Social rank overrides environmental and community fluctuations in determining meat access by female chimpanzees in the Taï National Park, Côte d'Ivoire

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Meat, long hypothesized as an important food source in human evolution, is still a substantial component of the modern human diet, with some humans relying entirely on meat during certain times of the year. Understanding the socio-ecological context leading to the successful acquisition and consumption of meat by chimpanzees (*Pan troglodytes*), our closest living relative, can provide insight into the emergence of this trait because humans and chimpanzees are unusual among primates in that they both (i) frequently hunt mammalian prey, (ii) share meat with community members, and (iii) form complex social hierarchies within their communities. However, females in both human hunter-gatherer societies as well as chimpanzee groups rarely hunt, instead typically access meat via males that share the prey with conspecifics. In female chimpanzees, dominance rank affects feeding competition in general, but the effect on meat access found different results within and across study groups. Here we contribute to this debate on how rank influences meat access while controlling for a wider spectrum of socio-ecological control variables than has previously been considered. Multivariate analyses of 773 separate meat-eating events collected from more than 25 years from two Taï chimpanzee communities were used to test the importance of female dominance rank for being present, and for acquiring meat during meat-eating events. We found that high-ranking females were more likely to be present during a meat-eating event and, in addition, they were more likely to eat meat compared to the subordinates. These findings of the importance of female social rank were robust to large demographic changes (decrease of community size) and as well as seasonal ecological changes (fruit abundance dynamics).

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22 **Abstract**

23   Meat, long hypothesized as an important food source in human evolution, is still a

24 substantial component of the modern human diet, with some humans relying entirely on meat

25 during certain times of the year. Understanding the socio-ecological context leading to the

26 successful acquisition and consumption of meat by chimpanzees (*Pan troglodytes*), our closest

27 living relative, can provide insight into the emergence of this trait because humans and

28 chimpanzees are unusual among primates in that they both (i) frequently hunt mammalian prey,

29 (ii) share meat with community members, and (iii) form complex social hierarchies within their

30 communities. However, females in both human hunter-gatherer societies as well as chimpanzee

31 groups rarely hunt, instead typically access meat via males that share the prey with conspecifics.

32 In female chimpanzees, dominance rank affects feeding competition in general, but the effect on

33 meat access found different results within and across study groups.

34   Here we contribute to this debate on how rank influences meat access while controlling for

35 a wider spectrum of socio-ecological control variables than has previously been considered.

36 Multivariate analyses of 773 separate meat-eating events collected from more than 25 years from

37 two Taï chimpanzee communities were used to test the importance of female dominance rank for

38 being present, and for acquiring meat during meat-eating events. We found that high-ranking

39 females were more likely to be present during a meat-eating event and, in addition, they were more

40 likely to eat meat compared to the subordinates. These findings of the importance of female social

41 rank were robust to large demographic changes (decrease of community size) and as well as

42 seasonal ecological changes (fruit abundance dynamics).

43   In addition to social rank, we found that other female properties had a positive influence

44 on meat access and presence at meat-eating events, including oestrus status, nursing of a small

45 infant, and age. Similar to findings in other chimpanzee populations, our results suggest that

46 females reliably acquire meat over their lifetime even if they are rarely active hunters. We discuss

47 our findings and offer implications of this study for chimpanzee understanding.

48

49 **Introduction**

50   Hunting and meat eating are considered important behaviors shaping early hominid

51 evolution and are proposed to be key innovations in the evolution of Australopithecines to *Homo*

52 *erectus* (Isaac, 1978; Washburn, 1978; Leakey, 1981; Hill, 1982). In particular, meat consumption

53 has for at least several decades been suggested as the food that powered brain expansion in human

54 evolution (Washburn & Lancaster, 1968; Milton, 1999). Meat has become a substantial component

55 in many modern human diets, recently averaging 42 kg of meat per capita per year (Faostat, 2014).

56   Placed within the context of human evolution, observations of hunting and meat eating

57 in our closest living relatives, chimpanzees (*Pan troglodytes*), are critical in helping to reconstruct

58 early human behaviors (Wrangham, 1987; Boesch-Acherman & Boesch, 1994). Since early-

59 published records of chimpanzee hunting and meat eating by Jane Goodall (1963), numerous other

60 field studies have reported these as common chimpanzee behaviors (Boesch & Boesch, 1989;

61 Uehara et al., 1992; Boesch & Boesch-Achermann, 2000; Mitani & Watts, 1999). Although

62 chimpanzee diets are composed primarily of fruits (Goodall, 1968; Sugiyama & Koman, 1992;

63 Morgan & Sanz, 2006), meat is considered an important food source year round, making up to 9%

64 of their activity budget, with males and females eating an average of 186 g and 25 g of meat per

65 day, respectively (Boesch & Boesch-Achermann, 2000). Because of its high quality calorific

66 package of protein, fat and micronutrients that are difficult to find in plant foods (Milton, 2003;

67   Tennie et al., 2009); the nutritional value of meat is not easily to substitute (Goodall, 1986; Boesch

68   & Boesch-Achermann, 2000).

69   Yet how meat is acquired, and the value of meat across individuals is not uniform within

70   and across gender. A stable isotope study of hair and bones confirmed sex differences in meat

71   consumption, with higher levels of meat eating among Taï chimpanzee males compared to females

72   (Fahy et al., 2013).

