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Social environments shape repertoire composition but not repertoire size in close-range chimpanzee communication

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Article

Keywords:

Posted Date: October 21st, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11049465/v1

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Additional Declarations: There is **NO** Competing Interest.

Abstract

Communication is a fundamental skill for managing social relationships, and it has been hypothesised that more complex social systems are associated with more complex forms of communication. This study investigates the sources of variation in the size and composition of chimpanzees' multimodal communicative repertoires for close range dyadic interactions across zoo, sanctuary and wild settings. Specifically, the influence of social complexity and environmental variables on individual repertoire size and repertoire similarity among individuals was examined. Substantial individual differences were revealed in both repertoire size and composition. Surprisingly, repertoire size was influenced only by the number of expressed social goals, whereas differences in the composition of individual repertoires were greater among groups than among settings. These findings support a link between social and communicative complexity, but also highlight that, at the individual level, variation explained by social factors lies more in repertoire composition than size.

1. Introduction

Although group living confers substantial benefits — reduced predation risk, collective defence, enhanced access to mates — it is nevertheless associated with considerable costs. The *social complexity* and *social intelligence hypotheses* propose that part of these costs lies in the cognitive skills required to efficiently manage social relationships [1,2], primarily through communication, directly linking communicative and social complexity. Indeed, social complexity may increase with the frequency and diversity of communicative interactions: larger and denser social groups are associated with greater degrees of individual discrimination, more numerous and diverse interaction partners and contexts, and possibly a greater variety of social roles [3–6], and individuals are likely to spend more time maintaining their relationships, and employ a wider range of communicative strategies [7,8]. Therefore, the *social complexity hypothesis for communicative complexity* posits that the latter increases with the former [2,3] to compensate for increased uncertainty and unpredictability [8], partly in relation to the dominance structure (e.g. egalitarian societies are associated with more tolerant but less predictable relationships; Aureli et al. 2022). The communicative repertoire of signals, specifically, is strongly influenced by variation in social systems. Both vocal and facial repertoire size have been shown to increase with group size across non-human primate species [9,10]. More diverse repertoires may allow individuals to adjust more easily to a range of communicative situations, thereby enhancing communicative effectiveness [8]. Social structure is another key factor shaping communication: primate species where males and females form long-term associations tend to have larger vocal repertoire sizes than species where male-female associations take the form of temporary consortships where communication is restricted to the reproduction context [11], while in birds, cooperative breeding is associated with expanded vocal repertoires [12]. In tolerant groups of primates, individuals express more explicit reconciliatory signals after conflicts [13], and signal use is generally more flexible than in despotic groups where it is more rigidly tied to specific contexts [14].

As discussed above, the primary approach to communicative complexity focuses on repertoire size as the number of expressed signal types. Although gaining interest, other communicative features — such as multimodality and signal combinations — have so far been neglected [2,15]. Yet, multicomponent and multisensory communicative strategies have been shown to help primates cope with social uncertainty, navigate unpredictable interactions, and improve communicative effectiveness [16–18]. These strategies are especially worth investigating within the social complexity hypothesis for communicative complexity framework, as they inherently represent greater complexity than unimodal signals by involving multiple signal types and sensory channels. Whether signals are used multimodally or unimodally can affect their function [19,20], and researchers focusing on only a single modality may overlook certain elaborate communicative expressions, ultimately underestimating the communicative complexity of interest [2].

Great apes, and chimpanzees in particular, serve as an ideal model to explore this hypothesis due to their complex social system, including fission-fusion dynamics, which increase uncertainty by influencing party size, composition and density (Aureli and Schino 2019; Aureli et al. 2022). Additionally, they exhibit diverse communicative repertoires and strategies, including multimodality [17,18,22]

The first aim of this study was thus to focus on close range, dyadic signal repertoires (hereafter, repertoire; e.g. Hobaiter and Byrne 2011; Roberts et al. 2019; Oña et al. 2019) to investigate the impact of the socio-ecological environment on the communicative complexity of adult chimpanzees and the role of multimodality in this relationship. To do so, the study included individuals from six social groups and three different settings: three groups from zoos, two from a sanctuary and one wild group. We identified a number of social variables that varied at the level of (i) setting (wild, sanctuary, zoo) (ii) group and (iii) individual, that may affect close-range communicative repertoires. First, at the level of setting, the extent to which chimpanzees living in these three settings can rely on non-communicative strategies to manage competitive relationships, such as avoidance of certain individuals, varies: individuals in the wild can capitalise on a fission-fusion system to maintain spatial distance with those they are competing against. In contrast, zoo-housed chimpanzees are usually in constant close physical proximity to group members, and cannot use space to manage competition, likely increasing the need for communicative strategies to manage social relationships. Sanctuaries provide an intermediate setting. Thus, it was predicted that zoo-housed chimpanzees would have the largest repertoires of close-range signals to effectively manage constant social proximity and aggression risk, followed by sanctuary chimpanzees and then by wild chimpanzees. Second, at the level of group, the six studied social groups differed in total size and in terms of the number of adult males in the group. We predicted that individuals with more interaction partners—representing more diverse social interactions (Freeberg et al. 2012)—and living in groups with many adult males—who impact dominance hierarchy steepness and interaction risk (Taborsky and Oliveira 2012; Aureli et al. 2022)—would express more diverse communicative repertoires. Lastly, on an individual level, repertoire size was predicted to vary with the number of expressed social goals, reflecting the variety of social situations an individual encounters. Indeed, some individual differences can impact the number of social goals expressed by the individuals: less social individuals might reduce their aims to the most necessary ones (and for example initiate play less), higher ranking males rarely

