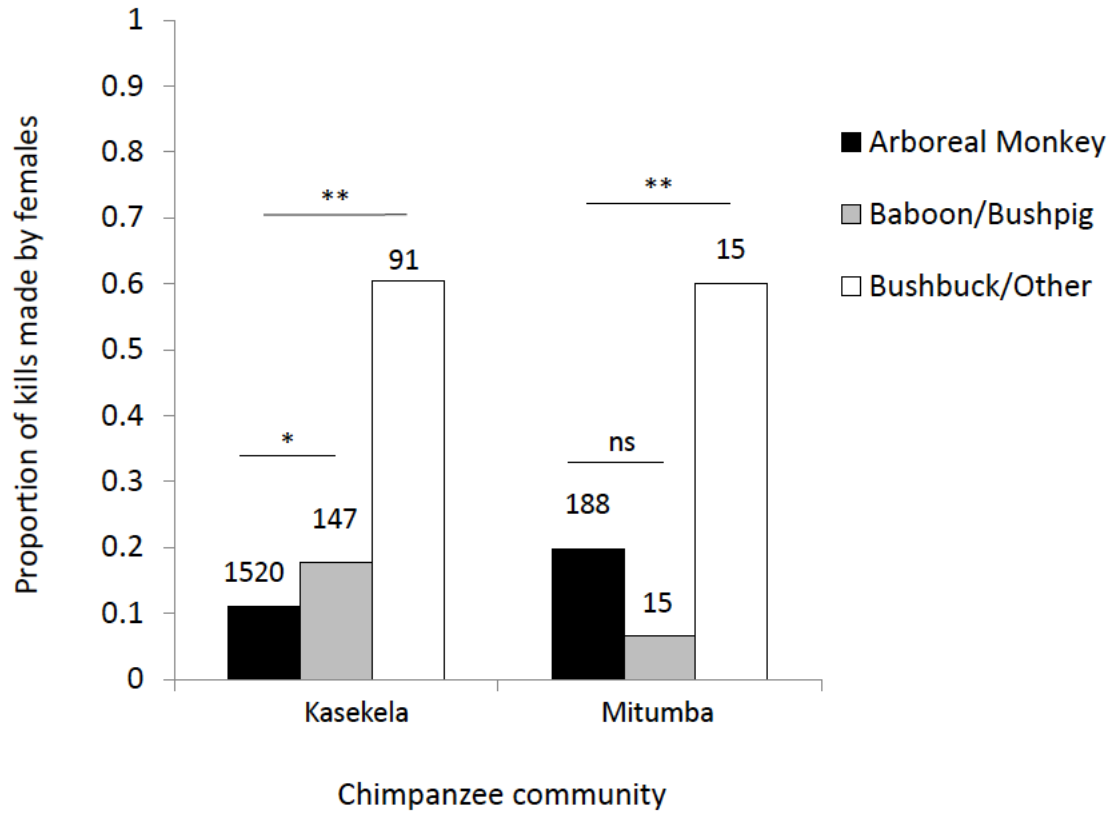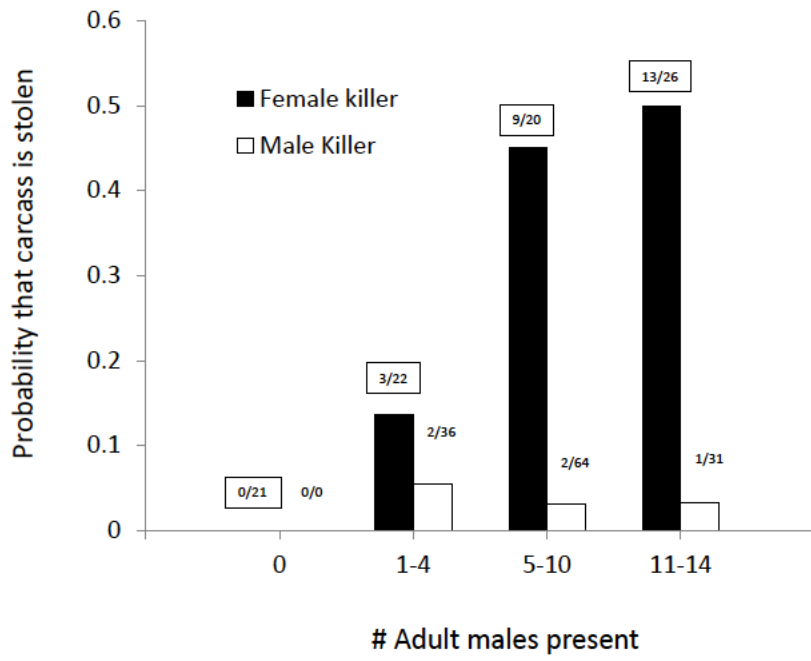
895

896

897   Fig. 1

898

899

900

901   Fig. 2

902

903

904

905

906   Fig. 3

907

908