73   Social rank can also play an important role in the access and consumption of meat

74   (O'Malley et al., 2016, but see Samuni et al., 2018b). A study of Gombe chimpanzees showed that

75   females use their dominance rank position to maximize their access to meat, with high-ranking

76   females consuming more meat than subordinates (O'Malley et al., 2016). Further, it has been

77   shown that meat is an important food source for female chimpanzees during periods of pregnancy

78   and nursing (O'Malley et al., 2016), a nutritionally and energetically costly body state for females

79   (Clutton-Brock & Harvey, 1978; Thompson et al., 2012). The Gombe study found an interaction

80   between reproductive state and rank, and revealed that high-ranking females do not differ in meat

81   consumption between different reproductive states, but low-ranking females do, with low-ranking

82   females consuming more meat during pregnancy than during lactation and baseline (not pregnant/

83   not lactating females) (O'Malley et al., 2016). In Sonso chimpanzees of the Budongo forest in

84   Uganda, high-ranking individuals monopolize meat irrespective of their own hunting role, whereas

85   in the neighbouring Waibira community no rank effect on meat access was found (Hobaiter et al.,

86   2017). Dominance rank has been shown to affect sociality, ranging, and feeding competition in

87   female chimpanzees at Gombe (Pusey et al., 1997; 2005; Williams et al., 2002a;b; Murray et al.,

88   2006; 2007) and Kibale (Thompson et al., 2007; 2010; Kahlenberg et al., 2008).

89   In the Taï National Park in Côte d'Ivoire, male chimpanzees are primarily the hunters; they

90   capture the prey in most cases, and subsequently share it with their community members (Boesch

91   & Boesch-Achermann, 2000; Samuni et al., 2018b). Females participate in hunts much less than

92   males, with their involvement in hunting being approximately 13%-15% (Boesch & Boesch, 1989;

93   Samuni et al., 2018b). The majority of meat (98%) in these groups is accessed via sharing (Samuni

94   et al., 2018b). Because hunting participation can largely determine meat access (Boesch & Boesch-

95   Achermann, 2000; Samuni et al., 2018b), the consumption of meat is not evenly distributed

96   between community members, resulting in some individuals frequently not receiving meat while

97   others obtain it regularly (Boesch & Boesch, 1989; Boesch, 1994; Boesch & Boesch-Achermann,

98   2000).

99   In the absence of hunting participation, "cheating", defined as consuming meat from a

100   successful hunt that an individual did not participate in, can occur. By cheating, females are able

101   to increase their caloric intake without suffering the energetic costs related to hunting. Females are

102   more successful at cheating than males because male hunters tolerate female cheaters much more

103   than male cheaters (Boesch & Boesch-Achermann, 2000). Female cheaters also receive more meat

104   than male cheaters, accessing meat in 15% versus 48% by males of the all prey captures (Boesch

105   & Boesch-Achermann, 2000).

106   Male hunters share meat unevenly with females, and males might share with cheating

107   females because females copulated more with males who shared meat with them than with males

108   who did not share meat with them, irrespective of e.g. male rank, female rank, or age (Gomes &

109   Boesch, 2009). Despite the low frequency in which females participate in hunting, some high-

110   ranking females in the Taï North group can reach a very high status in the meat access order

111   although they did not participate in the hunt, occasionally even surpassing low and middle ranking

112   males (Boesch & Boesch-Achermann, 2000). Because females can benefit from sharing by males,

113   it is of interest whether social rank can increase cheating opportunities. In the Taï North group,

114   high-ranking females monopolize and possess the food after a dyadic female/female food conflict

115   (Wittig & Boesch, 2003). Recent results investigating all food sharing events in Taï South and East

116   groups found a three-way interaction between rank of the beggar and the possessor with sex on

117   food access through sharing (Samuni et al., 2018a), indicating that rank neighbours were sharing

118   more than dyads with a larger rank asymmetry. When investigating access to meat only, however,

119   another study on the same chimpanzee groups found an impact of hunt participation, age, prey size

120   and fruit availability on meat consumption, but none by sex or dominance rank (Samuni et al.,

121   2018b).

122   Here we utilize a large, long-term (greater than 25 years) dataset that enables a wider

123   spectrum of socio-ecological control variables, such as community size and fruit abundance, to

124   detect the long-term importance of different social factors on female success to access meat. The

125   central two hypotheses tested here are that in comparison to lower ranking females, high-ranking

126   females are more likely to (1) be present during a meat eating event, and to (2) have increased

127   access to meat given both are at a meat eating event. The primary predictor variable of interest

128   here is female dominance rank, while controlling for age, oestrous status and the nursing of a small

129   infant, important factors in determining feeding competition more broadly (Riedel et al., 2011;

130   O'Malley et al., 2016) and hence important control variables to include when testing for the

131   importance of rank. We added socio-ecological control variables such as community size and fruit

132   abundance to test for the robustness of rank effects besides seasonal ecological changes and large

133   demographic changes (decrease of community size).

134

135 **Materials & Methods**

136 *Study site and data collection*

137   We analysed meat-eating data from two habituated chimpanzee communities in Taï

138 National Park, henceforth labelled North and South due to the relative geographic locations of

139 their territories. Habituation of the North and South groups started in 1979 and 1989, respectively.

140 Researchers and local field assistants have since continuously observed both communities. During

141 the study period, the North group decreased from 76 to 19 individuals and the South group from

142 56 to 39 chimpanzees (Figure 1), largely related to disease outbreaks, poaching and not to food

143 availability.

144   Human observers carried out daily focal animal follows (Altmann, 1974) using

145 standardised check-sheets and shifted to *ad libitum* data recording for hunting and meat eating

146 events. Inter-observer reliability among Taï assistants is very good (Deschner et al., 2004; Riedel

147 et al., 2011). During the daily focal animal follows, the observers make continuous records of

148 social interactions, party composition, and number and identity of females in oestrous encountered

149 by the focal chimpanzee throughout the observation day. From these focal data, we were able to

150 identify female dominance rank and the oestrous status. At hunting and meat eating events, the

151 assistants changed the focus from the focal animal to the whole hunting and meat-eating situation

152 and recorded as much information as possible about all visible individuals and interactions

153 between them. At meat eating events, observers noted which chimpanzees were present, who held

154 the prey, dyadic membership in meat sharing events, who was begging, who ate meat, who was

155 aggressive and received aggression, as well as consumption time and prey details such as species

156 and age-class. From the *ad libitum* data, we obtained information on whether a female was present

157 or not within the meat-eating party, and whether the female got meat or not. The dataset covers a

158   27-year period for the North group (1987 - 2014) with 451 meat-eating events, and a 15-year period

159   for the South group (1999 - 2014) with 376 meat-eating events. Due to logistical constraints, not

160   all meat-eating events during this period were recorded.

