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ABSTRACT

Many group-living animals coordinate movements with acoustic signals, but so far most studies have focused on how group movements are initiated. In this study, we investigated movement patterns of wild sooty mangabeys (*Cercocebus atys*), a mostly terrestrial, forest-dwelling primate. We provide quantitative results showing that vocalizations can be utilized in more general terms during movements, by moderating movement speed and changes in direction of individuals. Particularly, we show that collective vocalization rates of the subgroup an individual was part of, rather than the individual's own vocalizations, predicted changes in future speed and, to a lesser degree, travel direction, although this was dependent on subgroup size and the presence of poly-specific associations. These results suggest that in this primate species vocal behaviour during movements goes beyond travel initiation to function more generally in coordination and regulation of group movements.

Keywords: group movement, vocal communication, poly-specific association

INTRODUCTION

Living in groups can convey considerable benefits for individuals, such as increased predator detection and foraging success. Nevertheless, individuals incur costs, for example through increased competition for resources or exposure to diseases (Krause and Ruxton, 2002; Majolo et al., 2008; Elgar, 1989; Sterck et al., 1997; Altizer et al., 2003). To benefit from the presence of others, individuals need to regulate group cohesion, especially during travel, and signals such as vocalizations are likely to play a key role (Fischer and Zinner, 2011a,b; Boinski and Garber, 2000; Conradt and Roper, 2005; Petit and Bon, 2010).

Most previous research in this domain has focused on how movements are initiated (e.g., Stewart and Harcourt, 1994; Bousquet et al., 2011; Radford, 2004), which has revealed a variety of mechanisms (Conradt and Roper, 2005; Petit and Bon, 2010). In contrast, we are not aware of empirical work that has looked at the role of vocalizations in how movements are coordinated during travel, how speed and changes in direction are determined, and how movements are terminated. As such, initiation and termination of group movements may only represent the extreme ends of a more complex phenomenon, which may include additional communicative mechanisms that are used to regulate movement patterns along the way.

In addition, researchers working on movement initiations normally study discrete bouts of movements, such as when travelling from a resting place to a food resource. In such situations typically a leader individual is followed or a group consensus is reached, through the production of specific vocal and other behavioural signals (e.g., Black, 1988; Fletcher, 2007; Bousquet et al., 2011). While it is possible that such discrete and conspicuous movement bouts are only typical for species that exploit clumped food or water resources (e.g., Noser and Byrne, 2014; Asensio et al., 2011), mechanisms for species foraging on relatively evenly distributed food resources may be different, especially if foraging involves more or less continuously travelling.

Vocalizations are particularly well studied with respect to their role in initiating movements (e.g., Poole et al., 1988; Bousquet et al., 2011; Fischer and Zinner, 2011a), perhaps because acoustic signals can bridge the continuum between local and global information of individuals within a group much better than visual signals. The latter can function only in the local domain (Conradt and Roper, 2005; Petit and Bon, 2010, see also Couzin et al. (2005) and Strandburg-Peshkin et al. (2015)) and the use of which is

therefore constrained by habitat characteristics. Thus, vocalizations might be particularly well suited for the propagation of local information through large groups, especially if individuals are spread beyond an individual's visual range in dense habitats.

In this study, we investigated whether vocal behaviour plays a role in regulating group movements beyond travel initiations. We conducted our study on sooty mangabeys (*Cercocebus atys*), a forest dwelling, terrestrial primate species that lives in relatively large groups of up to 100 individuals (McGraw et al., 2007). Sooty mangabey foraging behaviour consists of individuals searching for edible items throughout the forest floor (McGraw et al., 2007). As a result, their movements are rarely in the form of distinct travel bouts but are characterised by continuously moving with variable speed in a general direction. Note that despite the group following a general direction it is possible for individuals to change direction *within* the group.

Our focus here is on describing these movement patterns during foraging in association with vocal production. Particularly, we studied the relationship between vocal rates of focal individuals and individuals in their immediate vicinity (subgroup) and individual movement speed and direction. We focused on two particular mangabey vocalizations, grunts and twitters, because they were the most frequently produced calls and while their exact function is currently unknown, they are predominantly given in the foraging context (Range and Fischer, 2004) with preliminary observations suggesting a role in group coordination. All other vocalizations of mangabeys were pooled into an 'other vocalizations' category. Second, we studied the relationship between the described vocal rates and changes in direction of focal individuals. In addition, sooty mangabeys frequently form associations with other, arboreal primate species (mostly Diana monkeys, *Cercopithecus diana* and red colobus, *Procolobus badius*, McGraw et al. (2007)), presumably to increase predator detection (Bergmüller, 1998; McGraw and Bshary, 2002; Heymann, 2011), which enabled us to test whether movement patterns were influenced by vocal rates of other species and/or their mere presence.

METHODS

We observed adult individuals in a wild, habituated group of sooty mangabeys of approximately 90 individuals at Taï National Park in Côte d'Ivoire (McGraw et al., 2007; Janmaat et al., 2006; Range and Fischer, 2004). During focal animal follows, we used a combination of all-occurrence and instantaneous sampling (Altmann, 1974). Data on the focal individual's vocalizations (grunts, twitters, other vocalizations) were collected continuously. In two-minute intervals, we noted the behaviour of the focal individuals and the number of individuals present within 10m. Every 10min we noted the number of other primate species associated with the mangabey group. Another species was associated if we detected the presence of at least one individual of another species within 50m from the focal individual (McGraw and Bshary, 2002). GPS coordinates were recorded automatically every 30s with a Garmin Rhino 650 unit. We continuously recorded the soundscape around the focal individual (Sennheiser MKH-416 microphone, Marantz PMD660 recorder). From these audio recordings, we counted the number of monkey vocalizations audible and assigned them to either mangabeys (distinguishing grunts, twitters and others) or any of the associated primate species to calculate rates of vocalizations. Rates of mangabey vocalizations in the soundscape were positively correlated with subgroup size (grunt: $r = 0.22$; twitter: $r = 0.20$; other: $r = 0.34$), but model diagnostics suggested that this unproblematic (see ESM) and from here on we refer to these vocalization rates in the soundscape as subgroup grunts, subgroup twitters and subgroup other vocalizations.

