1 **Coordination during group departures and group progressions in the tolerant**

2 **multilevel society of wild Guinea baboons (*Papio papio*)**

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4 Davide Montanari[1], Julien Hambuckers[2,3], Julia Fischer[1,4,5*] & Dietmar Zinner[1,4*]

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6 [1]Cognitive Ethology Laboratory, German Primate Center, Kellnerweg 4, 37077 Göttingen, Germany

7 [2]HEC Liège, University of Liege, Liège, Belgium

8 [3]Chair of Statistics, Georg-August-University of Göttingen, Humboldtallee 3, 37073 Göttingen,

9 Germany

10 [4]Leibniz-ScienceCampus Primate Cognition, Göttingen

11 [5]Department of Primate Cognition, Georg-August-University of Göttingen, Göttingen, Germany

12

13 Correspondence to: Dietmar Zinner, Cognitive Ethology Laboratory, German Primate Center,

14 Kellnerweg 4, 37077 Göttingen, Germany. E-mail: dzinner@gwdg.de Tel: +49 551 3851-129

15 * shared last authorship

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17 **Running title**

18 Group coordination in Guinea baboons

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20 **Research Highlights**

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22 • In wild Guinea baboons, both adult males and females initiated group departures

23 • Initiators signaled during departures, but this did not affect initiation success

24 • Solitary males were predominantly found at the front during group progression

25

26 **Abstract**

27 **Objectives:** Most primate species live in groups, and temporal and spatial coordination of activities of

28 individuals is essential for maintaining group cohesion, and there is still considerable debate to which

29 degree social organization, the extent of despotism, and resource distribution shape group

30 coordination processes. As different baboon species exhibit considerable variation in all of these

31 factors, they constitute an excellent test case to resolve this debate.

32 **Materials and Methods:** We analyzed group departures and progressions of Guinea baboons, *Papio*

33 *papio*, in the Niokolo Koba National Park in Senegal. Guinea baboons live in a multi-level society with

34 strong male bonds and a lack of a clear dominance hierarchy between males.

35 **Results:** Two-thirds of departures were initiated by adult males, and one third by adult females.

36 Although initiators were more likely to signal than followers, signaling did not affect the initiation

37 success. During group progression, males that were not affiliated with females were predominantly

38 found in the front, while affiliated males, females and young were observed more frequently closer

39 to the center of the group, and no preferences for rear positions. Overall, affiliated subjects were

40 more likely to depart and travel together.

41 **Discussion:** The group departures in Guinea baboons differed strikingly from the elaborate

42 'negotiation' behaviors among male hamadryas baboons, *Papio hamadryas*. We did not observe that

43 specific individuals dominated the group coordination. Neither social organization, variation in

44 despotism, nor resource distribution alone explain variation between species. Future studies should

45 test whether specific combinations of factors promote the occurrence of negotiation processes.

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2

50 **1 INTRODUCTION**

51 Taking advantage of the benefits of group living requires the temporal and spatial coordination of

52 activities of individuals (Conradt & Roper, 2003; King & Cowlishaw, 2009; Krause & Ruxton, 2002).

53 The coordination of individual movements in particular is essential for maintaining group cohesion

54 (Couzin, Krause, Franks & Levin, 2005; Petit & Bon, 2010; Westley, Berdahl, Torney & Biro, 2018).

55 These coordination processes differ between species and contexts. Many of the coordination

56 patterns seen in swarms, flocks and certain social groups such as desert locusts, *Schistocerca*

57 *gregaria* (Bazazi et al., 2008), European starlings, *Sturnus vulgaris* (Ballerini et al., 2008), three-spined

58 sticklebacks, *Gasterosteus aculeatus* Jolles, Boogert, Sridhar, Couzin & Manica, 2017), but also some

59 mammal species (e.g., herds of domestic sheep, *Ovis aries*, Toulet, Gautrais, Bon, & Peruani, 2015)

60 can be explained by simple rules characterizing the attraction, alignment, repulsion and mimetism

61 between neighboring individuals (Couzin & Krause, 2003; Deneubourg & Goss 1989; Sueur &

62 Deneubourg, 2011). However, especially in socially complex societies, several other factors can

63 modulate group coordination mechanisms and processes, such as individual traits (Couzin et al.,

64 2011; del Mar Delgado et al., 2018), heterogeneous social relationships (Nagy, Ákos, Biro & Vicsek,

65 2010), or landscape features (Strandburg-Peshkin, Farine, Crofoot & Couzin, 2017).

66 To investigate how group coordination arises from individual decisions, most studies focused

67 on the initiation of collective movements after the group had been stationary for a while (e.g.,

68 Kummer 1968a; Stueckle & Zinner, 2008). Key questions here are who attempts to initiate group

69 movements and whether attempts are successful, i.e. whether other group members follow and in

70 which order (e.g., Black, 1988; Lorenz, 1931; Stolba, 1979; Sueur & Petit, 2008a,b; Walker, King,

71 Mcnutt & Jordan, 2017). In some species, the initiation of group movements is highly biased towards

72 certain individuals, often dominant or old and experienced group members (e.g., mountain gorillas,

73 *Gorilla beringei beringei,* Watts, 2000; bottlenose dolphins, *Tursiops* sp., Lusseau & Conradt, 2009).

74 Such cases have been described as consistent leadership (Conradt & Roper, 2005; Pyritz, King, Sueur

75 & Fichtel, 2011a; Strandburg-Peshkin, Papageorgiou, Crofoot & Farine, 2018). In other species,

76 initiation attempts are distributed among many or all (often only adult) group members (e.g.,

77 meerkats, *Suricata suricata*, Bousquet, Sumpter & Manser, 2011; white-faced capuchins, *Cebus*

78 *capucinus*, Leca, Gunst, Thierry & Petit, 2003). These cases have been characterized as distributed or

79 variable leadership (Conradt & Roper, 2005; Pyritz et al., 2011a; Strandburg-Peshkin et al., 2018).