161   Our meat eating analyses focused on adult females, defined to be 13 years or more (Boesch

162   & Boesch-Achermann, 2000), with 39 adult females from the North group and 33 females from

163   the South group. Females in Taï give birth to their first infant when they are approximately 13

164   years old, at this age they are also fully grown and defined to be adult (Boesch & Boesch-

165   Achermann, 2000).

166   From the 827 observed meat-eating events, 773 had at least one adult female present and

167   these were used for analysis. Analysis of data for which at least one female from each rank category

168   was present (N=464) did not differ from the results using the full dataset; thus we present results

169   based on the entire 773 events dataset. The meat eating events were almost entirely on separate

170   days (to 94%) with a mean interval of 17 days (range of 1-254) for South and 25 days (range 1-

171   289) for North group.

172   Assistants trained in botanical monitoring censused fruit tree phenology every month using

173   established routes in both chimpanzee territories. They also noted the presence of ripe fruits of tree

174   species whose fruits were chimpanzee foods (Anderson et al., 2002; 2005; Polansky & Boesch,

175   2013).

176   All field protocols, data collection procedures, and data analyses were conducted in

177   accordance with wildlife research protocols and ethical standards of the Max Planck Society in

178   Germany, "Ministère de l'Enseignement supérieur et de la Recherche scientifique", "Ministère des

179   Eaux et Forêts", and "Office Ivoirien des Parcs et Réserves" in Côte d'Ivoire.

180

181   *Data analysis, model predictors and motivations*

182   We constructed and analysed two models for the response variables of (i) whether a female

183   was present or absent in the meat eating party (hypothesis 1) and (ii) whether the female did or did

184   not receive meat (hypothesis 2). Both models therefore have a bivariate response variable. We

185   considered four 'individual female' properties and 'socio-ecological' properties as predictor

186   variables, with interactions between some of these predictors, which we describe next.

187   Dominance rank

188   According to Wittig and Boesch (2003), we expected linear dominance hierarchies for the

189   adult females in Taï. Using the software package MatMan (De Vries 1995), we determined annual

190   linear dominance hierarchies following the direction of greeting behaviour: pant-grunts (PG),

191   greeting-hoohs (GH) and greeting-pants (GP) (Wittig & Boesch, 2003). Only 6 out of 44 annual

192   dominance hierarchies reached significance. The reasons why we rarely detected linear female

193   hierarchies are a high percentage of unknown dyadic dominance relationships between females

194   and years with just four adult females in the North group. Due to this, we implemented three rank

195   categories (high, middle and low) following the method used in Gombe by Pusey and colleagues

196   (1997). We determined rank categories as follows. High-ranking females either gave no greetings

197   to any females or gave occasional greetings to other high-ranking females and received greetings

198   from middle- and low-ranking females. Middle-ranking females greet to high- and some middle-

199   ranking females, and received greetings from low- and some middle-ranking females. Low-

200   ranking females rarely, if ever, received greetings from any adult females but often gave them to

201   middle- and high-ranking females. When there was no greeting behavior observed between a

202   female dyad in a certain year, we considered the ranks and interactions between these females in

203   the year before and after. Furthermore, we consulted other rank data published about the Taï

204 females (Boesch & Boesch-Achermann, 2000; Wittig & Boesch, 2003) and have always been able

205 to assign females to one of the three categories. Female rank categories remained stable across

206 years in both communities, with 58 of 80 females maintaining a single rank category over the study

207 period. Twenty-two females moved to the adjacent category, mostly from low to middle (10

208 females) and from middle to high (10 females). Only two females (one in each community)

209 dropped in rank from high to middle during the last years before death, as their physical condition

210 deteriorated. A recent study from Taï also found that female dominance hierarchies of both the

211 North and South group were largely stable over time and only few rank changes were described

212 (Mielke et al., in press).

213 Nursing a small infant

214   We controlled whether the female was nursing a small infant ($\leq$ 2 years old) at the day of

215 the meat-eating event because several studies have shown that chimpanzee mothers are less

216 gregarious (Goodall, 1986; Takahata, 1990; Sakura, 1994; Wrangham, 2000; Williams et al.,

217 2002b; Otali & Gilchrist, 2006; Murray et al., 2007; but also see Riedel et al., 2011). This suggests

218 that mothers with small infants avoid meat-eating events for the protection of their infants because

219 of the large party sizes and competitive interactions to access meat at these events (Boesch &

220 Boesch-Achermann, 2000). Alternatively, nursing females may disproportionately benefit from

221 the nutritive value of meat, so it is also plausible to predict that they would try to join meat-eating

222 events at higher frequencies. Males might prefer to share meat with mothers and their infants

223 (potentially their own offspring) as a provisioning strategy. In Gombe chimpanzees, the

224 reproductive state of females influenced meat consumption, with pregnant females consuming

225 more meat than lactating and not pregnant/ not lactating females (O'Malley et al., 2016).

226 Oestrous status

227   We controlled for oestrous state as females with a maximal sexual swelling are more

228   gregarious (Boesch & Boesch-Achermann, 2000) and adult males tend to share more meat with

229   oestrous than with anoestrous females in Taï National Park given their proportional representation

230   in hunting parties (Gomes & Boesch, 2009). Assistants recorded the oestrous status, which coded

231   sexual skin swellings after visual inspection following Furuichi (1987). Three stages of

232   tumescence were coded: (1) no swelling: minimal size and maximal degree of wrinkling; (2) partial

233   swelling: relative increase/decrease in size and loss/appearance of wrinkles compared with stage

234   1 or 3; (3) maximum swelling: maximum size with no wrinkles and tight appearance. For the

235   analysis we used whether the female had a maximal swelling at the meat-eating event.

