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Contact call acoustic structure is associated with inter-individual distances during antiphonal vocal exchanges in wild red-tailed monkeys (*Cercopithecus ascanius schmidti*)

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Abstract

Contact calls allow animals to maintain group cohesion when visibility is restricted. To maximise call detection, animals should produce calls that are audible to closest neighbours or respond to individuals that produce preceding calls (i.e., antiphony). Antiphonal exchanges are more likely to occur between older conspecifics that respond more reliably or close neighbours that are more likely to detect calls when groups are travelling. Because animals should produce calls that are optimised for propagation, call structure should be associated with the distance between individuals calling in antiphonal exchanges. I investigated whether acoustic structures of red-tailed monkey (*Cercopithecus ascanius*) contact calls (phrased grunts) reflected increased sound propagation as nearest neighbour distances increased, depending on three factors: (1) the occurrence of a preceding grunt, (2) neighbour age-sex class, and (3) group travel speed. I recorded grunts from five habituated monkey groups at Kibale National Park, Uganda. Per grunt, I measured five parameters associated with sound propagation. Grunt mean entropy and frequency related negatively to neighbour distance when the neighbour produced a preceding grunt or when there was no preceding grunt, but not when a more distant individual grunted prior. Neighbour age-sex class and group travel speed did not influence whether grunt structure was associated with neighbour distance, but monkeys produced grunts with higher mean entropy and frequency as groups travelled faster. Variation in grunt mean entropy and frequency was associated with propagation to either nearest neighbours or more distant individuals that produced preceding calls, providing quantitative evidence for antiphonal calling. By calling antiphonally, animals in cohesive groups can spread out to

avoid intra-group competition while maintaining contact with other group members. Higher grunt entropy and frequency as groups travel faster may counteract more variable sound attenuation as animals move through acoustically complex (e.g., densely vegetated) environments.

Keywords
animal communication, antiphonal calling, turn-taking, vocalising behaviour, guenon.

1. Introduction

To benefit from sociality, group-living animals must be able to maintain and adjust group cohesion (the relative spatial positioning of individuals within a group; Trillmich et al., 2004; Ward & Webster, 2016). Group members often need to communicate rapidly and across long distances to mediate inter-individual distances and track locations of specific individuals (e.g., to maintain social bonds; Cheney et al., 1996; Oda, 1996). Efficient mechanisms of communication allow individuals to adjust spatial positioning and minimise costs of sociality, such as increased competition for food or reproductive opportunities from other group members, that determine maximum group size and social structure (Krause & Ruxton, 2002; see also, e.g., Chapman & Chapman, 2000). Communication behaviour should therefore reflect adaptations to social and ecological pressures that influence animal sociality (Ord et al., 2010).

Acoustic communication is an energetically expensive modality of communication (Ryan, 1986). In complex (e.g., densely vegetated) environments, vocalisations that are not optimised for propagation can quickly attenuate or reverberate before being detected by another group member (Brown & Waser, 2017). Antiphonal vocalising, where two or more animals call in response to preceding calls, is an adaptation that can increase chances of call detection and reduces redundancy of calls that are energetically costly to produce (Yoshida & Okanoya, 2005; Pika et al., 2018). By responding to a preceding call, individuals can validate successful transmission of information and minimise overlap in calls that degrades vocalisation quality and risks miscommunication (Snowdon, 2001; Yoshida & Okanoya, 2005; Inoue et al., 2013).

Contact calls that communicate animal locations between group members are often produced in antiphonal exchanges (Carter et al., 2008; Candiotti et al., 2012). Antiphonal contact calling is especially important for animals in aquatic, densely vegetated, or dark environments, where visual and tactile

communication are limited (Brown & Waser, 2017; e.g., orcas, *Orcinus orca* — Miller et al., 2004; Cape mole-rats, *Georychus capensis* — Narins et al., 1992; naked mole-rats, *Heterocephalus glaber* — Yosida et al., 2007; white-winged vampire bats, *Diaemus youngi* — Carter et al., 2008; reviewed in Pika et al., 2018). By calling antiphonally, animals can maximise likelihood of vocalisation detection without needing to increase call rate or propagation distance, which may expend more energy (e.g., pygmy marmosets, *Cebuella pygmaea* — Snowdon & Hodun, 1981; de la Torre & Snowdon, 2002). Optimising contact calls for detectability as an alternative to increasing call rate can also reduce the risk of alerting potential predators to animal locations. Investigating antiphonal contact calling therefore provides insight into how animals maintain cohesive groups, even when conspecifics are not visible and vocal communication is expected to increase predation risk.

Demographic factors should influence which animals engage in antiphonal exchanges. For example, older group members may be more likely to participate in antiphonal exchanges because they are more reliable sources of information or more likely to respond to preceding calls than younger, inexperienced animals (Lemasson et al., 2010; Henry et al., 2015; Briseno-Jaramillo et al., 2018). Among primates, older individuals are more likely to engage in antiphonal exchanges in common marmosets (*Callithrix jacchus* — Chen et al., 2009) and Japanese macaques (*Macaca fuscata* — Lemasson et al., 2013). In contrast, juveniles are more likely to interrupt or break antiphonal exchanges, especially if exchanges are learned behaviour (e.g., common marmosets — Chow et al., 2015; Japanese macaques — Bouchet et al., 2017; Campbell's monkeys, *Cercopithecus campbelli* — Lemasson et al., 2010, 2011; humans — Henry et al., 2015).