80 The propensity to initiate group movements can be affected by individual, social or

81 environmental factors (Farine, Strandburg-Peshkin, Couzin, Berger-Wolf, & Crofoot, 2017). Initiators

82 often belong to specific age and sex-classes. For instance, old female bonobos, *Pan paniscus*

83 (Tokuyama & Furuichi, 2017) or adult female European bisons, *Bison bonasus* (Ramos, Manizan,

84 Rodriguez, Kemp & Sueur, 2018) initiate the majority of movements. Individual physiological needs

3

85 can also modulate the initiation process: lactating plain zebra females (*Equus burchellii*) initiate

86 collective movements more frequently than non-lactating females (Fischhoff et al., 2007). Bolder

87 individuals may initiate group movements more often than shy group members (e.g., domestic

88 horses, *Equus ferus caballus*, Briard, Dorn, & Petit, 2015; red-fronted lemurs, *Eulemur rufifrons*,

89 Sperber, 2018). In groups where power differentials play an important role, that is in more despotic

90 societies, high ranking subjects are more likely to initiate group movement (e.g., despotic rhesus

91 macaques, *Macaca mulatta*, than in more egalitarian Tonkean macaques, *Macaca tonkeana*, Sueur &

92 Petit, 2008a). The social organization (uni-level vs. multi-level) is also expected to modulate group

93 coordination processes (Fishhoff et al., 2007; Ozogány & Vicsek, 2015; Sueur et al., 2011). Finally,

94 environmental heterogeneity could modulate the propensity to initiate a group movement as it

95 modulates collective behavior in a variety of ways (e.g., Bonnell, Henzi & Barrett, 2019; King et al.,

96 2018; Strandburg-Peshkin et al., 2017).

97   Baboons (genus *Papio*) are an intriguing model to study the impact of social factors on group

98 coordination, as they exhibit considerable variation in mating system, social organization and social

99 structure (Anandam et al., 2013; Fischer et al., 2017; Swedell, 2011). Olive (*P. anubis*), yellow (*P.*

100 *cynocephalus*), chacma (*P. ursinus*) and Kinda baboons (*P. kindae*) usually live in a uni-level,

101 multimale-multifemale group (Anandam et al., 2013). Their societies reveal a linear rank hierarchy,

102 determined through agonistic interactions in males and inherited in females (Anandam et al., 2013;

103 Barrett & Henzi, 2008; Swedell, 2011). Hamadryas (*P. hamadryas*) and Guinea baboons (*P. papio*), in

104 contrast, live in multilevel societies based on monandric-polygynic reproductive units (one-male units

105 or OMUs) at the base of the societies (Fischer et al., 2017; Goffe, Zinner & Fischer, 2016; Kummer,

106 1968a,b; Patzelt et al., 2014; Pines & Swedell, 2011; Schreier & Swedell, 2009). Thus, baboons

107 provide a useful model to compare group coordination in uni-level and multi-level societies.

108   Studies of group coordination in uni-level baboon societies have shown heterogenous results.

109 In some groups, dominant males predominantly initiated and directed troop movements (chacma

110 baboons, Byrne, Whiten & Henzi 1990; Stoltz & Saayman, 1970; but see Buskirk, Buskirk & Hamilton,

111 1974). In a further study of chacma baboons, adult males were more likely to initiate group

112 movements but the likelihood of being successful was similar for males and females (Stueckle &

113 Zinner, 2008). However, when provided with incentives, the dominant male led groups to

114 experimental food patches (King et al., 2008). In olive baboons at Gombe, the highest-ranking male

115 was also more likely to determine the direction and timing of group movements than lower ranking

116 subjects (Ransom, 1981), whereas in Queen Elizabeth National Park high ranking males often

117 attempted to initiate a group movement, but they were only successful when old females followed

118 him (Rowell, 1969). A similar impact of high-ranking females has been observed in yellow baboons in

119 Mikumi National Park (Norton, 1986). A recent study in which olive baboons were tracked with a

120 high-resolution global positioning system revealed a process of shared decision-making
121 characterizing group movement. Rather than preferentially following dominant individuals, these
122 baboons were more likely to follow when multiple initiators agreed (Strandburg-Peshkin, Farine,
123 Couzin & Crofoot, 2015).

124   In hamadryas baboons, which live in a multi-level society (Grueter & Zinner, 2004; Kummer,
125 1968a), the reproductive males of the OMUs almost exclusively initiated group movements, while
126 females had only a little impact on group coordination (Kummer, 1968a, 1995; Stolba, 1979). In
127 subgroups of two OMUs, Kummer (1968a) described the decision making process as a "negotiation"
128 among males with different roles, the initiator and the decider male (ID-system). Initiators moved
129 away from the center of the band followed by their females. If another male (decider) from the band
130 did not follow, the initiator moved back to the center. The ID-system was, however, not confirmed in
131 a subsequent study on the same population, when larger social entities were taken into account (e.g.
132 clans, bands; Stolba, 1979).

133   Guinea baboons live in a similar multi-level social organization as hamadryas baboons. If the
134 social organization affects decision making, one could expect a similar strong impact of OMU males
135 on the initiation of collective movements as in hamadryas baboons. However, Guinea baboon males
136 are socially more tolerant than hamadryas baboon males and Guinea baboon females are not as
137 strictly controlled by their males (Fischer et al., 2017; Kummer, 1968a), which might also affect the
138 females' role in initiation collective movements. Thus, if the socially more tolerant style modulates
139 the decision-making process during group departures, one would expect that females take a share in
140 the initiation of group movement.