236   Age

237   We controlled for the age of the adult female although Wittig and Boesch (2003) found

238   that female linear hierarchy in Taï was related to the outcome of the contest, while it was

239   independent of age. Other studies in Gombe and Mahale found that females increased their rank

240   as they aged (Nishida, 1989; Pusey et al., 1997). Older Taï chimpanzees gained more access to

241   meat (Samuni et al., 2018b).

242   Number of females and males

243   We controlled for the number of adult females and males present at the meat-eating event

244   because an increase in competitors also increases the within-group contest competition over food

245   (Wittig & Boesch, 2003), although sub-group size previously had no effect on meat consumption

246   in Taï East and South group (Samuni et al., 2018b).

247   Community ID

248   We controlled for potential differences across the two chimpanzee communities (Luncz et

249   al., 2012) and included to which community the female belonged (either North or South group).

250 Community size

251   Demography is a potential major driver of hunting behaviour whereby in large

252 communities hunting frequency increases as well as the number of hunters acting together (Boesch

253 & Boesch-Achermann, 2000; Mitani & Watts, 1999). Both affect the amount of meat available

254 within one community. Since over the study period, the community sizes of both communities

255 decreased dramatically (Figure 1), and for South group later increased again, we included into our

256 analysis monthly community size to test for the potential demographic effect that could

257 importantly affect the role of dominance on securing food and female meat access. Community

258 size for each of the two communities was recorded at monthly intervals and the size recorded

259 closest to the meat-eating event was used.

260 ---
261   Insert Figure 1 here
262 ---

263 Fruit abundance index

264   In Taï chimpanzees, meat accessibility increased with a decrease in fruit availability

265 (Samuni et al., 2018b). Therefore, we considered a monthly fruit abundance index (FAI) as an

266 ecological predictor variable for presence at meat-eating events and meat access. Chimpanzee

267 hunting behavior and meat eating frequency in Taï National Park is seasonal and peaks in

268 September / October each year (Boesch & Boesch-Achermann, 2000) at the beginning of a major

269 peak in the FAI (Figure 2; see also Polansky & Boesch, 2013). To obtain a monthly FAI we used

270 the monthly percentage of observed trees presenting ripe fruits eaten by the Taï chimpanzees

271 following Wrangham and colleges (1998).

272 ---
273   Insert Figure 2 here
274 ---

275   Interactions between some predictors

276   Rank effects might be different in North and South group, so we included an interaction of

277   female dominance rank and community ID into both models. Because intra-annual dynamics of

278   FAI are substantial (Anderson et al., 2005, Polansky & Boesch, 2013), we included an interaction

279   between FAI and female dominance rank into both models. In the presence model, community

280   size and number of adult females were highly correlated (Pearson coefficient = 0.97), so we choose

281   between the two variables and excluded community size from the analysis to test for the effect of

282   number of adult females. We included the interaction of number of females with rank into both

283   models. Female dominance rank might have less of an influence for presence at meat eating events

284   if the number of adult females is low and therefore there is less competition. The same might be

285   true for the access to meat, when there are many other female competitors at the meat-eating event,

286   high rank might have a strong influence on the chances of accessing meat. Whereas when there is

287   only a small number of other females present all of them independently of their rank might receive

288   parts of the males share.

289   In addition, we included the interaction between female dominance rank and oestrous status

290   into both models, because females in oestrous are very social and interesting for the males

291   (Deschner et al., 2004), and independent of their rank they might be present and access meat. So

292   not only high-ranking females in oestrus might get meat, but also low ranking females in oestrus.

293

294   *Statistical Analyses*

295   Generalized linear mixed models (GLMM) with a logit link function were built to analyze

296   the significance of the factors described above. The GLMM framework accommodates the

297   bivariate data (indicating either female presence or absence or whether or not she received meat,

298   given presence at a meat eating event), while the mixed structure (both fixed and random effects)

299   allows proper treatment of repeated measurements on individual females and meat eating events

300   due to unobserved variables (e.g. total amount of meat available). Fixed effect predictor variables

301   were adult female dominance rank, age, oestrous status, whether the individual was nursing an

302   infant, community ID, FAI, the number of adult males present, and number of adult females

303   present (community size was highly correlated with number of adult females in the presence

304   model). Random effects grouping variables were the individual female ID and the meat-eating

305   event ID. As discussed previously, for both models we included the interactions of dominance

306   rank and FAI, dominance rank and community ID, dominance rank and number of adult females

307   present, and dominance rank and oestrus status.

308   We fit models in the R version 3.5.2 environment (R Development Core Team, 2018) using

309   the lme4 package (Bates et al., 2015) and following the general guidelines described by Bolker

310   and colleges (2009). The general model building process proceeded by first fitting a model with

311   only random effects to ensure estimated standard deviations were not close to zero. For the

312   presence model, this revealed numerical issues when random slopes were allowed for categorical

313   predictor variables (oestrus, nursing an infant, and dominance rank), so these were removed prior

314   to estimating a null model with only an intercept and supported random effects. For the meat access

315   model, no random slopes were included to avoid numerical issues. Given the null model consisting

316   only of an intercept, random effects, and an overall variance estimate, the full model including

317   main effects and interactions along with random effects was compared to the null model using a

318   likelihood ratio test (LRT). Interaction terms were removed one at a time from the full model and

319   their statistical support quantified using LRTs. Because the interactions were not statistically

320   supported, reduced models that excluded all interaction terms was re-fit to facilitate direct

321   interpretation of the coefficient estimates, and the support for each of these main effects was

322   evaluated using LRTs by removing each predictor variable one at a time.