Several factors associated with group travel may also influence which individuals engage in antiphonal exchanges. Animals create ambient noise as they travel due to breaking vegetation or water splashes, for example. As groups travel faster, tracking positions of moving group members may also become more challenging without visual contact or if animals spread out while travelling. Animals that are travelling may therefore be less likely to detect vocalisations or produce calls that are audible to group members, particularly if call frequencies overlap those of ambient noise. Producing calls that are most likely to be detected by a particular individual may also be harder if the location of the recipient is more difficult to identify in fast-moving groups (Snowdon & Hodun, 1981; Brown, 1989; Lohr et al., 2003).

To communicate more efficiently and improve the likelihood of call detection, animals in faster-moving groups should therefore produce calls that are more likely to be detected by closer, visible individuals (see also Koda et al., 2008).

Analysing recordings of calls can provide insight into antiphonal calling in wild animals when vocalising behaviour is difficult to observe and experimental approaches (e.g., manipulating calling dyad combinations — Yosida et al., 2007; playback experiments — Miller & Wren Thomas, 2012) are not feasible. Acoustic properties such as duration, entropy, and frequency are directly associated with how far a sound should propagate (Table 1). For example, sounds with longer durations should attenuate over distance more slowly, particularly in enclosed, densely-vegetated environments where reverberation may degrade shorter sounds but increase reflection of longer sounds (de la Torre & Snowdon, 2002; Naguib, 2003; Nemeth et al., 2006). Wider inter-individual distances relate to longer duration of contact calls in

Table 1.
Call acoustic parameters selected a priori for investigation with assumed effects on call propagation distance.

Acoustic parameter	Definition (this study)	Unit	Assumed relationship with call propagation distance
Duration	Total duration of call	Milliseconds (ms)	Positive
Mean entropy	Function of energy distribution across frequencies, with more tonal, narrowband sounds having lower entropy than noisier, broadband sounds	Bits	Negative
Maximum frequency	Frequency at which maximum power (dB/sample unit) of call occurs	Hertz (Hz)	Negative
Mean frequency	Mean of centre frequency ("the frequency that divides the spectrogram slice into two frequency intervals of equal energy" — Charif et al., 2010) across duration of call		Negative
Minimum frequency	Minimum centre frequency across duration of call		Negative

Japanese macaques (Sugiura, 2007) and isolation calls in squirrel monkeys (*Saimiri sciureus* — Masataka & Symmes, 1986; see also Brumm et al., 2004; Ey et al., 2009; but see Oda, 1996).

A sound's entropy also affects its propagation. Entropy is a measure of the distribution of energy across frequencies (i.e., the degree of 'noise'), which ranges from 0 (a pure tone with energy concentrated at a single frequency) to 1 (white noise, where energy is distributed equally across all frequencies; Ríos-Chelén et al., 2020). At low frequency ranges (0–2000 Hz), assuming the same total energy and lack of interference from ambient noise or reflective surfaces in the environment, more 'tonal' sounds with lower entropy should travel further than 'noisier' sounds with higher entropy (Waser & Waser, 1977). Lower entropy is also associated with higher amplitude (Ríos-Chelén et al., 2020; see also Liao et al., 2018; Fuong & Blumstein, 2020).

Sounds with concentrations of energy at lower frequencies attenuate over distance more slowly and propagate further (Marten et al., 1977; Brenowitz, 1986; Waser & Brown, 1986; Ey et al., 2009). Sounds are also reflected more effectively by objects with reflective surface diameters at least equal to the sound wavelength, which lengthens as frequency decreases (e.g., at 20°C ambient temperature, $\geqslant$33 cm diameter to reflect a 1000 Hz sound; $\geqslant$69 cm for a 500 Hz sound; Naguib, 2003). In densely vegetated environments with many small leaves, low frequency, long wavelength sounds should therefore attenuate less and propagate further (Naguib, 2003; Nemeth et al., 2006).

Variation in duration, entropy, and frequency is associated with the distance at which a sound should be detectable. Animals also adjust call acoustic structure to maximise chances of detection (Ey & Fischer, 2009; Ey et al., 2009). Variation in acoustic parameters should therefore be associated with receiver location; that is, animals located further away from a calling individual should be more likely to detect a call when the call acoustic structure is associated with a longer propagation distance (Table 1). Moreover, selection should favour greater modulation of contact call structure in animals that (1) live in large or widely spread groups, where individuals communicate with group members that frequently change position (Sugiura, 2007) and (2) exhibit complex, long-term social bonds (e.g., many primates; Miller & Wren Thomas, 2012).

I investigated antiphonal contact calling in the red-tailed monkey (*C. ascanius*), a social primate that lives primarily in densely vegetated forests

(Sarmiento et al., 2001). Groups are typically relatively large (15–35 individuals) and exhibit wide inter-individual distances (e.g., >50 m group diameter). Adult females and subadults and juveniles of both sexes produce contact calls (phrased grunts) that are associated with group cohesion; that is, maintaining contact between an individual and at least one other group member (Marler, 1973; Cords & Sarmiento, 2013).