141   In both types of baboon social organization, individuals appear to preferentially follow closely
142 affiliated group members, irrespective of who initiates a group movement (olive baboons, Farine et
143 al., 2016; chacma baboons, King et al., 2008, 2011). In hamadryas baboons the departure process
144 relies on unit member cohesiveness (Kummer, 1968a, 1995). We therefore expected that the
145 relationship strength affects who is likely to follow whom during group departures, with animals
146 having stronger relationships being more likely to depart in close succession.

147   We additionally investigated the function of signals in group departures. Signals are conceived
148 as indicators of specific behavioral dispositions (Fischer & Price, 2017). Thus, subjects who are
149 motivated to initiate a group movement should express this motivation using signals (e.g., bonobos,
150 *Pan paniscus*, Schamberg, Cheney & Seyfarth, 2017). We therefore predicted that subjects who
151 initiated group departures were more likely to signal compared to individuals whom we classified as
152 followers. We furthermore predicted that subjects who signaled may indicate a greater decisiveness
153 to initiate group movement, and therefore might be more successful in recruiting followers.

154   In the second part of this study, we investigated progression order. We focused on situations

155   when the baboons moved in more or less a single-file. The progression order has been regarded as

156   an adaptation to predation risk (DeVore & Washburn, 1963; Rhine, 1975; Rhine, Forthman, Stillwell-

157   Barne, Westlund & Westlund, 1981; Rhine, Bioland, & Lodwick, 1985). DeVore and Washburn (1963)

158   reported a socio-spatial order in which the most vulnerable group members (adult females, juveniles

159   and infants) took central positions close to the dominant adult males, whereas low-ranking adult

160   males and older immature males occupied the more risk prone positions in the front and rear of the

161   progression. However, this male-centered order was not observed in other baboon populations

162   (Altmann, 1979; Rowell, 1969; Harding, 1977; Rhine, 1975; Rhine & Westlund, 1981; Rhine et al.,

163   1985; Rhine & Tilson, 1987). For multi-level hamadryas baboons, Kummer (1968a) reported that the

164   frequency with which adult and subadult males appeared at the front was twice that which would be

165   expected by chance, whereas males were found at the rear with a frequency equal to chance.

166   Regarding group progressions, we therefore contrasted two possible scenarios: if Guinea

167   baboons conform to other baboon species, adult males should be found more frequently in front and

168   rear positions, while adult females and youngsters should mainly travel in the middle of the

169   progression. Alternatively, units may retain their cohesiveness during group movement. In this case,

170   the progression would resemble the male centered pattern with primary unit males moving with

171   their females and offspring in the center of a progression.

172

2 MATERIALS AND METHODS

2.1 Field site and study subjects

175   The fieldwork was conducted in the surroundings of the field station "Centre de Recherche de

176   Primatologie (CRP) Simenti" (13°01'34" N, 13°17'41" W), in the Niokolo-Koba National Park, south-

177   eastern Senegal. The multi-level system of Guinea baboons consists of "units" (usually one adult

178   male and one to several females with their young), units are nested within "parties" and parties are

179   nested within "gangs" (Fischer et al., 2017). The study subjects were fully habituated baboons

180   belonging to five parties, that formed two gangs (Table 1). Subjects were individually identified,

181   although the identification of juveniles was not always possible. The home ranges of the parties

182   covered on average 30.3 km^2 of largely overlapping territories (Kernel density estimations 95%,

183   unpubl. data, M. Klapproth).

184

185 **Table 1.** Average composition of study groups. Party sizes (i.e. total number of party members)
186 varied due to births, deaths, disappearances, between-parties transfers of individuals and difficulties
187 in recognizing young weaned individuals.
188

Gang	Party	Number of units	Number of adults		Size
"Mare"	"4"	2-3	5 ♂	3 ♀	15
	"9"	5-6	12 ♂	17 ♀	45
	"10"	1-2	2 ♂	2 ♀	8
"Simenti"	"5"	3-4	10 ♂	9 ♀	25
	"6"	4-5	12 ♂	11 ♀	38

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191 **2.2 Data collection**

192 Data collection was conducted from January to August, in 2016 and 2017, for a total of 16 months, 6

193 days per week. Observation days started before sunrise (at 6:00 or 6:30) to locate the baboons at the

194 sleeping site. Data were recorded on Samsung Note 3 handhelds using forms created with Pendragon

195 7.2 (Pendragon Software Corporation, USA). Every day, all researchers working at CRP collect census,

196 ad libitum, scan, and focal data of the baboons to investigate the demography, reproductive success,

197 association data, and behavioral patterns (Altmann, 1974). These data were used to determine

198 female-male associations. Data on group movement were collected with the all-occurrence sampling

199 method (Altmann, 1974). Two types of events were distinguished during the group movement

200 process: group departures and group progressions (see below). We classified individuals according to

201 age (Category "young" including infants, yearlings, and juveniles; Category "adult" including

202 subadults and adults) and sex. We further noted the unit identity for primary males and the

203 associated members of the unit. Non-primary adult males (i.e. secondary and unaffiliated ones) and

204 young individuals which could not be unambiguously identified as members of one unit were labelled

205 by their own IDs. In addition we considered the unit size (number of adult subjects). Non-associated

206 animals had a unit size of 1, units comprised of an adult male and one female had a size of 2, and so

207 on. The largest unit size was 7.

208

209 **2.2.1 Operational definition of group departures**

210 A group departure occurred when a group of baboons was collectively leaving a confined area where

211 they had been stationary for a set time. We collected data on events of group departures throughout

212 the day, whenever visibility allowed it and certain conditions were met. Specifically, the group had to

213 consist of one or more complete units or a complete party. The confined area where the individuals

214 stayed stationary before a group departure was named the pre-departure area. The size of the pre-

215 departure area was 20 m in diameter at maximum. The individuals had to be isolated from

216 conspecifics outside the area for at least 20 m. The individuals had to stay stationary, either feeding,

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217   resting, or socializing in the pre-departure area for at least 15 minutes, to ensure a certain degree of

218   independence in timing and direction from previous movements (comparably to e.g., Leca et al.,

219   2003; Pyritz, Kappeler & Fichtel 2011b; Seltmann, Majolo, Schülke & Ostner, 2013; Sueur & Petit,

220   2008a,b). We excluded movements prompted by predation risks, alarm calls or social interactions

221   such as threats or chases. When these conditions were met, the identity of all individuals moving

222   away from the pre-departure area and the starting time and the direction of their movements were

223   voice recorded.