323   Prior to fitting the full GLMMs, we standardized continuous predictor variables to have

324   mean = 0 and standard deviation = 1 to increase model fitting stability. Furthermore,

325   multicollinearity was checked by examining the generalized variance inflation factors (GVIF; Zuur

326   et al., 2009) as implemented in the car package (Fox & Weisberg, 2011) in a full model without

327   interactions or random effects. This indicated that community size and number of females were

328   too correlated (GVIF = 21.094) to simultaneously include in the presence model. We checked

329   residual temporal autocorrelation and correlation with time since last observation within

330   individuals across events to ensure no systematic bias in predictions related to time. We remark

331   that there was no strong evidence (GVIF values always less than 2) that female age and dominance

332   rank were correlated.

333

334   **Results**

335   Seventy-two different adult females were observed, two of which never were present at

336   any meat-eating event. Of the 773 events, at least one low, middle, and high-ranking adult female

337   attended 530 (69%), 677 (88%), and 697 (90%) events. The number of events at least one female

338   of a given rank received meat given that rank class was present was 329 (62%), 556 (82%), and

339   619 (89%) for low, middle and high rank class, respectively.

340

341   *Probability of females being present at meat eating events*

342   The full model (including interactions) for the probability of being present at meat eating

343   events was significantly better than a null model with only random effects and an overall intercept

344   (test statistic 234.331, df=17, P-value<0.001). All proposed interactions were not significant

345   (Table 1). The reduced model refit without including these interactions was also significantly

346   better than the null model (test statistic 224.385, df=9, P-value<0.001) but not worse than the full

347   model (test statistic 9.946, df=8, P-value=0.269).

348   Parameter values and individual term significance of the reduced model are shown in Table

349   1. This indicates that female dominance rank, nursing a small infant, oestrus status, and the

350   increased fruit abundance (FAI) have significant positive influence on the probability of females

351   being present at a meat eating event. Increased number of males in the community resulted in a

352   decrease in the probability of being present. Not significant was age, number of females, and

353   community ID.

354   --
355   Insert Table 1 here
356   --

357

358   *Probability of females accessing meat given presence at a meat-eating event*

359   The full model (including interactions) for the probability of accessing meat given presence

360   at a meat eating event was significantly better than a null model with only random effects and an

361   overall intercept (test statistic 166.142, df=18, P-value<0.001). All proposed interactions were not

362   significant (Table 2). The reduced model refit without including these interactions was also

363   significantly better than the null model (test statistic 158.007, df=10, P-value<0.001), but not

364   worse than the full model (test statistic 8.135, df=8, P-value=0.420).

365   Parameter values and individual term significance of the reduced model are shown in Table

366   2. This indicates that female dominance rank, age, nursing a small infant, and oestrus status have

367   significant positive influence on the probability of females accessing meat, while increased

368   community size and increased number of females statistically decreased the likelihood to obtain

369   meat. The number of males, FAI, and community ID were not significant.

370   --
371   Insert Table 2 here
372   --

373

374   **Discussion**

375   We found support for our two principle hypotheses, that high-ranking females were more

376   likely to be present during a meat-eating event and that they were more likely to eat meat when

377   they were present compared to the subordinates. This research contributes to a growing body of

378   literature on the topic, where high female rank has also been shown to provide priority of access

379   to high quality foods in Kibale and Gombe chimpanzees (Murray et al., 2006; 2007; Kahlenberg

380   et al., 2008; Williams et al., 2002a).

381   For chimpanzees at Taï National Park, our analyses further indicated that this positive

382   effect of female dominance rank on acquiring meat was stable for the two chimpanzee

383   communities (North and South) over a long period (more than 25 years). During this time, both

384   communities experienced large declines in size with associated demographic changes that include

385   different numbers of adult females and adult males and important changes in the communities'

386   dominance hierarchies. In addition, the intra-annual fruit food fluctuations in Taï National Park

387   are quite strong and have been increasing in the past decade (Anderson et al., 2005, Polansky &

388   Boesch, 2013). Despite these changes in demographic and environmental conditions, no

389   interactions between female social rank and the different socio-ecological variables was detected;

390   the rank related behaviors of these female chimpanzees are both stable and robust across the two

391   communities. Further, the rank contribution to meat access remained constant across all these

392   social changes.

393   In humans, sharing of food has been proposed to be the result of a collective action problem

394   due to living in a risky foraging niche that produces a set of social norms of production and sharing

395   (Jaeggi & Gurvgen, 2013). In other words, humans live in a niche were food sharing became a

396   necessity. Considering that meat brings along a number of important micronutrients (Milton, 2003;

397   Tennie et al., 2009), it seems that meat, acquired through the presence of sharing, is an important

398   component of the diet in Taï chimpanzees.

399   Two recent studies in Taï, focusing on dyadic interactions or detailed hunting

400   characteristics, have shown that social rank independent of sex has only a limited effect in the food

401   sharing behaviour of the Taï chimpanzees or their ability to access meat after a hunt (Samuni et

402   al., 2018a;b). In contrast, focusing on the characteristics of the females, here we found a clear

403   effect of rank on meat access by females, with dominant females accessing more often meat than

404   subordinates. At least three reasons may account for this difference: (1) since we used data over

405   25 years the analysis had to fit the available long-term data, preventing us from analysing for

406   example the effects of hunt participation or reciprocal relationships on meat access; (2) our

407   research question was different and we did not include dyadic relationships; and (3) due to missing

408   dyadic dominance relationships, we used three rank categories, which may provide a slightly

409   different picture compared to linear dominance hierarchies. Our result, nonetheless, provides

410   evidence that female dominance rank has an effect on the accessibility of valuable resources,

411   indicating an advantage for dominant females as expected with contest competition over food

412   similar to Wittig & Boesch (2003).

413   In Gombe and Kibale, high ranking females occupied higher-quality areas while

414   subordinates had to settle elsewhere (Murray et al., 2006; 2007; Kahlenberg et al., 2008; Williams

415   et al., 2002a) resulting in higher reproductive success for dominant females (Pusey et al., 1997;

416   2005; Thompson et al., 2007). A better-fed female can invest more energy in reproduction and

417   thereby produce more offspring, or she can supply more food to her offspring. In Gombe, the five

418   most successful females at getting large amounts of meat had more surviving offspring than did

419   the five least successful females (Mc Grew, 1992).