We used linear mixed models to address our questions. We created time-blocks of five minutes, for which we established the distance covered by the focal animal (numeric, hereafter: speed), whether or not the focal animal produced at least one grunt or other vocalization (binary), the average number of individuals within 10m of the focal animal (numeric, hereafter: subgroup size), vocal rates of mangabeys as audible in the soundscape around the focal individual (grunts, twitters and other vocalizations, excluding the focal animal's vocalizations, all numeric), the sex of the focal individual (binary), the number of associated primate species (numeric), and the rate of primate, non-mangabey vocalizations. Vocalizations of focal animals were too infrequent to allow calculating meaningful calling rates and hence were coded binary. For the same reason, we could not include twitter production of focal individuals as predictor variable because during our observations no focal animal produced a twitter. We did not consider

97 behaviour/activity as variable in our models, because pure travel behaviour was rare (2.3% of activity
98 budget, see ESM). We incorporated an auto-correlation term to control for temporal dependence of data
99 points (Fürtbauer et al., 2011) and fitted individual ID and calendar date as random intercepts.

100 Change points, i.e. points in space and time at which individuals modified the direction into which they
101 moved, were assessed following procedures described by Byrne et al. (2009). In brief, the change point
102 test decomposes an individual track into smaller segments and examines whether a given track segment is
103 aligned with systematically varied numbers of segments before and after it (Byrne et al., 2009). A more
104 detailed description of the method can be found in Byrne et al. (2009) and examples of its application
105 are Asensio et al. (2011), Janmaat et al. (2013) and Noser and Byrne (2014). We used the following
106 parameters to calculate change points: $q = 6, \alpha = 0.05, N = 1000$ and a tolerance of 0.00002.

107 Our approach was two-fold. First, we aimed to describe the co-variation between speed and the
108 predictor variables within the same 5-minute time blocks. Second, within a given time block we used
109 our variables to predict speed in the following time block, i.e. future speed, while controlling for current
110 speed. We followed the same approach for modelling probabilities of direction changes (presence or
111 absence of 'change points') in current and future time blocks. Table 1 summaries the design. Our sample
112 comprised 16 individuals comprising 175 5-min data points totalling 14.6h of focal observations.

113 All models were built in R 3.1.1 (R Core Team, 2014) with the lmer and glmer functions in the lme4
114 package (v. 1.1.11, Bates et al., 2015). Statistical significance was established using likelihood ratio
115 tests (LRTs, Dobson, 2002) comparing full models with their respective null model. These null models
116 contained the same random effects as the full models and sex as fixed effect. Depending on the model,
117 we also included the auto-correlation term and speed or direction change in the previous time block
118 as additional terms in the null models. R^2 values were computed following Nakagawa and Schielzeth
119 (2013) using the MuMIn package (Bartoń, 2016). We tested several two-way interactions in each model,
120 which were retained only if they improved model fit as determined by LRTs and were otherwise removed
121 to allow interpretation of main effects (Mundry, 2011; Hector et al., 2010). Specifically, we included
122 interactions between subgroup size and vocalizations of mangabeys (both focal individuals' (grunt, other)
123 and subgroups' (grunt, twitter, other)), reasoning that effects of vocalizations may differ according to the
124 number of individuals in proximity of the focal individual. We also included the two-way interaction
125 between number of associated species and calling rate of associated species. More details on methods,
126 analyses and checks of model assumptions can be found in the ESM.

127 This study was entirely observational and adhered to the legal requirements of Côte d'Ivoire and
128 Switzerland, as well as to the Animal Behavior Society Guidelines for the Use of Animals in Research.
129 Research permissions were granted by the Ministère de la Recherche Scientifique et Technique of Côte
130 d'Ivoire.

RESULTS

Travel speed

133 Both models for current and future travel speed were different from their respective null models
134 (current: $\chi^2_{14} = 36.59, p = 0.0009, R^2_m = 0.36$; future: $\chi^2_{14} = 26.60, p = 0.0217, R^2_m = 0.34$; LRT; table 1;
135 full model results in tables 2 and 3).

Current travel speed

137 We found no strong relationships between vocalizations of focal animals and their current travel speed
138 (grunts: $\beta \pm se = -0.142 \pm 0.107, t = -1.332$; other vocalizations: $\beta \pm se = -0.049 \pm 0.132, t = -0.372$;
139 twitters: not tested, see methods).

140 In contrast, high rates of twitters in the soundscape (subgroup twitters) were associated with low
141 current speed of the focal individual ($\beta \pm se = -0.108 \pm 0.051, t = -2.146$, figure 1). We found no
142 such significant effect for subgroup grunts ($\beta \pm se = -0.068 \pm 0.049, t = -1.383$). For other subgroup
143 vocalizations the effect of calling rate was mediated by subgroup size (interaction: $\beta \pm se = -0.140 \pm$
144 $0.041, t = -3.410$, figure 2), insofar as in smaller subgroups, higher call rates were associated with higher
145 current speed, while the opposite was the case for larger subgroups.