I tested the hypothesis that animals modulate call acoustic structure based on distance to the nearest neighbour. I predicted that red-tailed monkey call duration increases and call entropy and frequency decrease as the distance between the caller and the nearest neighbour increases. I expected three factors to influence the strength of these relationships: whether the nearest neighbour produces a preceding call; nearest neighbour age-sex class; and group travel speed. I predicted that variation in call acoustic structure is more likely to relate to nearest neighbour distance when (1) a preceding grunt is produced by the nearest neighbour (versus an individual further away), (2) the neighbour is an adult female (versus a subadult or juvenile) and (3) groups are travelling faster (Tables 1 and 2).

2. Material and methods

2.1. Data collection

I collected data at Ngogo, Kibale National Park (Uganda), a mosaic of predominantly closed-canopy primary forest and mixed-canopy secondary forest (Struhsaker, 1997). I followed five habituated red-tailed monkey groups, each comprising one adult male and multiple adult females, subadults, and juveniles (16–35 total individuals per group; median = 21 individuals; Table 3). I followed groups from 07:00 to 19:00 daily and typically in sets of six consecutive follow days between March–October 2017 and January-June 2019 (24–112 follow days per group; Table 3). I followed each group in at least one rainy season month and one dry season month during the study, although there is substantial monthly and annual variation in rainfall at Ngogo that means seasons are not consistent between years (Struhsaker, 1997). No other observers collected data or were present during follows. In each group, I could individually identify the adult male, most or all adult females and subadults, and a few (2–3) juveniles. I also collected data while still learning identities, in which case I only recorded the identity of the focal individual if I was certain.

Table 2.
Predicted and observed influence of three factors on the strength of the relationship between increasing nearest neighbour distance and call duration, entropy, and frequency.

Factor	Levels	Predicted relative strength of relationship between call acoustic structure and nearest neighbour distance	Prediction supported?
Occurrence of preceding grunt	No preceding grunt Preceding grunt — produced by nearest neighbour Preceding grunt — unknown if produced by nearest neighbour Preceding grunt — not produced by nearest neighbour	Stronger relationship Weakest relationship	Yes — the relationship was stronger when there was no preceding grunt or a preceding grunt was made by the neighbour or an unknown individual, than when a preceding grunt was made by an individual further away than the nearest neighbour
Nearest neighbour age-sex class	Adult female Subadult Juvenile Adult male	Stronger relationship for adult females versus subadults, and subadults versus juveniles Weakest relationship	No — neighbour age-sex class did not influence the relationship
Group travel speed	NA (continuous measure)	Stronger relationship as travel speed increases	No — travel speed did not influence the relationship

Predicted strengths of this relationship for a given level are relative to other levels within the same factor. Individual levels are shown for categorical fixed effects included in statistical models (see Methods and Table A2 in the Appendix at 10.6084/m9.figshare.19317536).

I recorded grunts ad libitum from all group members using a Sennheiser MKH 416-P48U directional microphone and a Marantz PMD661MKII solid-state recorder (channels, mono; bit depth, 24-bit PCM; sampling rate 96 kHz). I did not record consecutive grunts from the same focal individual to minimise temporal autocorrelation. I recorded grunts from individuals within 12 m of the microphone and with a clear line of sight (i.e., without obstruction from vegetation; following Fischer et al., 2013). For each grunt from a focal individual, I noted the following: focal age-sex class (adult male,

Table 3.
Follow days, age-sex class compositions, and recording sample sizes by age-sex class for each focal group.

Group	Follow period (n follow days)	Group composition					Sample size (n recorded grunts)				
		Total size	Adult males	Adult females	Subadults	Juveniles	Adult female	Subadult	Juvenile	Unknown	Group total
R6	Mar–Jun 2017 (n = 71)	Approx. 35	2	Approx. 20 adult females and subadults		Approx. 8	141	28	4	4	177
R5	Jul–Oct 2017 (n = 89)	Approx. 25	1	Approx. 16 adult females and subadults		Approx. 5	214	44	2	4	264
	Jan–Feb 2019 (n = 23)	Approx. 30	1	14–16	9–10	4–5					
R2	Jan–Mar 2019 (n = 24)	16	1	7	6	2	64	20	–	–	84
RSW	Jan; Mar–Apr 2019 (n = 22)	16–19	1	9	6–7	0–2	41	15	–	1	57
RGS	Apr–Jun 2019 (n = 72)	17–19	1	5	7	4–6	217	90	4	6	317
Total											899

adult female, subadult, or juvenile), identity (if known), and vegetation class (primary forest, secondary forest, or edge); nearest neighbour age-sex class and distance from the focal individual (metres). Because monkeys spent most of their time arboreal, I estimated the linear distance (horizontal or vertical) between animals to account for differences in how high individuals were positioned in trees. To keep estimates of distance consistent, I used a set of 10 stakes positioned at consecutive 1 m intervals at the Ngogo camp as a reference, which I checked en route to the forest each follow day. For each grunt, I also noted whether a different individual had grunted in the preceding five seconds; if so, I noted whether the preceding caller was the focal animal's nearest neighbour or not. This resulted in a categorical factor with four levels for analyses (no preceding grunt; preceding grunt produced by nearest neighbour; preceding grunt produced by an individual further away than the nearest neighbour; preceding grunt produced by either the nearest neighbour or an individual further away that I could not differentiate). I used a 5-s window to identify antiphonal calls because this window is short enough to ensure subsequent calls were most likely responses in the same exchange and long enough to allow for variation between individuals in inter-call intervals (Yoshida & Okanoya, 2005; following Oda, 1996; Miller et al., 2009). While following groups, I positioned myself in the group centre of mass as often as possible when not recording vocalisations and used a Garmin Rino 650 unit to log GPS coordinates at automatic 1-minute intervals.