420   The effect of female dominance rank on feeding competition appears across chimpanzee

421   populations besides differences in demography and female sociality (Wrangham, 2000; Fawcett,

422   2000; Boesch & Boesch-Achermann, 2000; Williams et al., 2002a;b; Lehmann & Boesch, 2008).

423   Taï females are more gregarious compared to those from Kibale and Gombe where females were

424   relatively asocial (Wrangham & Smuts, 1980; Goodall, 1986; Wrangham et al., 1992; Pusey et al.,

425   1997; Williams et al., 2002b). Females in Kibale and Gombe seem to disperse and to be less

426   gregarious to reduce within-group contest competition. In contrast, the females in Taï remain

427   highly gregarious and build a formal hierarchy to reduce contest competition (Wittig & Boesch,

428   2003) also at meat-eating events. Higher gregariousness in Taï females may result from a

429   combination of higher fruit abundance (Boesch, 2009) and higher predation pressure at Taï

430   (Boesch, 1991; 2009) compared to the other study populations. Unequal access to monopolizable

431   food, such as meat, might be an explanation for the development of the linear hierarchy in Taï

432   females (Wittig & Boesch, 2003). Female dominance rank might help to reduce direct dyadic

433   fighting by giving access to the dominant individual before even a conflict or fight have to evolve.

434   Samuni and colleges (2018b) found a positive effect of age on meat access in Taï

435   chimpanzees, which we confirmed. It remains unclear why older chimpanzees are more likely to

436   access meat. It may be due to better begging and/or hunting skills. One hypothesis is that older

437   females can have stronger friendships with chimpanzees in their community and can rely on long-

438   term cooperative exchanges that gives them access to shared foods such as meat (Samuni et al.

439   2018a). In addition, older females are also preferred mating partners by male chimpanzees (Muller

440   et al. 2006).

441   Another female property proposed to play a role for presence and meat access was the

442   oestrous status of the female. We found that oestrous females in Taï National Park were more

443   likely to be present and to get meat than females with no oestrous. This agrees with the findings

444   that oestrous females were more gregarious than anoestrous ones (Boesch & Boesch-Achermann,

445   2000), and that adult males share more meat with oestrous than with anoestrous females, when

446   controlled for their proportional representation in hunting parties (Gomes & Boesch, 2009).

447   Our results show that a nursing female with a small infant in Taï did not avoid meat eating

448   events where elevated levels of intra-group aggression can occur. The increased need for high

449   value food such as meat to support nursing an infant is a likely factor motivating these females to

450   acquire meat. Chimpanzee mothers in Taï National Park remained as gregarious as non-mothers

451   (Riedel et al., 2011), in contrast to other study populations, where mothers are less gregarious than

452   non-mothers (Goodall, 1986; Murray et al., 2007; Williams et al., 2002b; Takahata, 1990; Sakura,

453   1994; Wrangham, 2000; Otali & Gilchrist, 2006). Our results about lactating females accessing

454   meat better than non-lactating females, confirms the findings from Gombe, where pregnant

455   females consumed more meat than lactating and not pregnant/not lactating females (O'Malley et

456   al., 2016). An interaction between reproductive state and rank in Gombe females, revealed that

457   high-ranking females do not differ in meat consumption between different reproductive states, but

458   low-ranking females do, with low-ranking females consuming more meat during pregnancy than

459   during lactation and not pregnant/ not lactating females (O'Malley et al., 2016).

460   For the ecological variable that we studied, we found that fruit abundance had no

461   significant effect on female meat access, but plays a role on female presence at meat eating events,

462   with more females being present during times of high fruit abundance. That those periods of high

463   fruit abundance result in higher party sizes and sociality in Taï chimpanzees has been shown before

464   (Doran, 1997; Riedel et al., 2011).

465   Females hunt much less than males, involvement in hunting was only 13%-15% (Boesch

466   & Boesch, 1989; Samuni et al., 2018b). Nevertheless, we can report that adult females continued

467   hunting and meat eating behaviors also during years when there were no or just one adult male in

468   the North group. The North group had no adult males for four years and only one adult male for

469   another six years, but a minimum of four adult females that continued to hunt and eat meat during

470   this period. Although hunting frequencies seemed reduced, it is impressive that females engaged

471   successfully in this behavior, further supporting the evidence that meat has a high nutritional value

472   for chimpanzees. Impressively, low-ranking females and even nursing mothers joined these

473   aggressive meat-eating events and were successful in accessing meat, which strengthens further

474   the importance of meat in the female chimpanzee diet.

475

476   **Conclusion**

477   The benefits of female dominance rank for accessing meat are positive and robust to fruit

478   abundance variations and large demographic changes (and hence some group level social changes

479   such as in dominance hierarchies). Taken together this indicates that this female social property is

480   persistent even when the competition for resources declines because of overall community size

481 declines or fruit abundance increases. Furthermore, other female properties such as age, oestrus

482 status and the nursing of a small infant positively influenced meat access.

483

484 **Acknowledgments**

485   We thank the Ministère des Eaux et Forêts, Ministère de l'Enseignement supérieur et de la

486 Recherche scientifique, and the Office Ivoirien des Parcs et Réserves for permitting this research,

487 and the Centre Suisse de Recherche Scientifique at Abidjan in Côte d'Ivoire for their logistical

488 support; and the Max Planck Society. We thank the Taï Chimpanzee Project (TCP) and especially

489 the TCP field assistants Camille Bolé, Nicaise Oulaï, Honora Kpazahi, Grégoire Nohon and Nestor

490 Gouyan Bah, who collected the long-term data presented here. We are grateful to Roger Mundry

491 for statistical advice, Robert Power for insights into human meat eating literature and three

492 anonymous referees for valuable comments on an earlier version of the manuscript. This research

493 was conducted in accordance with the animal care regulations and national laws of Côte d'Ivoire

494 and Germany. The viewpoints expressed are those of the authors and do not necessarily reflect the

495 opinions of the U.S. Department of the Interior or the U.S. Fish and Wildlife Service.