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146 Finally, the calling rate of other primate species also influenced current speed and this was mediated
147 by the number of associated species ($\beta \pm \text{se} = 0.101 \pm 0.050, t = 2.021$): with fewer associated species,
148 higher call rates were associated with lower current speed, while the opposite was the case for larger
149 poly-specific groups consisting of many species (figure 3).

Future travel speed

151 As with current speed, we found no statistically significant effects of focal animal vocalizations
152 on future travel speed (grunts: $\beta \pm \text{se} = -0.107 \pm 0.143, t = -0.744$; other vocalizations: $\beta \pm \text{se} =$
153 $-0.280 \pm 0.169, t = -1.652$; twitters: not tested, see methods).

154 Focal individuals decreased future speed (i.e. travelled slower in the future) if the subgroup produced
155 more other vocalizations ($\beta \pm \text{se} = -0.154 \pm 0.062, t = -2.497$, figure 4). Subgroup grunt rate was also
156 associated with future speed, but this relationship depended on subgroup size (interaction: $\beta \pm \text{se} =$
157 $-0.130 \pm 0.055, t = -2.349$, figure 5): in small subgroups, individuals travelled faster in the future if the
158 subgroup produced grunts at higher rates, while the opposite was found for large subgroups. There was
159 no statistically significant effect of subgroup twitter rate on future speed ($\beta \pm \text{se} = -0.026 \pm 0.064, t =$
160 -0.406).

161 The number of associated species and calling rate of other primate species appeared to have no
162 pronounced effect on future travel speed of focal individuals (number of species: $\beta \pm \text{se} = -0.051 \pm$
163 $0.104, t = -0.489$; calling rate of other species: $\beta \pm \text{se} = -0.014 \pm 0.068, t = -0.208$).

Direction changes

165 Regarding changes in direction, neither the 'current direction changes' nor the 'future direction
166 changes' full model was significant at $\alpha = 0.05$ (current: $\chi^2_{14} = 20.35, p = 0.1194, R^2_m = 0.28$; future:
167 $\chi^2_{14} = 23.36, p = 0.0546, R^2_m = 0.30$; table 1; full model results in tables 4 and 5). Given the low p value
168 of the future model, we continued to explore this model.

Future direction changes

170 Focal animals' vocalizations did not significantly predict the probability of a change in future travel
171 direction (grunts: $\beta \pm \text{se} = 0.458 \pm 0.482, z = 0.950$; other vocalizations: $\beta \pm \text{se} = 0.499 \pm 0.635, z =$
172 0.786; twitters: not tested, see methods).

173 Individuals were more likely to change direction in the future if the rate of twitters in the subgroup
174 increased ($\beta \pm \text{se} = 0.494 \pm 0.255, z = 1.941$, figure 6). The probability of an individual changing direction
175 in the future also depended on the interaction between subgroup size and rate of other vocalizations in
176 the subgroup (interaction: $\beta \pm \text{se} = -0.559 \pm 0.288, z = -1.944$, figure 7). In smaller subgroups, future
177 direction changes were more likely with high rates of vocalizations compared to low vocalization rates. In
178 larger subgroups, this pattern is reversed, such that direction changes in the future were more likely with
179 low vocalization rates compared to high vocalization rates. There was no statistically significant effect of
180 subgroup grunt rate on the likelihood of changing direction in the future ($\beta \pm \text{se} = -0.095 \pm 0.241, t =$
181 -0.396).

182 As in the model of future speed, neither the number of associated species nor the calling rate of other
183 primate species appeared to have a pronounced effect on the probability of the focal individual changing
184 direction in the future (number of species: $\beta \pm \text{se} = -0.306 \pm 0.252, t = -1.215$; calling rate of other
185 species: $\beta \pm \text{se} = -0.027 \pm 0.228, t = -0.118$).

DISCUSSION

187 Our results indicate that the travel speed and changes in direction of focal individuals co-varied with
188 complex interactions of conspecific and heterospecific vocalizations. Notably, our results indicate that
189 individual movement patterns were largely independent of the focal animal's own vocal behaviour. In
190 contrast, we found effects of the subgroup's collective vocal behaviour, the subgroup's size, and the
191 number of associated primate species, which all were related to individual movement patterns.

Interestingly, differences in vocal rates were often not directly linked with differences in travel speed and direction changes, but were mediated by the social environment, i.e. subgroup size. The only vocal predictor of future speed that was independent of social factors was how many 'other' vocalizations were produced in the subgroup, which generally slowed down individuals. Most likely, this was a consequence of high rates of vocalizations produced during important social interactions, such as aggression and mating, which tend to take place while animals remain stationary.

Our results also suggest that the rate of twitters in the soundscape around the focal animal predicted whether or not this individual changed direction: individuals were more likely to change direction if twitters were more frequent as compared to when twitters were rare. Whether or not these direction changes led individuals towards the source of twitters is hitherto unknown and we do not have information about where these twitters originated from the focal individual's perspective. Given the proposed function of twitters in foraging (Range and Fischer, 2004), it would be interesting to see whether these calls serve as food calls similar to those described in chimpanzees, for example (Schel et al., 2013). Similar to our results on future speed, we found that the effect of the subgroup's 'other vocalizations' rate on the probability of changing future direction was modulated by subgroup size. As with changes in speed, it is most likely that these effects are a consequence of relevant social interactions nearby, for which 'other vocalizations' may be indicators and which may subsequently trigger changes in direction of focal individuals. Note, however, that our results on direction changes did not reach the conventional level of statistical significance and therefore have to be interpreted with some caution.