2.2. *Data analyses*

I analysed recordings in Raven Pro v1.6 (Center for Conservation Bioacoustics, 2019; spectrograms: Fast Fourier transformation length = 1024 samples, window = Hann, hop size = 0.1 ms, frequency resolution = 2.93 Hz; Figure 1). I discarded recordings in which grunts overlapped with conspecific grunts or loud ambient sounds in the same frequency range (e.g., cicada vocalisations; snapping branches). To reduce interference from ambient noise, I used only recordings with a signal-noise ratio of ⩾6 dB. I calculated signal-noise ratio as the difference in inband power (dB) between each grunt spectrogram sample and an identically sized (duration and frequency bounds) sample comprising only ambient noise within 500 ms (mean 50.1 ms) of the corresponding grunt, following Charif et al. (2010). For each grunt, I measured call duration, mean entropy, and maximum, mean, and minimum frequency (Table 1). I measured minimum and mean frequency

from the 50% frequency contour, which best ignored gaps within grunt structures that would otherwise have led to measurements including sections of ambient noise (compared to using the peak frequency contour, for example). I used QGIS v3.10 (QGIS Development Team, 2019) to calculate 15-minute group travel speed as the summed Euclidean distance (metres) between the 16 consecutive 1-minute GPS coordinates of group centre of mass preceding the grunt.

2.3. Statistical analyses

For grunts where GPS coordinates were missing ($N = 54$ grunts; 6% of observations), I used the package *mice* in R 3.6.2 (van Buuren & Groothuis-Oudshoorn, 2011; R Core Team, 2020) to regress suitable values of group travel speed from time of day and vegetation class, which are known to correlate to hourly travel speeds in red-tailed monkeys (method: predictive mean matching; following van Buuren & Groothuis-Oudshoorn, 2011; see McLester et al., 2019). I visually inspected pair-wise correlograms and calculated pair-wise Pearson correlation coefficients to check that multi-collinearity between acoustic parameters was not present.

To test predictors of acoustic parameters (call duration, mean entropy, and maximum, mean, and minimum frequency), I used the package *MCMCglmm* (Hadfield, 2010) to build five Bayesian linear mixed models with Gaussian error distributions. I fitted each acoustic parameter as a response and interactions between nearest neighbour distance and (1) occurrence of preceding grunt (four level factor), (2) nearest neighbour age-sex class (four level factor), and (3) group travel speed (continuous), as predictors (Table 2). I fitted vegetation class (three level factor) as a fixed control effect because *Cercopithecus* species are known to alter call structure depending on vegetation density (Brown & Waser, 2017). I fitted focal ID (or age-sex class where identity was unknown; both nested in focal group ID) as a random intercept effect to control for baseline variation in call structure between both individuals and groups (e.g., because the number of neighbours and preceding calls to which monkeys were responding may have been greater in larger groups) and differences in the number of grunts recorded from each individually identified monkey.

I centred responses and continuous predictors to a mean of zero and a standard deviation of one to improve model fitting and interpretation of continuous main effects in interactions (following Schielzeth, 2010). There
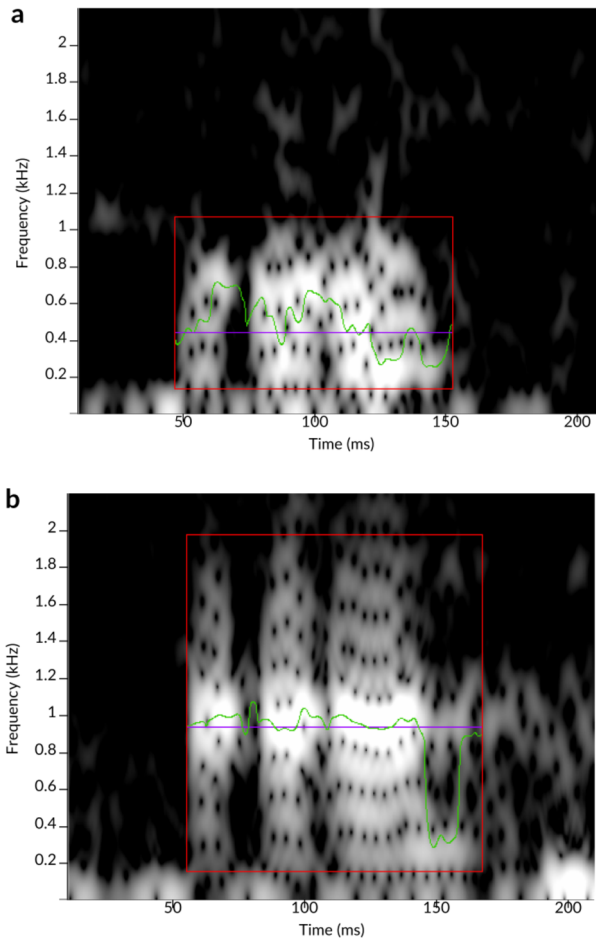
Figure 1. Example spectrograms illustrating grunts from an adult female (a) and subadult (b). The red border indicates the selection box drawn in Raven Pro, from which grunt duration (selection box width), maximum frequency (horizontal purple line), and 50% frequency contour (green line; for mean and minimum frequency) are measured. Lower mean entropy is indicated by energy (white areas) concentrated at a narrower range of frequencies, i.e., the vocalisation in (b), which has most energy concentrated between 0.8–1.2 kHz, has lower entropy than the vocalisation in (a), which has energy distributed more uniformly across the entire frequency range of the call.