ask for grooming (lower ranking individuals usually initiate these interactions) or express submissive signals, while females with infants express some specific goals (e.g. climb on me) that others do not. Chimpanzees flexibly associate many of their signals with social goals [26–29] and the more social goals an individual communicates towards, the more signals they may need to express them.

In addition to our predictions regarding repertoire size, we also wanted to test the degree to which repertoire composition varied between individuals and is influenced by social and environmental factors. In order to do this, we assessed the degree of signal and multicomponent repertoire similarity among individuals. Simultaneously, comparisons between and within groups and settings were conducted to evaluate the impact of social and environmental pressures respectively on the composition of the individual repertoires. We expected individuals to share a substantial portion of their repertoires but also to exhibit some level of individual variation. Repertoire similarity was expected to be higher among individuals of the same group and setting than between groups and settings, as similar socio-environmental conditions would likely result in more shared signals. In particular, repertoire overlap was expected to increase with higher levels of captivity (the zoo and wild settings providing both extremes of the spectrum and the sanctuary setting an intermediate position), due to increased proximity among group members.

2. Materials and methods

a) *Data collection*

Data on zoo-housed chimpanzees were collected by ALo and ALu. from two social groups at Zoo Leipzig, Germany, from January to March 2022 (group A comprised 21 individuals, including 13 adult subjects; group B comprised 6 adult subjects) and one social group at Leintalzoo Schwaigern, Germany, from May to June and from September to November 2022 (group L, 33 individuals, including 30 adult subjects). Data on sanctuary-housed chimpanzees were collected by ALu at Chimfunshi Wildlife Sanctuary, Zambia, between July and August 2022 from two social groups: group C2 with 56 individuals, including 29 adult subjects; and group C4 with 13 individuals, including 9 adult subjects. Detailed descriptions of the enclosure characteristics have been provided in Lombrey et al. (2025). Data on wild individuals were collected by C.W. in the Kanyawara community (hereafter labelled group K, 53 individuals, 27 adults), Kibale National Park, Uganda, from February to May 2013 and from June 2014 to March 2015. Details on the study site and subjects can be found in Wilke et al. (2017). The majority of individuals included in this study were adults over the age of 15 years, or having given birth to an infant (one individual aged 13) to ensure focus on mature communicative repertoires [30]. However, captive subjects under 15 years of age who exhibited adult-like behaviours, such as actively participating in reciprocated grooming with adults or not playing with other juveniles anymore, were also included (two 14-year-olds in group C2 and one 13-year-old in group C4; see electronic supplementary material, Tab. S1 for detailed information on group composition).

Dyadic social interactions were recorded using a high-definition camera (Panasonic models HC-VXF 999, HDC-SD90 or HDC-SD40) and an external directional microphone (Sennheiser models MKE 600 or MKE 400). In wild chimpanzees, 15-minute focal videos were collected throughout follows of individual that were aimed at lasting all day (6:00am-18:30pm; see electronic supplementary material, Tab. S2, for detailed information on sample size per individual). In the zoos, data collection was carried out during the zoo opening hours (from 9 am to 5 pm) and video recordings were taken when the focal animal came into proximity with other group members during 15-minute focal follows. In the sanctuary setting, data were collected on most days (five to seven days a week, from 8 am to 4 pm) when the sanctuary-housed chimpanzees were relatively close to the fences and the feeding area (provisioning twice a day, 11:30 am to 1:30 pm and 1:30 pm to 3:30 pm), where we could film them. When individuals stayed in sight, 15-minute focal follows were conducted with videos being recorded as soon as the focal individual was in proximity with other group members. However, the enclosures at Chimfunshi were very large (65 ha for group C2 and 25 ha for group C4; van Leeuwen et al. 2022) and chimpanzees roam freely in their enclosures, meaning they often moved out of sight of the observer. We thus also collected ad libitum video data on visible individuals [32,33]. .