A major focus of studies on animal travel is to look at how group movements are initiated and how cohesion is maintained (Boinski and Garber, 2000; Fichtel and Manser, 2010), yet close to nothing is known about how group movement and cohesion are regulated once individuals are on their way. While it is known that vocalizations can play a role in group cohesion (e.g., Ramos-Fernández, 2005; Fischer et al., 2001; Cheney et al., 1996), the results of our study suggest that individual movement patterns, i.e. changes in speed and direction, need to be addressed as a potential proximate mechanism as to how groups, which are made up of individuals, achieve cohesion.

We propose that acceleration and deceleration of movements and adjustment of direction – in addition to initiating – is a domain that requires communication and our current findings support this view. In fact, fine-tuned regulation of group movements may be a common, hitherto largely overlooked, mechanism that is crucial in many group living species that depend on cohesion and occupy large home ranges. As such, vocally mediated movement regulation may be the default mechanism on a continuous scale with the more conspicuous initiation and termination of movements at the extremes.

Our hypothesis is that species that are constantly on the move, such as sooty mangabeys and other scramble foragers, may benefit specifically from a communication system that enables individuals to continuously regulate group movements as opposed to species for which group movements occur in discrete bouts for example to exploit clumped food resources (Kinnaird and O'Brien, 2000).

We might even expect that within-species variation exists as to what a coordination signal may mean. For example, frugivorous species are likely to travel in bouts during periods of high fruit availability and switch to continuous travelling in periods when food sources are dispersed, which is likely to exert different evolutionary pressures on a communication system. Sooty mangabeys exhibit such flexibility in their feeding ecology (Bergmüller, 1998, see also Janmaat et al. (2006)). Our data collection took place when food sources were dispersed, and it will be interesting to see how movements in this species are coordinated when resources are clumped (Janmaat et al., 2006).

Our results also indicate that associations with other primate species and their vocalizations influence mangabey movements. Poly-specific associations among Taï monkeys are common (McGraw et al., 2007), offering mutually increased predator detection (Bergmüller, 1998; McGraw and Bshary, 2002). The cost/benefit ratio of these associations is high, given that they do not lead to increased food competition. Yet again, most data on communicative mechanisms so far demonstrate how associations are formed, rather than maintained and regulated (Heymann, 2011). Our results suggest that mangabeys adapt and coordinate their movements according to the presence and vocalizations of other primate species. These results suggest that the underlying communicative mechanisms of interspecific movement coordination may be more complex than previously thought.

In sum, our results represent the first example of vocalizations being used in the context of movement regulation of wild primates, and draw a complex picture of how vocalizations of mangabeys and their association partners alongside the immediate social environment of individuals need to be integrated to understand movement patterns of individuals. Future playback experiments will elucidate whether the relationships we suggest are indeed causal.

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REFERENCES

Altizer, S., Nunn, C. L., Thrall, P. H., Gittleman, J. L., Antonovics, J., Cunningham, A. A., Cunnningham, A. A., Dobson, A. P., Ezenwa, V., Jones, K. E., Pedersen, A. B., Poss, M., and Pulliam, J. R. C. (2003). Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics*, 34:517–547.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49(3):227–266.

Asensio, N., Brockelman, W. Y., Malaivijitnond, S., and Reichard, U. H. (2011). Gibbon travel paths are goal oriented. *Animal Cognition*, 14(3):395–405.

Bartoń, K. (2016). MuMIn: Multi-Model Inference.

Bates, D. M., Mächler, M., Bolker, B. M., and Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1):1–48.

Bergmüller, R. (1998). Nahrungsökologie der Rauchgrauen Mangabe (*Cercocebus torquatus atys*) [Feeding ecology of sooty mangabeys].

Black, J. M. (1988). Preflight signalling in swans: a mechanism for group cohesion and flock formation. *Ethology*, 79(2):143–157.

Boinski, S. and Garber, P. A., editors (2000). *On the move: how and why animals travel in groups*. University Of Chicago Press, Chicago.

Bousquet, C. A. H., Sumpter, D. J. T., and Manser, M. B. (2011). Moving calls: a vocal mechanism underlying quorum decisions in cohesive groups. *Proceedings of the Royal Society B: Biological Sciences*, 278(1711):1482–1488.

Byrne, R. W., Noser, R., Bates, L. A., and Jupp, P. E. (2009). How did they get here from there? Detecting changes of direction in terrestrial ranging. *Animal Behaviour*, 77(3):619–631.

Cheney, D. L., Seyfarth, R. M., and Palombit, R. A. (1996). The function and mechanisms underlying baboon 'contact' barks. *Animal Behaviour*, 52(3):507–518.

Conradt, L. and Roper, T. J. (2005). Consensus decision making in animals. *Trends in Ecology & Evolution*, 20(8):449–456.

Couzin, I. D., Krause, J., Franks, N. R., and Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, 433(7025):513–516.

Dobson, A. J. (2002). *An introduction to generalized linear models*. Chapman and Hall, Boca Raton, 2nd edition.

Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews*, 64(1):13–33.

Fichtel, C. and Manser, M. (2010). Vocal communication in social groups. In Kappeler, P. M., editor, *Animal behaviour: evolution and mechanisms*, pages 29–54. Springer, Berlin/Heidelberg.

Fischer, J., Hammerschmidt, K., Cheney, D. L., and Seyfarth, R. M. (2001). Acoustic features of female chacma baboon barks. *Ethology*, 107(1):33–54.

Fischer, J. and Zinner, D. (2011a). Communication and cognition in primate group movement. *International Journal of Primatology*, 32(6):1279–1295.

Fischer, J. and Zinner, D. (2011b). Communicative and cognitive underpinnings of animal group movement. In Boos, M., Kolbe, M., Kappeler, P. M., and Ellwart, T., editors, *Coordination in human and primate groups*, pages 229–244. Springer, Berlin/Heidelberg.