was no confounding effect of predictor multicollinearity (maximum variance inflation factor = 1.04). I included observations with unknown values for categorical predictors in models but did not analyse effects for these levels unless there was a valid interpretation.

I used the default *MCMCglmm* priors for fixed effects, weakly informative priors for random effects ($V = 1$; $\nu = 0.002$), and the standard inverse-gamma prior for residual variance. Markov chains (Monte Carlo) ran for 800,000 iterations with a burn-in of 100 000 iterations and a thinning interval of 100 iterations. After running each model, I checked trace plots to confirm autocorrelation was not an issue and that effective sample sizes were adequate (all models — minimum effective sample size = 6614; mean effective sample size = 7993). I calculated the Gelman-Rubin diagnostic for three other equivalent models to confirm chain convergence (maximum point estimate across all models = 1.0).

For each response, I compared deviance information criterion (DIC) between models with each combination of fixed interaction effects and a null model fitted with only control effects. Lower DIC and higher corresponding weights indicate better relative model fit. I selected the model with the lowest DIC compared to the null model and inferred fixed effect sizes by examining posterior distributions (widths and overlap of 95% credible intervals with zero) and posterior probabilities (the probability a predictor relates to the response; calculated as the proportion of samples in each distribution with the same sign as the mean).

3. Results

3.1. Model selection for each acoustic parameter

I followed five red-tailed monkey groups comprising a total of approximately 144 individuals for 301 follow days (Table 3). I analysed a total of 899 grunts ($N = 57$–317 grunts per group; Table 3). For 451 grunts, I was able to identify the age-sex class, but not individual identity, of the caller. For the remaining 448 grunts, I was able to individually identify the caller. Individually identified callers each produced 1–68 grunts (median = 3 grunts; mean = 11 grunts). For each grunt, the neighbour of the focal monkey was positioned between 0 m (directly adjacent) and 15 m away (median = 5 m).

For grunt duration, maximum frequency, and minimum frequency, none of the predictive models fitted the data better than the null model (minimum DIC vs. null model: $+1.31$–13.14; Table A1 in the Appendix at 10.6084/m9. figshare.19317536). For mean entropy and mean frequency, the best fitting models included an interaction between nearest neighbour distance and preceding grunt (DIC vs. null model: -10.53 and -3.78, respectively; Table A1 in the Appendix at 10.6084/m9.figshare.19317536).
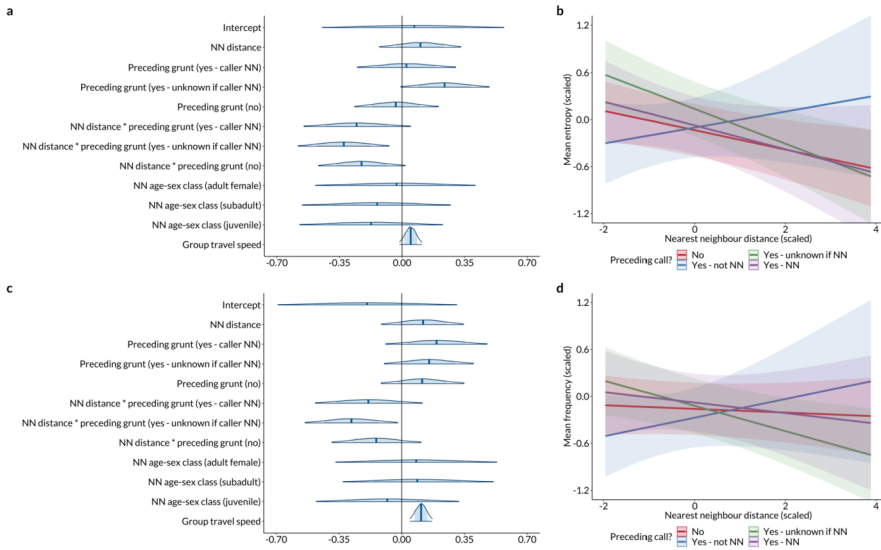
Figure 2. Fixed effects in selected best models of grunt mean entropy (a, b) and mean frequency (c, d; Table A2 in the Appendix at 10.6084/m9.figshare.19317536). (a, c) Upper and lower 95% (distributions) and 75% (blue shading) highest posterior density intervals. Reference levels: preceding grunt = "yes — caller not nearest neighbour"; Nearest neighbour age-sex class = "adult male". (b, d) Interaction effects between nearest neighbour distance and preceding grunt for each response. Bands indicate confidence intervals derived from equivalent generalized least squares regression.