224   The first individual leaving the area was defined as attempting an initiation of group departure.

225   The individuals moving away from the pre-departure area in the same direction as another one

226   before, within a 5-minute interval time, were considered followers. When an individual was heading

227   more than 45° to the left or right from the direction chosen by the previous individual, and/or was

228   starting to move away more than 5 minutes after the previous individuals, it was coded as

229   attempting another initiation of group departure. Therefore, an initiation attempt was coded as

230   successful when some or all individuals in the pre-departure area followed. All individuals of the

231   subject group were hence classified as successful initiators, unsuccessful initiators, or followers.

232   Unsuccessful initiators were subsequently coded either as followers, successful initiators or again as

233   unsuccessful initiators on the following initiation attempt. When two successful initiations were

234   coded in one event, this implied group fission.

235   We furthermore recorded whether any one of the following signals occurred, to test whether

236   they signaled the readiness to initiate a group departure or affected the likelihood to succeed in

237   initiation:

238   •   Back glance: once the individual has started to move away from the pre-departure area and it

239   looks back in the direction of other group members. Empirically defined as the turn of the head

240   of more than 90° towards the direction of the pre-departure area.

241   •   Branch shaking display: rapid repeated bouncing in place while the individual stands

242   quadrupedal grasping a flexible branch, shaking it (Mehlman, 1996).

243   •   Pause: once the individual has started to move away from the pre-departure area and it stops

244   moving for more than 2 seconds within the first 20 m of movement.

245   •   Vocalizations: individual call, classified per type: keck, grunt, roar grunt, scream, bark, wahoo

246   (Fischer et al., 2017; Maciej, 2013).

247   •   Greeting: "exchange of non-aggressive signals that consist of species-specific behavioral

248   patterns, […] ranging from touches and embraces to genital manipulation and same-sex

249   mounts" (Dal Pesco & Fischer, 2018, p. 88).

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2.2.2 Operational definition of group progressions

A group progression was defined as the instance when a group of travelling baboons was positioned in an approximate single-file and jointly moved in (largely) the same direction. Single-file travel progressions typically occur along delineated pathways such as roads and on open areas. We collected data on events of group progressions throughout the day, whenever visibility allowed it and the following conditions were met: the progressing group had to consist of one or more complete parties and the first data regarding a group progression event had been collected at least 30 minutes after the end of a previous event. When these conditions were met, D.M. advanced a few meters in front of the moving group, stopped and set a virtual reference line on the ground in front of the arriving group. Whenever a baboon crossed this reference line, its identity and time of crossing (to the nearest second) were voice recorded.

2.3 Data analyses

All models and plots were fitted in R (version 3.5.0; R Core Team, 2018), using RStudio interface (version 1.1.383; RStudio Team, 2016). The only exception concerns the representation of posterior probability distributions of the order of group progression. These plots were created with MATLAB (version 9.4; The MathWorks, Inc., 2018).

2.3.1 Group departures

We first tested whether the likelihood of attempting an initiation of group departure was influenced by sex, age and/or unit size. To this end, we ran a Generalized Linear Mixed Model (GLMM; Baayen, 2008) with a binomial response variable and logit link function. Sex, age and unit size were included as fixed effects, individual identity and event as random effects (both random intercept components) and time of the day as a polynomial predictor variable. To prevent any scaling issue, we applied a z-transformation of the time of the day. We used the function glmer provided by the R package lme4 (version 1.1-17; Bates, Mächler, Bolker & Walker, 2015), setting the optimizer to 'bobyqa' to prevent convergence issues. To test if the full model fits better than a simpler alternative with a likelihood ratio test (Dobson, 2002), we compared the full model to the null model containing only the random effects and time. The p-values for the distinct effects were derived comparing the full model with the model reduced of the predictor of interest, using the function drop1, argument 'test' set to 'Chisq'. To obtain the confidence intervals for the different regression coefficients, we used a bootstrap procedure using the function bootMer provided by lme4 (nboots = 1000). In a second step, with the same procedure, we tested whether the same set of independent variables was affecting the success of the initiation attempts.

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286   In order to approximate distances between individuals and to investigate the individual spatial

287   association within the party, we calculated interval times (to the nearest second) between dyads of

288   individuals succeeding each other. We restricted the analysis to those 40 events where at least one

289   complete party was present, and calculated interval times only for individually identified subjects

290   (omitting most of the juveniles).

291   To test whether interval times were influenced by unit identity, we used a linear mixed model

292   (LMM; Baayen, 2008) into which we included unit membership, that is, whether individuals belonged

293   to the same unit as fixed effect, and the identity of the individual following, i.e. for which we

294   calculated the interval time, as well as the event as random effects. The model was fitted using the

295   function lmer of the R package lme4 (version 1.1-17; Bates et al., 2015). Because the interval times

296   were highly skewed, they were log-transformed. We verified that the assumptions of normally

297   distributed and homogeneous residuals were met by visually inspecting a qqplot and a plot of the

298   residuals against the fitted values. Both plots indicated that the assumptions were met. We tested

299   model stability by excluding subjects one by one from the dataset and comparing the model estimate

300   outcomes of these subsets with those outcomes of the full dataset. This revealed no influential

301   subjects. We tested whether the full model was significantly better compared to the null model, in

302   which the fixed effect was omitted, with the R function anova (argument test 'Chisq'; Dobson, 2002;

303   Forstmeier & Schielzeth, 2011). The models were fitted using Maximum Likelihood, rather than

304   Restricted Maximum Likelihood, to allow for a likelihood ratio test (Bolker et al., 2009). The p-value

305   for the fixed effect was based on a likelihood ratio test comparing the full with the reduced model,

306   with the function drop1, argument 'test' set to 'Chisq' (Barr, Levy, Scheepers & Tily, 2013).