Fletcher, L. E. (2007). Vibrational signals in a gregarious sawfly larva (*Perga affinis*): group coordination or competitive signaling? *Behavioral Ecology and Sociobiology*, 61(12):1809–1821.

Fürtbauer, I., Mundry, R., Heistermann, M., Schülke, O., and Ostner, J. (2011). You mate, I mate: macaque females synchronize sex not cycles. *PLoS ONE*, 6(10):e26144.

Hector, A., von Felten, S., and Schmid, B. (2010). Analysis of variance with unbalanced data: an update for ecology & evolution. *Journal of Animal Ecology*, 79(2):308–316.

Heymann, E. W. (2011). Coordination in primate mixed-species groups. In Boos, M., Kolbe, M., Kappeler, P. M., and Ellwart, T., editors, *Coordination in human and primate groups*, pages 263–281. Springer, Berlin/Heidelberg.

Janmaat, K. R. L., Ban, S. D., and Boesch, C. (2013). Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons. *Animal Behaviour*, 86(6):1183–1205.

Janmaat, K. R. L., Byrne, R. W., and Zuberbühler, K. (2006). Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. *Animal Behaviour*, 72(4):797–807.

Kinnaird, M. F. and O'Brien, T. G. (2000). Comparative movement patterns of two semiterrestrial cercopithecine primates: the Tana River crested mangabey and Sulawesi crested black macaque. In Boinski, S. and Garber, P. A., editors, *On the move*, pages 327–350. University Of Chicago Press, Chicago.

Krause, J. and Ruxton, G. D. (2002). *Living in groups*. Oxford University Press, Oxford.

Majolo, B., de Bortoli Vizioli, A., and Schino, G. (2008). Costs and benefits of group living in primates: group size effects on behaviour and demography. *Animal Behaviour*, 76(4):1235–1247.

McGraw, W. S. and Bshary, R. (2002). Association of terrestrial mangabeys (*Cercocebus atys*) with arboreal monkeys: experimental evidence for the effects of reduced ground predator pressure on habitat use. *International Journal of Primatology*, 23(2):311–325.

McGraw, W. S., Zuberbühler, K., and Noë, R., editors (2007). *Monkeys of the Taï Forest: an African primate community*. Cambridge University Press, Cambridge.

Mundry, R. (2011). Issues in information theory-based statistical inference – a commentary from a frequentist's perspective. *Behavioral Ecology and Sociobiology*, 65(1):57–68.

Nakagawa, S. and Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2):133–142.

Noser, R. and Byrne, R. W. (2014). Change point analysis of travel routes reveals novel insights into foraging strategies and cognitive maps of wild baboons. *American Journal of Primatology*, 76(5):399–409.

Petit, O. and Bon, R. (2010). Decision-making processes: the case of collective movements. *Behavioural Processes*, 84(3):635–647.

Poole, J. H., Payne, K., Langbauer, Jr, W. R., and Moss, C. J. (1988). The social contexts of some very low frequency calls of African elephants. *Behavioral Ecology and Sociobiology*, 22(6):385–392.

R Core Team (2014). R: A Language and Environment for Statistical Computing.

Radford, A. N. (2004). Vocal coordination of group movement by green woodhoopoes (*Phoeniculus purpureus*). *Ethology*, 110(1):11–20.

Ramos-Fernández, G. (2005). Vocal communication in a fission-fusion society: do spider monkeys stay in touch with close associates? *International Journal of Primatology*, 26(5):1077–1092.

Range, F. and Fischer, J. (2004). Vocal repertoire of sooty mangabeys (*Cercocebus torquatus atys*) in the Taï National Park. *Ethology*, 110(4):301–321.

Schel, A. M., Machanda, Z., Townsend, S. W., Zuberbühler, K., and Slocombe, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour*, 86(5):955–965.

Sterck, E. H. M., Watts, D. P., and van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, 41(5):291–309.

Stewart, K. J. and Harcourt, A. H. (1994). Gorillas' vocalizations during rest periods: signals of impending departure? *Behaviour*, 130(1):29–40.

Strandburg-Peshkin, A., Farine, D. R., Couzin, I. D., and Crofoot, M. C. (2015). Shared decision-making drives collective movement in wild baboons. *Science*, 348(6241):1358–1361.

Table 1. Outline of analysis strategy and summary of results. We built four models that tested variation in current and future speed and probability of direction changes of sooty mangabeys. Results in the table represent comparisons of full versus null models using likelihood ratio tests.

	Speed	Change points
current time block	$\chi^2_{14} = 36.59$	$\chi^2_{14} = 20.35$
	$p = 0.0009$	$p = 0.1194$
future time block	$\chi^2_{14} = 26.60$	$\chi^2_{14} = 23.36$
	$p = 0.0217$	$p = 0.0546$

Table 2. Results of LMM testing variation in *current speed*. Given are results for the full model, including all interactions, and of the final model, from which non-significant interaction terms were removed. Significance of interpretable terms in the final model (interaction terms and main effects of terms not included in an interaction) was assessed with likelihood ratio tests. Reference levels of categorical variables are: focal grunt = 'no', focal other = 'no', and sex = 'female'. Test levels are given in parentheses. LRT = likelihood ratio test, IA = interaction.