3.2. Effect of preceding grunts

Whether grunt mean entropy and mean frequency were associated with nearest neighbour distance depended on if a different individual produced a grunt in the preceding five seconds. Grunt mean entropy related negatively to nearest neighbour distance when there was (1) a preceding grunt produced by the nearest neighbour ($n = 96$; posterior density (PD) $\bar{x} = -0.255$, posterior probability (PP) = 95.0; Figure 2a,b; Table A2 in the Appendix at 10.6084/m9.figshare.19317536), (2) a preceding grunt produced by either a nearest neighbour or non-nearest neighbour that I could not differentiate ($N = 266$; PD $\bar{x} = -0.326$, PP = 99.4), or (3) no preceding grunt ($N = 333$; PD $\bar{x} = -0.227$, PP = 96.5). In contrast, when a preceding grunt was produced by an individual further away than the nearest neighbour, mean entropy did not relate strongly to nearest neighbour distance ($N = 98$; PD $\bar{x} = 0.103$, PP = 81.1).

Grunt mean frequency related negatively to nearest neighbour distance when a preceding grunt was produced by either a nearest neighbour or non-nearest neighbour that I could not differentiate (PD $\overline{x} = -0.281$, PP = 98.3; Figure 2c,d; Table A2 in the Appendix at 10.6084/m9.figshare.19317536). Grunt mean frequency also related negatively, although less strongly, to nearest neighbour distance when a preceding grunt was produced by the nearest neighbour (PD $\overline{x} = -0.186$, PP = 88.5), or when there was no preceding grunt (PD $\overline{x} = -0.142$, PP = 87.6). Grunt mean frequency related even less strongly to nearest neighbour distance when an individual beyond the nearest neighbour produced a preceding call (PD $\overline{x} = 0.119$, PP = 84.6).

3.3. Modulating effects of nearest neighbour age-sex class and group travel speed

The relationship between nearest neighbour distance and grunt mean entropy and mean frequency did not change depending on neighbour age-sex class or how fast the group was travelling (Table A2 in the Appendix at 10.6084/m9.figshare.19317536). When groups were travelling faster, monkeys were more likely to produce calls with higher mean entropy (PD $\overline{x} = 0.048$, PP = 93.5; Figure 2a) and mean frequency (PD $\overline{x} = 0.108$, PP = 100.0; Figure 2c).

4. Discussion

Mean entropy and frequency of red-tailed monkey grunts related most strongly to nearest neighbour distance when the nearest neighbour called in the preceding 5 s or when there was no preceding grunt. In these instances, mean entropy and mean frequency both decreased as nearest neighbour distance increased, matching expected call structure for optimal propagation over longer distances (Table 1; Figure 2b,d). In contrast, when a preceding grunt was produced by an individual that was further away than the nearest neighbour, neither parameter related strongly to nearest neighbour distance. Monkeys produced calls that appeared better optimised for detection by the neighbour only when the neighbour — and not a more distant individual — produced the preceding call in an exchange. These results indicate red-tailed monkeys respond differently to calls produced by neighbours versus non-neighbours located further away, and demonstrate that variation in acoustic structure can provide broad quantitative evidence for antiphonal contact calling in this species.

Grunt mean entropy and frequency related to neighbour distance and preceding calls; however, minimum and maximum frequency and duration, which are similarly associated with sound propagation, did not relate to any predictor. It is possible that minimum and maximum frequency values may not have reflected the frequencies at which most energy was concentrated, especially in longer grunts where energy was distributed across a wider range of frequencies (i.e., grunts with relatively variable 50% frequency contours; for example, Figure 1a compared to Figure 1b). Although lengthening call duration should increase call propagation, producing relatively short calls (inter-quartile range $= 92$–123 ms; $\overline{x} = 109$ ms; Figure 3) and instead modulating call propagation primarily through the distribution of energy at different frequencies (i.e., entropy; mean frequency) may further reduce the risk of call overlap. I also modelled linear relationships between acoustic parameters and neighbour distance, meaning it is possible that duration relates non-linearly to neighbour distance and only varies significantly in grunts produced in response to individuals very far away (e.g., >15 m away, the maximum distance I modelled in analyses). Further studies could investigate whether red-tailed monkeys that exhibit wider group spread than Ngogo groups (e.g., those living in more open savanna-woodland environments; McLester et al., 2019) are more likely to produce calls with significantly greater duration and frequency ranges when calling antiphonally over longer distances.