307

308   **2.3.2 Group progressions**

309   To test whether specific individuals would be preferentially found in specific parts of the group, we

310   divided the sequence of individuals into equal thirds. We used a multinomial logit regression model

311   with random intercepts (Fahrmeir, Kneib, Lang & Marx, 2013). Progression-location was coded into

312   three categories (front, middle and rear), with the probability of belonging to the category

313   conditioned on age (adult vs young) and on one variable with three terms: female, primary male,

314   non-primary male ("f_pm_npm"). The model was estimated by means of Bayesian methods.

315   Posterior densities of the regression coefficients were obtained from Markov-chain Monte Carlo

316   (MCMC) procedures, using the R package MCMCglmm (Hadfield, 2010). From the resulting posterior

317   samples of progression-location regression coefficients, we calculated the distribution of the relative

318   frequency (i.e. the probability p) to observe a progression-location k = 1, 2, 3, conditional on age =

319   adult (ESM formula set 1), as well as the distribution of the relative frequency to observe

320   progression-location k = 1, 2, 3, conditional on f_pm_npm = female (ESM formula set 2).

321   In addition, we ran a post-hoc test to investigate whether non-primary males were occupying

322   edge positions during group progressions compared to primary males. To do this, we divided the

323   sequence of individuals of the front third and the one of the rear third in two equal parts. We ran a

324   GLMM with a binomial response variable and logit link function. We used the function glmer

325   provided by the R package lme4 (version 1.1-17; Bates et al., 2015). f_pm_npm was introduced as

326   one fixed effect with three levels: female, primary male, non-primary male. Individual identity was

327   included as a random effect. Model diagnostics were performed by creating scaled residuals through

328   simulations from the fitted model with the function simulateResiduals (number of simulations: 1000),

329   provided by the R package DHARMa (version 0.2.0; Hartig, 2017). We also plotted the residuals

330   against the predicted response from the model, using the function plotSimulatedResiduals, provided

331   by the R package DHARMa. The plot permits to detect deviations from uniformity in y-axis direction

332   and performs a quantile regression, which provides 0.25, 0.50 and 0.75 quantile lines across the

333   plots. Reported p-values for the individual effects were obtained from likelihood ratio tests

334   comparing the full with the respective reduced models (R function drop1, Barr et al., 2013).

335   Finally, we investigated the spatial association within the progressing party to test whether

336   interval times were influenced by unit membership, as for group departures. We measured the time

337   differences between individuals to the nearest second and used the same procedure applied to the

338   dataset of group departures. In brief, we used a linear mixed model (LMM; Baayen, 2008) into which

339   we included unit membership, that is, whether individuals belonged to the same unit as a fixed

340   effect, and the identity of the individual following, i.e. for which we calculated the interval time, as

341   well as the event as random effects.

342

343   **3 RESULTS**

344   **3.1 Group departures**

345   We collected data during 121 group departure events. Thirty-three events involved only one

346   complete unit, 48 events involved more than one complete unit, and 40 events involved a complete

347   party. In total, we sampled 146 attempts of group departure: 52 (35.6%) conducted by adult females,

348   91 (62.3%) by adult males and 3 (2.1%) by juveniles. Twenty-three attempts of initiation were not

349   successful (15.8%) (Table 2). In two events, the individuals in the departure area split during group

350   departure, after two successful initiation attempts within the same event. Fifty-eight different

351   individuals attempted to initiate a group departure: 28 different adult males, 27 different adult

352   females and three different juveniles.

353

354 **Table 2.** Number of initiation attempts by adult females, adult males, and young in relation to the
355 level of social organization and initiation success.
356

Level of social organization	initiation	adult female	adult male	young
one unit	successful	15	16	2
	unsuccessful	4	1	0
more units	successful	18	32	0
	unsuccessful	2	6	1
party	successful	9	31	0
	unsuccessful	4	5	0

357

358   Overall, the predictors age and sex had a clear impact on the probability of attempting an

359 initiation of group departure (likelihood ratio test comparing full and null model: χ^2 = 71.882, df = 6, P

360 < 0.001). Being male and of adult age strongly increased the likelihood of attempting an initiation.

361 Within the different adult age categories, there was no difference in the likelihood to initiate a group

362 departure (Table 3, Figure 1).

363

364 **Table 3.** Effects of age and sex category, as well as unit size, and time of day on the likelihood of
365 attempting to initiate a group departure. Estimated coefficients, standard errors, confidence
366 intervals, and test statistics.
367

	Estimate	Std. Error	CI $_{lower}$	CI $_{upper}$	χ^2	Df	P
Intercept	-6.113	0.793	-7.385	-4.898	(1)	(1)	(1)
sex Male	1.047	0.231	0.625	1.533	14.865	1	<0.001
age Mature adult	3.643	0.726	2.551	4.545	66.680[2]	4	<0.001[2]
age Old adult	3.878	0.766	2.619	5.022	(2)	(2)	(2)
age Subadult	3.591	0.764	2.387	4.734	(2)	(2)	(2)
age Young adult	3.399	0.745	2.249	4.389	(2)	(2)	(2)
unit size	0.028	0.078	-0.126	0.183	0.122	1	0.727
z.time	0.104	0.101	-0.108	0.317	(1)	(1)	(1)
I(z.time^2)	-0.057	0.063	-0.237	0.052	0.877	1	0.349