	full model		final model		LRT	
	$\beta \pm$ se	t	$\beta \pm$ se	t	χ^2_1	p
intercept	-0.35 ± 1.27	-0.28	-0.31 ± 1.27	-0.25		
subgroup size	-0.07 ± 0.05	-1.32	-0.05 ± 0.05	-0.99		
focal grunt (yes)	-0.15 ± 0.11	-1.44	-0.14 ± 0.11	-1.33	1.76	0.1844
focal other vocalization (yes)	-0.03 ± 0.13	-0.19	-0.05 ± 0.13	-0.37	0.14	0.7107
subgroup grunt	-0.07 ± 0.05	-1.44	-0.07 ± 0.05	-1.38	1.90	0.1680
subgroup other	0.11 ± 0.05	2.45	0.10 ± 0.05	2.16		
subgroup twitter	-0.12 ± 0.05	-2.28	-0.11 ± 0.05	-2.15	4.53	0.0333
number of associated species	-0.03 ± 0.08	-0.43	-0.00 ± 0.08	-0.06		
vocal rate of other species	-0.01 ± 0.05	-0.19	-0.03 ± 0.05	-0.53		
sex (male)	4.03 ± 2.27	1.78	3.99 ± 2.27	1.75	2.87	0.0901
auto-correlation	-2.60 ± 0.14	-18.53	-2.61 ± 0.14	-18.48	113.99	0.0000
IA subgroup size : focal grunt	0.19 ± 0.11	1.68				
IA subgroup size : focal other	-0.23 ± 0.18	-1.29				
IA subgroup size : subgroup grunt	0.03 ± 0.05	0.56				
IA subgroup size : subgroup other	-0.16 ± 0.04	-3.66	-0.14 ± 0.04	-3.41	11.18	0.0008
IA subgroup size : subgroup twitter	0.03 ± 0.05	0.74				
IA associated species : vocal rate of other species	0.10 ± 0.05	2.02	0.10 ± 0.05	2.02	4.01	0.0453

Table 3. Results of LMM testing variation in *future speed*. Given are results for the full model, including all interactions, and of the final model, from which non-significant interaction terms were removed. Significance of interpretable terms in the final model (interaction terms and main effects of terms not included in an interaction) was assessed with likelihood ratio tests. Reference levels of categorical variables are: focal grunt = 'no', focal other = 'no', and sex = 'female'. Test levels are given in parentheses. LRT = likelihood ratio test, IA = interaction.

	full model		final model		LRT	
	$\beta \pm$ se	t	$\beta \pm$ se	t	χ_1^2	p
intercept	0.16 ± 0.71	0.22	0.20 ± 0.69	0.28		
subgroup size	-0.01 ± 0.07	-0.12	-0.03 ± 0.06	-0.53		
focal grunt (yes)	-0.15 ± 0.14	-1.05	-0.11 ± 0.14	-0.74	0.55	0.4575
focal other vocalization (yes)	-0.31 ± 0.17	-1.77	-0.28 ± 0.17	-1.65	2.70	0.1007
subgroup grunt	0.16 ± 0.06	2.63	0.15 ± 0.06	2.36		
subgroup other	-0.15 ± 0.06	-2.45	-0.15 ± 0.06	-2.50	6.06	0.0139
subgroup twitter	-0.02 ± 0.07	-0.32	-0.03 ± 0.06	-0.41	0.16	0.6855
number of associated species	-0.05 ± 0.10	-0.49	-0.05 ± 0.10	-0.49	0.22	0.6354
vocal rate of other species	0.01 ± 0.07	0.07	-0.01 ± 0.07	-0.21	0.04	0.8378
sex (male)	0.67 ± 1.26	0.53	0.52 ± 1.24	0.42	0.18	0.6747
control speed	0.00 ± 0.06	0.02	0.02 ± 0.06	0.33	0.10	0.7461
auto-correlation	-1.60 ± 0.13	-12.76	-1.60 ± 0.13	-12.58	61.20	0.0000
IA subgroup size : focal grunt	-0.12 ± 0.15	-0.79				
IA subgroup size : focal other	0.00 ± 0.23	0.01				
IA subgroup size : subgroup grunt	-0.09 ± 0.06	-1.41	-0.13 ± 0.06	-2.35	5.39	0.0203
IA subgroup size : subgroup other	-0.10 ± 0.06	-1.70				
IA subgroup size : subgroup twitter	-0.02 ± 0.06	-0.33				
IA associated species : vocal rate of other species	0.08 ± 0.06	1.37				

Table 4. Results of GLMM testing variation in *current direction changes*. Given are results for the full model, including all interactions. Since the overall model was not statistically significant at $\alpha = 0.05$ no final model or tests of individual terms are presented. Reference levels of categorical variables are: focal grunt = 'no', focal other = 'no', and sex = 'female'. Test levels are given in parentheses. IA = interaction.

	$\beta \pm \text{se}$	z
intercept	-1.68 ± 0.34	-4.89
subgroup size	-0.78 ± 0.31	-2.54
focal grunt (yes)	-0.20 ± 0.49	-0.41
focal other vocalization (yes)	0.97 ± 0.65	1.49
subgroup grunt	0.01 ± 0.26	0.05
subgroup other	0.02 ± 0.25	0.07
subgroup twitter	0.14 ± 0.27	0.51
number of associated species	-0.14 ± 0.31	-0.45
vocal rate of other species	0.32 ± 0.27	1.19
sex (male)	0.05 ± 0.61	0.08
IA subgroup size : focal grunt	0.22 ± 0.60	0.36
IA subgroup size : focal other	2.34 ± 1.04	2.24
IA subgroup size : subgroup grunt	0.04 ± 0.30	0.12
IA subgroup size : subgroup other	-0.56 ± 0.28	-1.98
IA subgroup size : subgroup twitter	-0.08 ± 0.30	-0.26
IA associated species : vocal rate of other species	0.36 ± 0.20	1.77

Table 5. Results of GLMM testing variation in *future direction changes*. Given are results for the full model, including all interactions, and of the final model, from which non-significant interaction terms were removed. Significance of interpretable terms in the final model (interaction terms and main effects of terms not included in an interaction) was assessed with likelihood ratio tests. Reference levels of categorical variables are: focal grunt = 'no', focal other = 'no', and sex = 'female'. LRT = likelihood ratio test, IA = interaction.