I expected monkeys might be more likely to engage in antiphonal exchanges with older, more reliable monkeys, but nearest neighbour age-sex class had no effect on whether grunt structure was associated with neighbour distance. The difficulty of tracking group members in dense vegetation and over widely spread groups likely means if monkeys were to preferentially exchange calls with older individuals, callers may expend energy producing grunts that propagate across the group, without knowing if a particular recipient is still within hearing range. Instead, animals closer to the caller may remain in sight for longer than more distant individuals or provide other indicators of their general location (e.g., noise from moving through vegetation; scent signals) that callers cannot detect from group members positioned further away. Without a preceding call to respond to, initial callers may therefore produce calls optimised for detection by the nearest neighbour, irrespective of neighbour age-sex class, to increase chances of call detection. Initial grunts in antiphonal exchanges may therefore function foremost to
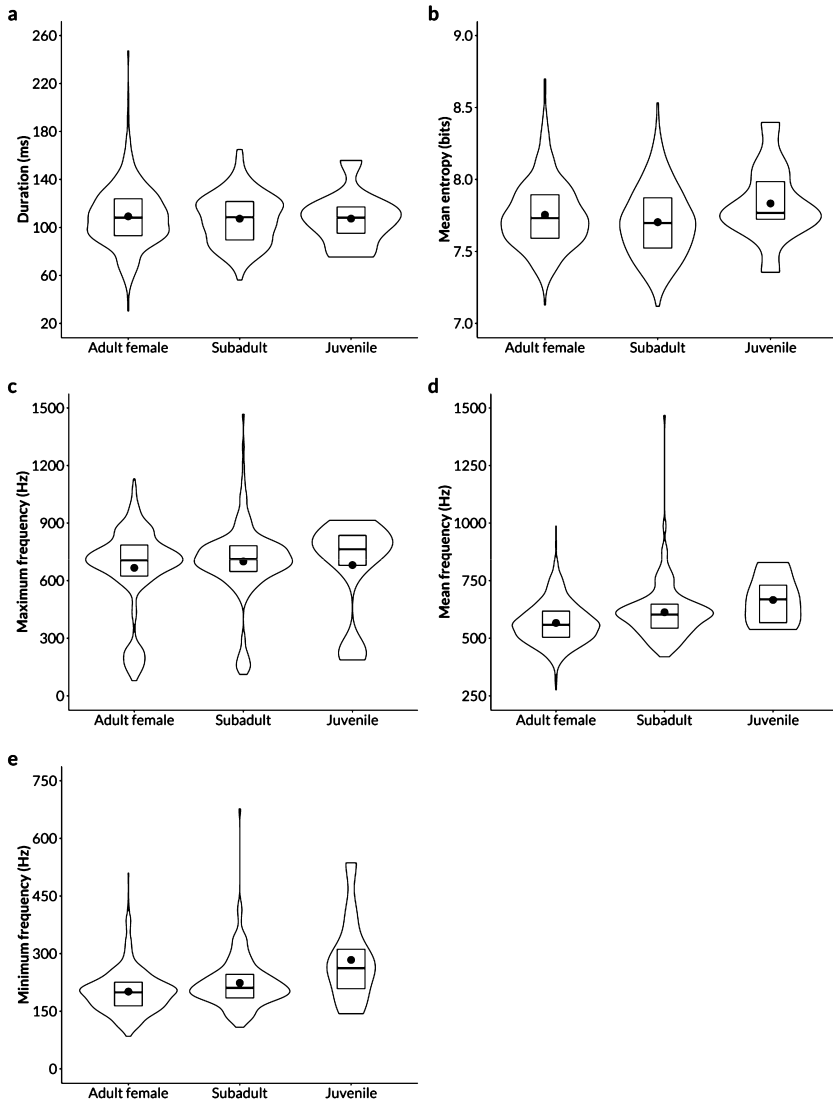
Figure 3. Summary of grunt ($N = 899$) measurements extracted in Raven Pro for five acoustic parameters by age-sex class: (a) grunt duration (ms); (b) mean entropy (bits); (c) maximum frequency (Hz); (d) mean frequency (Hz); (e) minimum frequency (Hz). Bars = median values; dots = mean values; boxes = inter-quartile range; outlines = sample distribution).

maintain contact between closely spaced neighbours. Nonetheless, in many taxa, individuals are more likely to associate with related or closely bonded individuals (including closely-related blue monkeys, *C. mitis* — Cords et al., 2018; also e.g., giraffes, *Giraffa camelopardalis* — Carter et al., 2013; bottlenose dolphins, *Tursiops* spp. — Diaz-Aguirre et al., 2018). Callers may therefore still be initiating exchanges with specific individuals who are simply more likely to be their nearest neighbour.

4.1. Acoustic flexibility in contact calls

I expected monkeys would be more likely to exchange calls with nearest neighbours as groups travelled faster because of the difficulty of pinpointing more distant individuals in quicker moving groups. Group travel speed had no effect on whether monkeys adjusted grunt structure in response to nearest neighbour distance, however. Depending on environmental conditions such as food availability, monkeys reduced inter-individual distances when travelling faster during the study (McLester, 2020). Closer proximity between individuals likely results in improved call detection for all group members, meaning callers may not always need to optimise calls to reach close neighbours to maximise call detection. Moreover, individuals that are separated by only a few metres may not produce calls with significant variation in acoustic structure that should otherwise reflect optimal propagation. For example, callers may not need to produce grunts that should propagate significantly further in response to an individual positioned two metres away versus an individual positioned one metre away.