368 [1] not meaningful in this context; [2] equal values because they refer to different terms of the same variable

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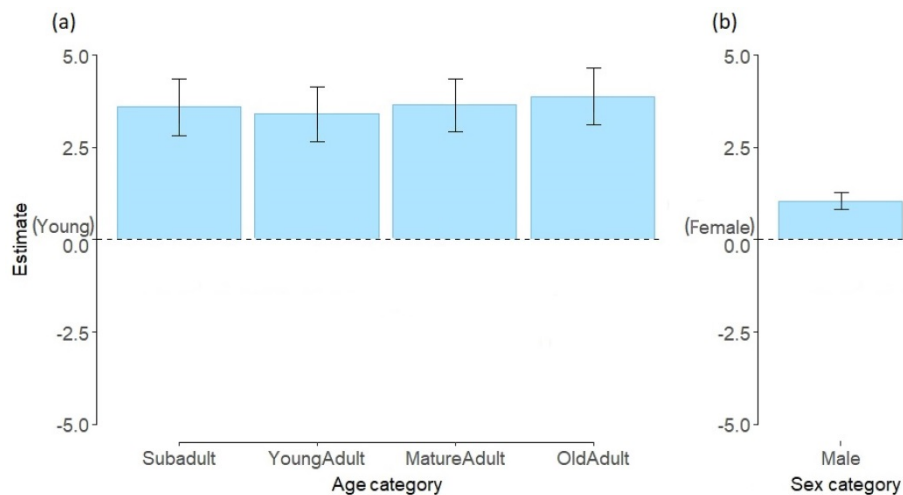
Figure 1. Estimates of the predictors age and sex on the likelihood of attempting an initiation of group departure, from GLMM (reference category being "young" and "female"). (a) All adult categories are significantly more likely to attempt than young individuals. (b) Males are significantly more likely to attempt than females.

Because only three group departures were initiated by young subjects, we excluded these from further analyses to avoid convergence issues. Out of the 52 initiation attempts by adult females, 42 (80.8%) were successful, while out of the 91 attempts by adult males, 79 (86.8%) were successful. Once failed, an individual that attempted to initiate tried again only twice in 23 occurrences of unsuccessful attempts. Adult age category, sex, and/or individual association did not explain the variation in success of initiation (likelihood ratio test: χ^2 = 3.309, df = 5, P = 0.653).

We next tested whether initiators and followers differed in signal usage during group departures. Initiators signaled in 57.7% of observations, while followers used signals only in 19.5 % of observations (Figure 2a; mean signaling rates across N = 86 individuals; N = 1102 events; P < 0.001; Table S1). Whether or not initiators used signals had no effect on their success rates. When a signal was used, the success rate was 83.6%; when no signal was used, it was 86.4 % (Figure 2b; N = 142 events; P = 0.947, see ESM for details Table S2). Note that signaling rates were first averaged for each individual and then across all individuals.

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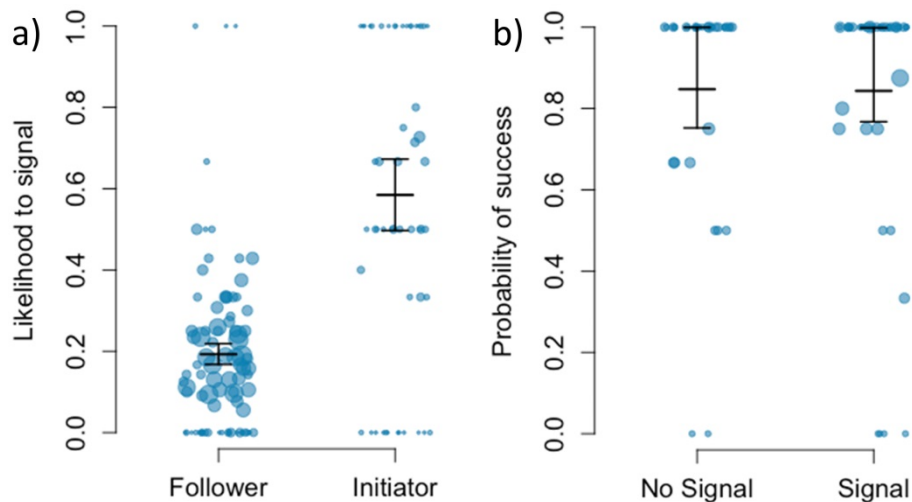
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Figure 2. (a) Likelihood of followers and initiators to signal during group departures. (b) Probability of success in relation to signaling during initiation.

When leaving the pre-departure area, the time intervals between two individuals that belonged to the same unit was significantly shorter (mean = 13.7 s; range: 0-260 s) than the interval time between two individuals who did not belong to the same unit (mean = 25.6 s; range: 0-910 s); Table S3; likelihood ratio test: χ^2 = 23.9, df = 1, P < 0.001, N = 813 intervals in 40 events).

3.2 Group progressions

We collected data on 100 events of group progression. Seventeen events involved more than one party. During the collected events, members of party 4 and 10 were always travelling with at least one of the other three parties. The number of events in which parties 4 and 10 were involved was very low (≤7 per party) compared to those in which party 5, 6 and 9 were involved (≥27 per party). Therefore, we excluded the individuals belonging to party 4 and 10 from the analyses, to achieve comparable numbers of events per party. Eleven events involved portions of a party because the party split for some hours or the whole day. In 6 of these events, the progressing group consisted of only 2 units.

Overall, the model outcomes revealed that age explained parts of the positioning of individuals during group progressions (i.e. 95% posterior density intervals do not include 0; Table 4). Adults were located more in front positions than middle or rear. It was also more likely to find adults in rear positions than in the middle of the group. Young individuals were somewhat less likely to take front positions compared to the other two categories (Figure 3a; the distribution of relative frequencies in Table S4).