496

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Figure 1: Yearly maximal community size during the study period for North group (grey line) from 1987 until 2014 and for South group (black line) from 1999 until 2014.

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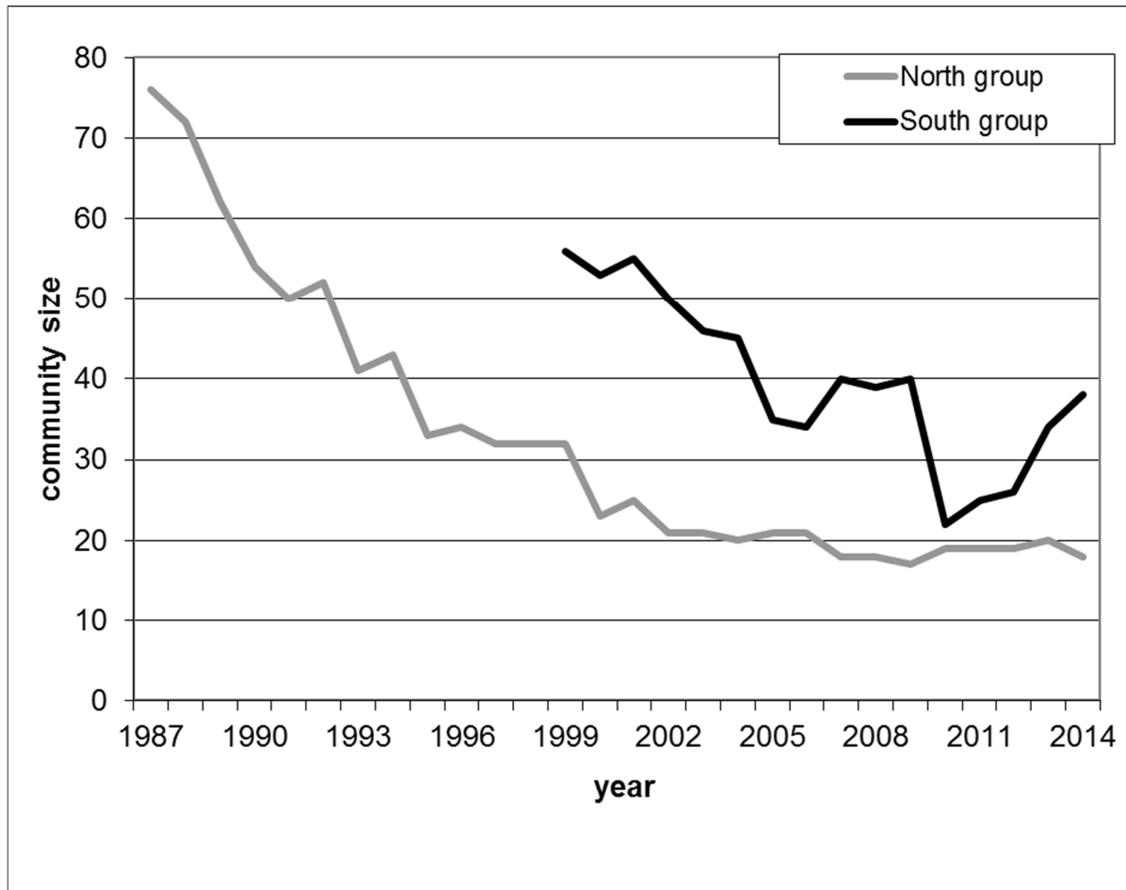
Figure 2: Monthly variation in the meat eating frequency controlled for the total observation time and monthly fruit abundance index (FAI).

Figure 2: Monthly variation in the meat eating frequency controlled for the total observation time (min) for North and South group with a peak in September and October. Second Y-Axis shows the monthly fruit abundance index (FAI) with an increase in FAI during the two meat eating peak months.
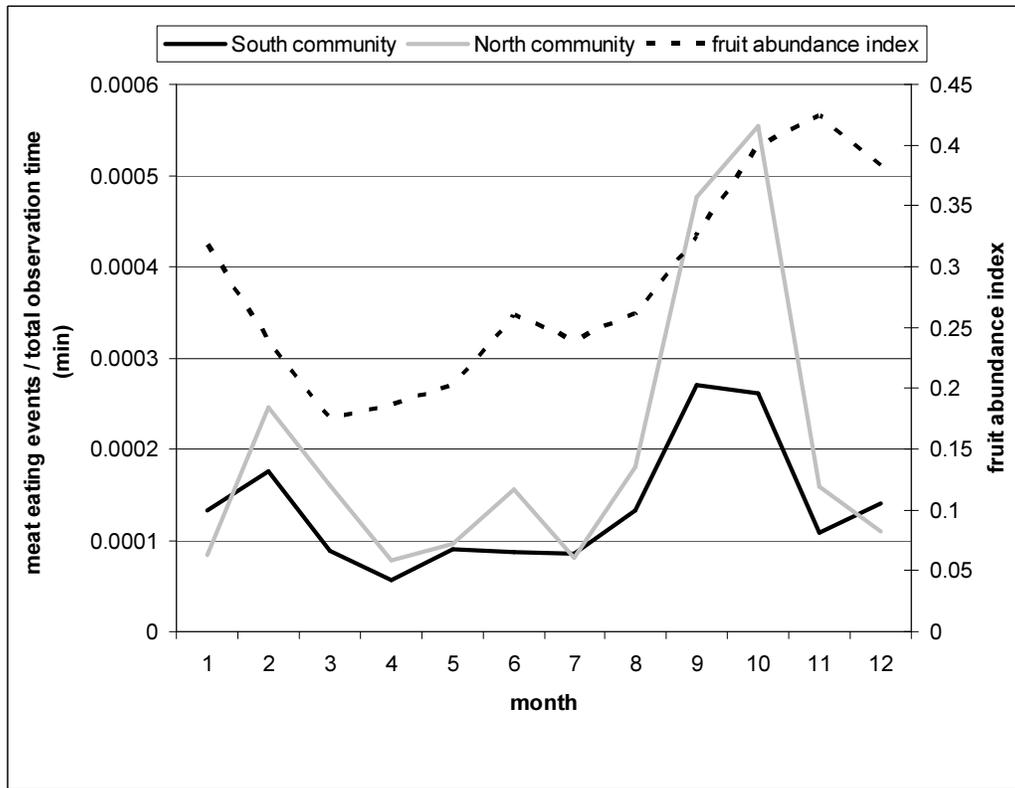
Table 1: Summary of models for the probability of being present at meat eating events.