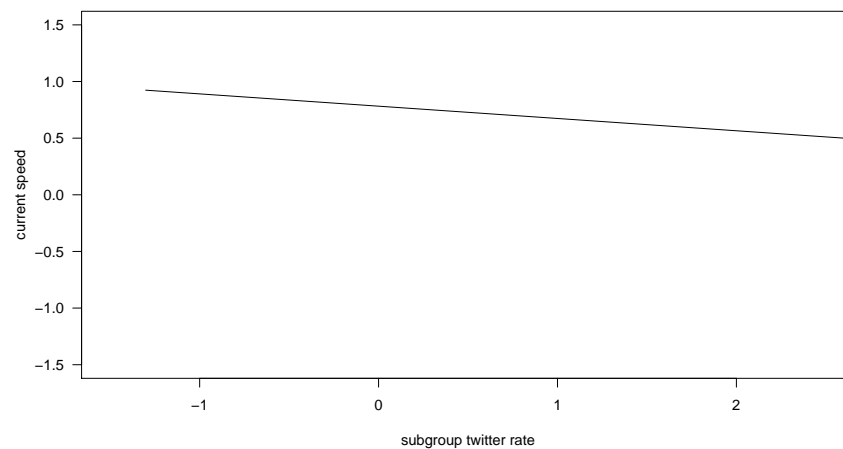|	full model		final model		LRT	
	$\beta \pm$ se	z	$\beta \pm$ se	z	χ^2_1	p
intercept	-1.80 ± 0.38	-4.72	-1.76 ± 0.36	-4.85		
subgroup size	-0.30 ± 0.33	-0.91	-0.43 ± 0.25	-1.69		
focal grunt (yes)	0.26 ± 0.52	0.51	0.46 ± 0.48	0.95	0.89	0.3444
focal other vocalization (yes)	0.79 ± 0.72	1.10	0.50 ± 0.63	0.79	0.61	0.4367
subgroup grunt	-0.03 ± 0.28	-0.11	-0.10 ± 0.24	-0.40	0.16	0.6917
subgroup other	-0.40 ± 0.27	-1.48	-0.32 ± 0.25	-1.30		
subgroup twitter	0.51 ± 0.30	1.69	0.49 ± 0.25	1.94	3.86	0.0493
number of associated species	-0.21 ± 0.28	-0.75	-0.31 ± 0.25	-1.22	1.48	0.2238
vocal rate of other species	0.15 ± 0.28	0.54	-0.03 ± 0.23	-0.12	0.01	0.9064
sex (male)	0.53 ± 0.63	0.84	0.71 ± 0.61	1.17	1.36	0.2437
control change point	1.19 ± 0.51	2.33	1.31 ± 0.48	2.76	7.50	0.0062
IA subgroup size : focal grunt	-1.25 ± 0.68	-1.84				
IA subgroup size : focal other	1.46 ± 0.93	1.58				
IA subgroup size : subgroup grunt	0.17 ± 0.28	0.61				
IA subgroup size : subgroup other	-0.79 ± 0.34	-2.28	-0.56 ± 0.29	-1.94	4.44	0.0352
IA subgroup size : subgroup twitter	0.04 ± 0.33	0.11				
IA associated species : vocal rate of other species	0.33 ± 0.21	1.57				

Figure 1. Higher rates of subgroup twitters were associated with lower travel speed.
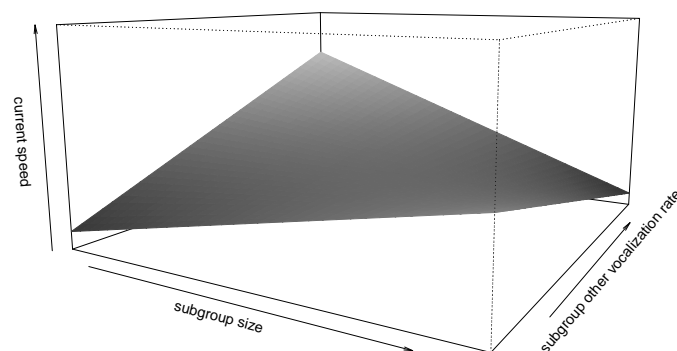