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Table 4. Effect of age (adult; young) on the likelihood for an individual to take a front, middle or rear position during a group progression. Reference category front and adult. Posterior means, confidence intervals, sample size and P-values derived from MCMC procedure.

	Posterior mean	CI lower	CI upper	effective sample size	P MCMC
middle and adult	-0.338	-0.526	-0.141	538.0	<0.001
rear and adult	-0.247	-0.436	-0.054	574.7	0.001
middle and young	0.542	0.177	0.886	648.9	0.004
rear and young	0.430	0.085	0.759	801.0	0.016

We then considered only adult individuals for testing the effect of being a female, a primary male or a non-primary male on the position during group progressions. Sex and the distinction between primary and non-primary males explained variability in the order of group progression (Table 5). Adult females were found in all thirds with similar likelihood. Primary males mainly took front positions during group progressions, and were least frequently observed in middle positions. The strongest effects were observed for non-primary males, who were more likely to move in the front third than in the middle or rear third; their pattern differed significantly from that of females (distributions did not overlap; Figure 3b; the distribution of relative frequencies in Table S5)

Table 5. Effect of being a female, a primary male or a non-primary male on the likelihood for an individual to take front, middle or rear positions during a group progression. Reference category front third and female. Posterior means, confidence intervals, sample size and P-values derived from MCMC procedure.

	Posterior mean	CI lower	CI upper	effective sample size	P MCMC
middle and female	0.057	-0.212	0.303	602.1	0.679
rear and female	0.050	-0.214	0.313	600.4	0.710
middle and primary male	-0.439	-0.912	0.060	593.8	0.086
rear and primary male	-0.276	-0.755	0.189	541.3	0.262
middle and non-primary male	-1.240	-1.758	-0.817	535.1	<0.001
rear and non-primary male	-0.968	-1.430	-0.563	542.2	<0.001

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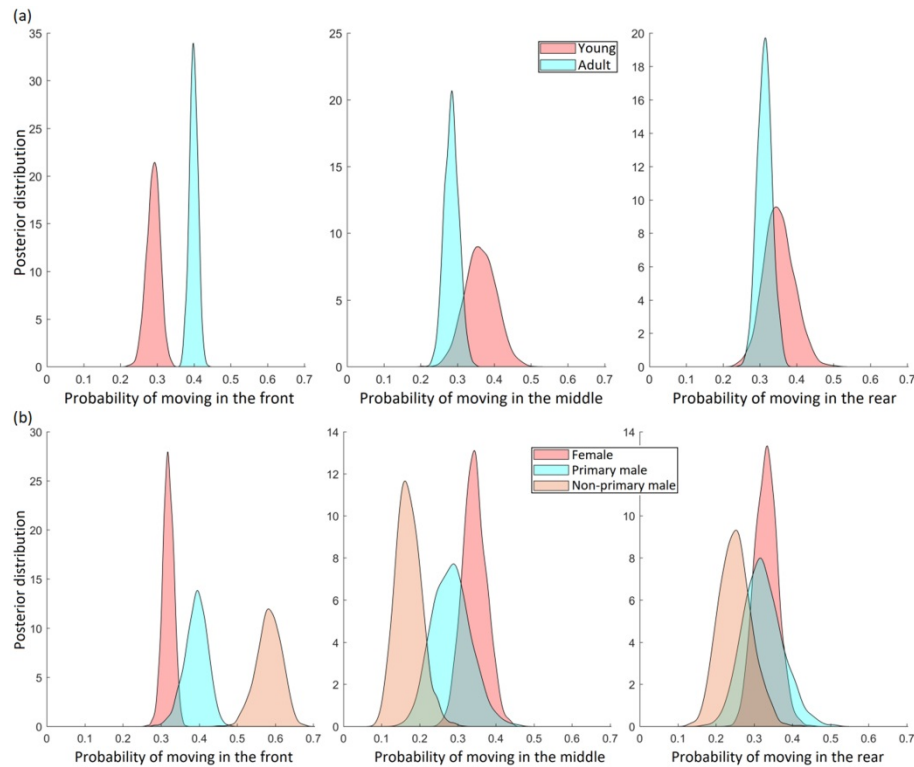
Figure 3. Posterior probability distributions to progress in front, middle or rear positions according to (a) age and (b) sex (adult subjects only). The distribution of relative frequency per category per third, i.e. estimated probabilities, in ESM.

Furthermore, non-primary males were observed significantly more often in the front half of the first third, as compared to females and primary males, which tended to progress in the half closer to the middle of the group (P < 0.001, Table S6). Non-primary males were also observed significantly more often in the back half of the rear third, as compared to females and primary males, which again progressed in the half closer to the middle of the group (P < 0.001, Table S7).

During group progressions subjects who belonged to the same unit were more likely to travel together, as evidenced by the interval time between two individuals belonging to the same unit (mean = 4.2 s; range: 1-70 s), which was significantly shorter than the interval time between two individuals that did not belong to the same unit (mean = 8.9 s; range: 1-293 s; likelihood ratio test: χ^2 = 201.5, df = 1, P < 0.001, N = 2226 intervals involving N = 120 individuals following in 100 events, Table S8).

4 Discussion

In our study population of Guinea baboons, collective movements were predominantly initiated by adult individuals. Adult males attempted initiations more often (62% of events) than adult females (36%, juveniles 2%). The vast majority of initiation attempts were successful (males 87%; females 80%). In other baboon species (olive, yellow and chacma), adult males were also reported as the major, but not exclusive, actors during group departures (King et al., 2011; Norton, 1986; Ransom,

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461   1981; Stueckle & Zinner, 2008). The patterns we observed in Guinea baboon group departures and
462   progressions were overall more similar to the patterns observed in uni-level species, such as chacma
463   and olive baboons (Strandburg-Peshkin et al., 2015; Stueckle & Zinner, 2008), than to the patterns
464   observed for hamadryas baboons.