Irrespective of whether a preceding grunt had been produced, monkeys produced grunts with higher mean frequency and entropy when groups were travelling faster. Given that this acoustic structure is not optimised for detectability over longer distances, increasing detection by close individuals may be a response to greater ambient noise during group travel. Red-tailed monkeys produced grunts at relatively low frequency ranges (mean range $=$ 207–672 Hz; $\bar{x} = 578$ Hz — Figure 3). Because low frequency sounds are generally difficult to localise (Waser & Waser, 1977), producing grunts with higher average frequencies should improve audibility. Several taxa, including humans, increase vocalisation frequencies in response to higher frequency and amplitude ambient noise (i.e., the Lombard effect — Zollinger & Brumm, 2011; e.g., elegant crested tinamous, *Eudromia elegans* — Schuster et al., 2012; horseshoe bats, *Rhinolophus ferrumequinum* — Hage et

al., 2013). Moreover, increasing entropy produces broadband calls, in which energy is distributed over a wider range of frequencies. These calls are more likely to propagate through a wider range of frequencies that do not overlap with ambient noise (Waser & Waser, 1977). For example, bottlenose dolphins produce contact whistles with wider frequency ranges as ambient noise from shipping traffic increases (Marley et al., 2017), while tamarins (*Saguinus oedipus*) produce calls with wider energy distributions when background noise is greater (Hotchkin et al., 2015). In acoustically complex environments such as forests, where vegetation results in many reflective surfaces, broadband calls may be a mechanism of counteracting fast changing attenuative properties of the environment as animals travel (Morton, 1975; Waser & Waser, 1977; Brown & Waser, 2017). Producing higher frequency, broadband calls that are more likely to be audible to fewer, close individuals may be a more efficient way of communicating than producing lower frequency, narrowband calls that are better optimised for responding to more individuals located further away but less likely to be detected when background noise is high.

4.2. *Socio-ecological drivers of antiphonal contact calling*

Antiphonal calling is an important adaptation that allows group-living animals to track and maintain contact with out-of-sight conspecifics in complex environments. When the costs of group-living (e.g., intra-group feeding competition) outweigh the benefits, groups should reduce in size through fission (Chapman & Chapman, 2000). During the study, monkeys frequently exhibited wide (>20 m) inter-individual distances, but groups rarely fissioned into clear, distinct subgroups irrespective of size ($N < 10$ observations in 301 follow days, each lasting <1 h). Monkeys likely benefit from antiphonal calling because exchanges mean individuals can increase inter-individual distances to mitigate costs of sociality without losing their group. Adjusting individual spatial cohesion in this way is an alternative to longer-lasting or permanent group fission, which would result in losing fitness benefits conferred by larger groups (Ward & Webster, 2016).

Environmental conditions associated with group-living behaviour may explain why animals call antiphonally. For example, food availability and competition with conspecifics influence group ranging and rates of inter-group aggression in red-tailed monkeys (Cords, 1987; Brown, 2013). Given that red-tailed monkeys are sympatric with a diversity of predators (chimpanzees, *Pan troglodytes* and raptors in rainforest; lions, *Panthera leo* and

leopards, *P. pardus* in savanna-woodland — Mitani et al., 2001; McLester et al., 2018), predation risk also influences ranging and foraging patterns (Treves, 2000). By calling in antiphonal exchanges, monkeys should reduce call redundancy and minimise inadvertently attracting con- and heterospecifics that may otherwise increase competition or predation risk (Yoshida & Okanoya, 2005). Increases in competition for resources and predation risk are generally associated with increases in group size and are key limiting factors on animal sociality (Janson & Goldsmith, 1995; Boinski et al., 2000; Ward & Webster, 2016). Providing evidence for antiphonal calling therefore builds on hypotheses of ecological constraints on sociality by demonstrating an adaptive behaviour through which animals can mitigate costs of living in groups.

Environmental influences on vocalising behaviour should also vary depending on social contexts. For example, though in this study I could not distinguish preceding callers beyond 'nearest neighbour or not', grunts following a single preceding grunt often appeared to be responses to the initial caller based on very short intervals between grunts (personal observation). For grunts preceded by multiple different callers, however, future studies could examine whether individuals produce calls that are optimised for detection by the initial caller, or simply the closest preceding caller (e.g., to prioritise call detection by at least one other individual without propagating calls further than necessary). More research on the function of red-tailed monkey grunts could help explain such variation in call propagation distances, especially if the adaptive benefits of the information conveyed in a call vary between receivers of different age-sex classes (Fuller & Cords, 2017). Moreover, in group-living animals with long-term social bonds, the cost-benefit ratios of calling (i.e., exchanging information at the risk of increasing conspicuousness to competitors or predators) should vary depending on relatedness or social affiliation between callers (Lemasson et al., 2013). Social affiliation networks in Japanese macaques and ring-tailed lemurs (*Lemur catta*) closely reflect calling networks; that is, closely bonded or related individuals are more likely to exchange calls than less closely affiliated individuals (Arlet et al., 2015; Kulahci et al., 2015). Neighbour age, as a broad proxy for social integration and reliability, had no effect on red-tailed monkey grunt structure, but comparing wide age-sex classes may not capture finer-scale variation in social bonds that could better predict participation in vocal exchanges. For example, although young individuals

typically become more socially integrated in groups as they grow up, this trend may revert in aging individuals that decline physically and cognitively (i.e., social aging; Almeling et al., 2017). How environmental drivers of contact calling are modulated by social determinants of call production (i.e., kinship; social network centrality) therefore remains to be investigated further in wild group-living animals.

Acknowledgements

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