Table 1: Summary of models for the probability of being present at meat eating events. The term estimates columns show the estimate (Est), standard error (SE), and Z-value for model parameters, where the entries along the rows that do not include interactions (denoted by a colon) are based on the fitted reduced model with no interactions and the entries for rows with interactions are based on the fitted full model with all interactions and main effects. The term significance entries show results of likelihood ratio tests between either the full (when testing the importance of an interaction) or reduced model (when testing the importance of a predictor variable in isolation) and a model with the corresponding term removed; χ^2- test statistic; df- degrees of freedom. Significant model parameters are marked bold.

1 **Table 1**: Summary of models for the probability of being present at meat eating events. The term
2 estimates columns show the estimate (Est), standard error (SE), and Z-value for model
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8 variable in isolation) and a model with the corresponding term removed; χ^2- test statistic; df-
9 degrees of freedom. Significant model parameters are marked bold.

	Term estimates			Term significance		
Terms	Est	SE	Z-value	χ^2	df	P-value
Intercept	-1.080	0.222	-4.871	-	-	-
Dominance rank (high-middle)	**1.086**	**0.199**	**5.449**	**32.255**	**2**	**<0.001**
Dominance rank (middle-low)	0.425	0.163	2.613	-	-	-
Age	0.194	0.112	1.736	2.735	1	0.098
Nursing a small infant (yes)	**0.243**	**0.075**	**3.250**	**10.312**	**1**	**0.001**
Oestrous status (yes)	**1.234**	**0.102**	**12.097**	**150.842**	**1**	**<0.001**
Fruit Abundance Index (FAI)	**0.157**	**0.062**	**2.539**	**6.325**	**1**	**0.012**
Number of males	**-0.340**	**0.099**	**-3.444**	**11.275**	**1**	**0.001**
Number of females	-0.181	0.103	-1.760	2.915	1	0.088
Community ID (South)	-0.190	0.273	-0.694	0.481	1	0.488
Dominance rank (high-middle) : No. of females	-0.240	0.156	-1.533	4.342	2	0.114
Dominance rank (middle-low) : No. of females	-0.288	0.138	-2.095	-	-	-
Dominance rank (high-middle) : FAI	0.088	0.082	1.079	1.971	2	0.373
Dominance rank (middle-low) : FAI	0.116	0.082	1.412	-	-	-
Dominance rank (high-middle) : Community ID (South)	0.069	0.436	0.159	1.898	2	0.387
Dominance rank (middle-low) : Community ID (South)	0.459	0.399	1.149	-	-	-
Dominance rank (high-middle) : Oestrous status (yes)	0.199	0.260	0.764	0.998	2	0.607
Dominance rank (middle-low) : Oestrous status (yes)	-0.044	0.236	-0.186	-	-	-

Table 2: Summary of models of the probability of meat access given presence at an event.

Table 2: Summary of models of the probability of meat access given presence at an event. See the caption for Table 1 for details on entries.

1   **Table 2**: Summary of models of the probability of meat access given presence at an event. See
2   the caption for Table 1 for details on entries.

Terms	Term estimates			Term significance		
	Est	SE	Z-value	χ^2	df	P-value
Intercept	-0.080	0.212	-0.376	-	-	-
Dominance rank (high – middle)	**1.090**	**0.208**	**5.232**	**26.206**	**2**	**<0.001**
Dominance rank (middle - low)	0.707	0.171	4.138	-	-	-
Age	**0.402**	**0.094**	**4.286**	**18.708**	**1**	**<0.001**
Nursing a small infant (yes)	**0.293**	**0.083**	**3.514**	**11.999**	**1**	**0.001**
Oestrous status (yes)	**0.459**	**0.138**	**3.335**	**10.9**	**1**	**0.001**
Fruit Abundance Index (FAI)	0.091	0.070	1.300	1.655	1	0.198
Number of males	-0.046	0.090	-0.507	0.259	1	0.611
Number of females	**-0.321**	**0.077**	**-4.184**	**17.57**	**1**	**<0.001**
Community size	**-0.193**	**0.095**	**-2.030**	**4.001**	**1**	**0.045**
Community ID (South)	-0.068	0.231	-0.295	-0.043	1	1
Dominance rank (high-middle) : No. of females	0.080	0.114	0.698	1.804	2	0.406
Dominance rank (middle-low) : No. of females	0.149	0.113	1.321	-	-	-
Dominance rank (high-middle) : FAI	0.160	0.109	1.465	2.385	2	0.303
Dominance rank (middle-low) : FAI	0.144	0.109	1.327	-	-	-
Dominance rank (high-middle) : Community ID (South)	-0.200	0.393	-0.511	0.45	2	0.798
Dominance rank (middle-low) : Community ID (South)	0.027	0.339	0.078	-	-	-
Dominance rank (high-middle) : Oestrous status (yes)	0.585	0.353	1.658	2.87	2	0.238
Dominance rank (middle-low) : Oestrous status (yes)	0.399	0.341	1.170	-	-	-