465   In hamadryas baboons, only adult males were observed to take part in the negotiation and
466   decision making on the direction and timing of coordinated departures of several OMUs (clans) from
467   the sleeping sites (Kummer, 1968a, 1995; Stolba, 1979). In Guinea baboons, in contrast, adult
468   females initiated group departures in about a third of the cases. Their greater share in initiating
469   departures compared to other hamadryas baboons may be a result of the higher degree of 'female
470   freedom'. More specifically, female Guinea baboons are not coerced to maintain constant close
471   proximity to their males and they have greater leverage in association patterns (Goffe et al., 2016).
472   Also, the complex "negotiating" behaviors described for hamadryas baboons were observed
473   extremely rarely. Instead, any adult Guinea baboon who moved off could trigger a group departure.

474   The observed differences between Guinea and hamadryas baboons likely reflect true species
475   differences, but they may also be due to differences in data collection procedures. Descriptions of
476   the hamadryas group departures by Kummer (1968a) and Stolba (1979) encompassed only
477   departures from the sleeping site in a relatively open landscape, whereas our observations
478   encompassed a mixture of observations in the early morning hours up to midday. We did not find
479   any differences in departure processes among early morning departures and departures later during
480   the day.

481   Although Byrne (1981) had observed negotiation processes similar to those described for
482   hamadryas baboons during morning departures of Guinea baboons, we recorded such behaviors only
483   in two cases. Males of two OMUs showed greeting interactions (Dal Pesco & Fischer 2018) before
484   both left the sleeping site in the same direction with their party members. We are therefore rather
485   confident that elaborate negotiation processes do not play a major role in group coordination in this
486   species.

487   Another reason for the differences between Guinea and hamadryas in pre-departure
488   coordination processes may be different ecological conditions of the two species (e.g. Chala, Roos,
489   Svenning & Zinner, 2019). Kummer (1968a) and Stolba (1979) speculated that the elaborate
490   coordination process of hamadryas baboons is an adaptation to their arid environment. To exploit
491   food resources hamadryas bands often need to fission. Bands may break up into clans and even
492   single OMUs during foraging, but have to fuse again at scarce water sources or sleeping sites. Since
493   habitats of Guinea baboons in most parts of their distribution range are more productive than the
494   average hamadryas baboon habitat, i.e. higher densities of food and water resources, an elaborate
495   decision process on the direction of the daily travel direction might not be necessary.

496   Although signalers were more likely to use signals during departures, which could be taken as

497   an expression of their intention to move (or perhaps their intention to initiate a group movement;

498   Fischer & Zinner, 2011), this had no significant effect on their success in initiating group movement.

499   However, the power to detect an effect of signaling was low, as initiators were generally highly

500   successful in initiating group movement. It might also be the case that initiators who signaled were

501   indeed more highly motivated than those who did not signal, while followers were not affected by

502   the initiator's expression of motivation (Fischer & Price 2017).

503   The spatial positioning of progressing baboons has been primarily seen as an adaptation to

504   terrestrial lifestyle with its respective predation pressure (DeVore & Washburn, 1963). Progressions

505   of olive baboons were led by low-ranking adult males and older immature males. The most dominant

506   adult males, females with infants, and the youngest juveniles were in the center of the troop. The

507   rear portion of the troop was a mirror image of the front, with low-ranking adult males and older

508   immature males (DeVore & Washburn, 1963). In other populations of olive, yellow and chacma

509   baboons, however, adult males predominantly occupied front positions, while young individuals

510   mainly occupied central positions and adult females were equally spread from the front to the rear

511   (Harding 1977; Rhine et al., 1985; Rhine & Tilson, 1987). The progression of Guinea baboons

512   resembled the pattern described by DeVore & Washburn (1963), with non-primary adult males at the

513   front and primary males in more central positions. Adult females, however, occupied front, center or

514   rear position with similar probabilities, similar to what Rhine (1975) and Rhine & Tilson 1987)

515   reported from yellow and chacma baboons. Positions at the rear of the group were equally taken by

516   individuals of all age/sex classes. In summary, no clear pattern emerged for the different baboon

517   species. The analysis of the interval times indicated that individuals belonging to the same units, i.e.

518   individuals with closer social bonds, were more likely to depart and travel in close proximity,

519   corroborating previous findings in other baboon species (Bonnell, Clarke, Henzi & Barrett, 2017;

520   Farine et al., 2017; King et al., 2008, 2011; Kummer 1968a).

521   A comparison of the available data for the different species suggests that neither social

522   organization nor ecological conditions fully account for differences in group coordination processes.

523   With regard to the social organization, we found substantial differences between hamadryas and

524   Guinea baboons; thus life in a multi-level society does not necessarily give rise to elaborate

525   negotiation processes. The alternative idea that the harsh semi-desert conditions promotes

526   negotiation behaviors and accounts for the observed variation neither seems to be true, as chacma

527   baboons living in the Namib desert do not conform to the hamadryas pattern either (King et al.,

528   2008, 2011). A possible explanation may be that it takes both factors together: a multi-level society

529   with rather shallow rank hierarchies between males, and a resource distribution promoting fission-

530   fusion dynamics. One way to test this conjecture would be to observe Guinea baboons living in harsh

531   environments, such as the Sahara desert in Mauritania. Such observations are presently beyond our

532   means, but could provide the answer to the question which combination of drivers accounts for the

533   regulation of group coordination processes in baboons.

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547   DATA AVAILABILITY STATEMENT

548   Data and code are available upon request.

549

550   COMPETING INTERESTS

551   The authors declare no competing interests.

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553   ORCID

554   Julia Fischer https://orcid.org/0000-0002-5807-0074

555   Dietmar Zinner http://orcid.org/0000-0003-3967-8014

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