Figure 2. Interaction effect of subgroup size and subgroup rate of other vocalizations. In smaller subgroups, higher calling rates were associated with faster travel speed. In larger subgroups, lower calling rates were associated with higher travel speed of focal individuals. Speed (along the z-axis) ranges between -1.5 and 1.5. Limits along the x- and y-axes correspond to the range of standardized values in the data.
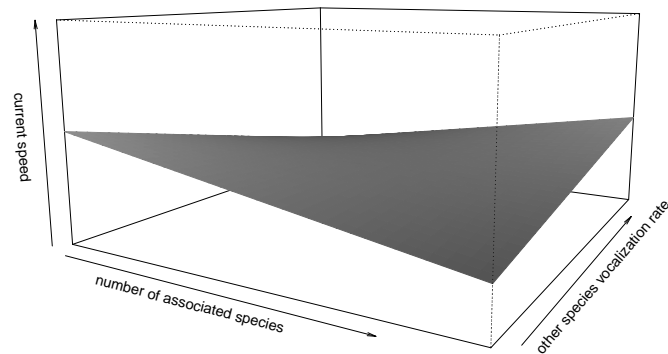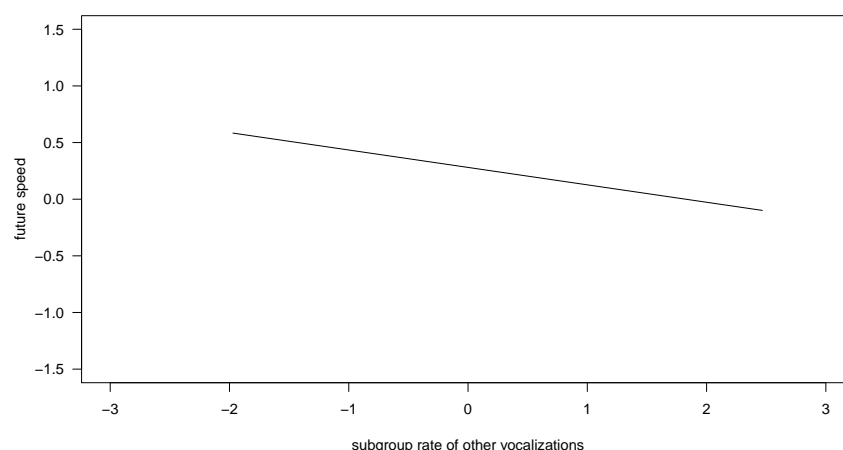
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Figure 3. Interaction effect of number of associated species and calling rate of other species. With fewer associated species, higher calling rates corresponded to lower travel speed. With more associated species, higher calling rates corresponded to higher speed of focal individuals. Speed (along the z-axis) ranges between -1.5 and 1.5. Limits along the x- and y-axes correspond to the range of standardized values in the data.

Figure 4. Individuals slowed down in the future if the subgroup produced other vocalizations at higher rates.
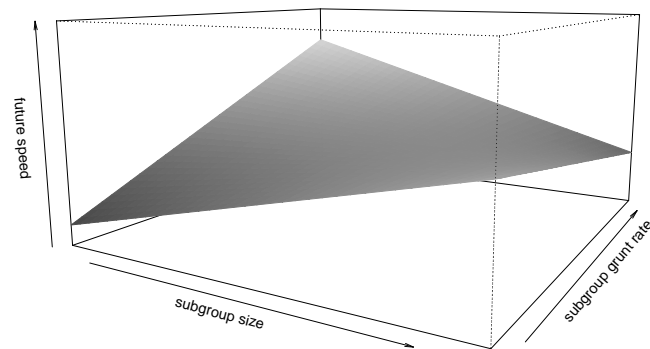
Figure 5. Interaction between subgroup size and subgroup grunt rate and its effect on future speed of individual mangabeys. In smaller subgroups, individuals increased future speed with higher subgroup grunt rates. In larger subgroups, individuals decreased future speed with higher subgroup grunt rates. Speed (along the z-axis) ranges between -1.5 and 1.5. Limits along the x- and y-axes correspond to the range of standardized values in the data.
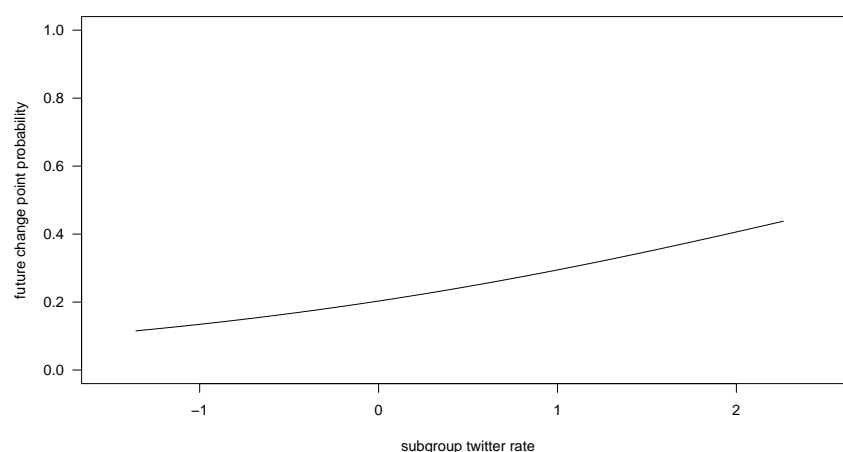

Figure 6. Individuals were more likely to change direction if the subgroup twitter rate was higher.
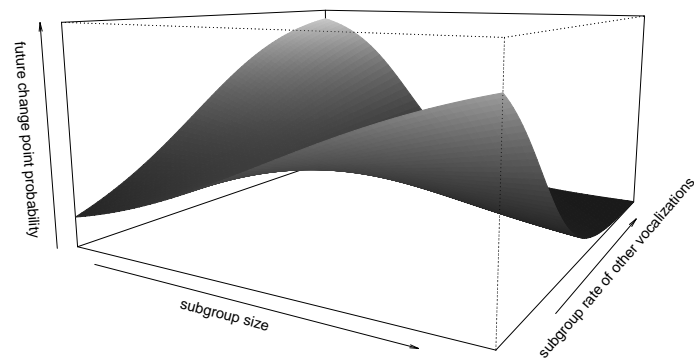
Figure 7. Interaction between subgroup size and subgroup rate of other vocalizations. Individuals were more likely to change direction in the future if the subgroup was small but vocalized at high rates or if subgroup size was large but produced little other vocalizations. Probability of a change in direction (along the z-axis) ranges between 0 and 1. Limits along the x- and y-axes correspond to the range of standardized values in the data.