Ethical approval

was granted by the Chimfunshi Research Advisory Board (CRAB) as well as the research boards of the Zoo Leipzig and the Leintalzoo Schwaigern for the study on captive chimpanzees and by the Animal Welfare Ethical Review Board in the Department of Biology (University of York) for wild chimpanzees. The Ugandan Wildlife Authority and the Ugandan National Council for Science and Technology granted permission to collect the data in Kibale National Park, Uganda.

b) *Video coding procedure*

A total of 10179 (zoo: 3953, sanctuary: 4464, wild: 1762) video-recorded intraspecific communicative acts were coded in BORIS v 7.13 [34] using a previously established list of 96 communicative acts based on the signals reported in Hobaiter and Byrne (2011) and Wilke et al. (2017), including vocalizations, manual and body gestures, and facial expressions. This study only included communicative behaviours that were mechanically ineffective and emitted in a dyadic interaction by a signaller, presumably to elicit a behavioural response by the receiver (e.g. Pika 2008; Hobaiter and Byrne 2014; Fröhlich et al. 2022). This definition thus excluded mechanically effective acts involving physical force, namely, when the "social goal" is achieved without requiring voluntary action from the recipient. Since this study focused on dyadic interactions, signals that were presumably directed towards several recipients or for which a specific recipient could not be clearly identified, such as signals produced in ambiguous interactions (e.g. multi-party conflicts), were not included. Additionally, ambiguity was reduced by focusing on signals which aim was to initiate an interaction or to elicit a behavioural change in the recipient. Signals emitted to maintain a social activity (e.g. during play) were not considered, as they do not fit this definition. Signals expressed simultaneously in the same or different modalities (i.e. gestural-manual, gestural-bodily, vocal, facial) were coded as multicomponent, and all the signal types involved within the

communicative act were indicated (e.g. gestural-manual+vocal). While the set of signallers was limited to mature individuals, no restriction was placed on the recipients of the signals which therefore included both other mature and immature individuals. Additionally, we assigned each communicative act to one of 17 social goals based on Cartmill and Byrne 2010 and Hobaiter and Byrne 2014 (attend to specific location, climb on me, follow me – sex, move closer, reposition body, start grooming, start play, travel with me, acquire object, dominance, affiliation/greeting, move away, tolerance, sexual attention, seek reassurance, give reassurance, stop action; see electronic supplementary material, Tab. S3 for definitions of the coding scheme) and chosen based on the presumed goal of the signaller, depending on its behaviour, the context of the interaction and the signal type [37].

Inter-rater reliability was assessed using Cohen's Kappa coefficient (K, [38]) to ensure that coding was consistent between all three coders (ALo, ALu, ND), which was the case (signal: K = 0.68; signal combination: K = 0.87; social goal: K = 0.86; 50 videos including 142 signal instances were used for the zoo groups, 48 videos including 130 signal instances for the sanctuary groups, and 10 videos including 38 signal instances for the wild group).

c) *Statistics and reproducibility*

Two response variables were used for the analyses of variation in close-range repertoire size. The signal repertoire contains all signal types expressed by an individual, regardless of whether they are associated with other signals (e.g. if an individual expressed a "reach" gesture and a "grunt" vocalisation simultaneously, both signals are included as separate entries in the signal repertoire). The multicomponent repertoire contains the specific signal combinations expressed by an individual. A signal combination represents the instances where at least two signals temporally overlapped within the same communicative act, regardless of their behavioural type (i.e. gestural, facial, or vocal). For example, if an individual expressed a reach and a grunt simultaneously, the combination of the two signals was treated as one entry ("Reach+Grunt") in the multicomponent repertoires.

In order to conduct more conservative and representative analyses, individuals contributing less than 30 instances of signal use to the dataset and signals expressed only once by a single individual were excluded from the signal repertoire dataset, while individuals contributing less than 2 instances of combinatorial signal use were excluded from the multicomponent repertoire dataset [16,36], resulting in a total dataset of 8807 communicative acts available for analyses on signal repertoires and 1393 instances for analyses on multicomponent repertoires. All statistical analyses were conducted using R v 4.3.1 [39].

First, the cumulative number of signals identified over the sampling period was plotted (Fig. S1) and approached an asymptote for all groups except L and C4. Since these groups also reached a plateau and approached stability, the data are likely representative of the study groups' communicative repertoires.

The effect of the social group (6 levels: A, B, L, C2, C4, K) and setting (3 levels: zoo, sanctuary, wild) on individual repertoire size was assessed using a linear mixed model. The model also included individual

characteristics (age with range = 13–56; sex with two levels: male and female; the number of expressed social goals with range = 1–11), variables related to the social group (the number of males in the group with range = 1–15; the number of interaction partners with range = 4–40), and sampling effort (range = 25–270 communicative acts), as has been done in previous studies on between-individual differences (Roberts 2018, see electronic supplementary materials Tabs. S1 and S2 for details on model variables). In the present study, the sampling effort was defined as the total of coded communicative acts per individual. To test the overall significance of our key test predictors (number of social goals, number of males in the group, number of interaction partners, social group, and setting), the full models were compared with null models, including only the control predictors (age, sex, sampling effort) and all random effects, using a likelihood ratio test [41]. The absence of collinearity between predictor variables was confirmed by assessing variance inflation factors (VIFs; Quinn and Keough 2002) from models including only the fixed effects (max VIF = 3.09), and the significance of fixed effects was assessed using likelihood ratio tests (R function drop1 with argument “test” set to “Chisq”).

In line with previous work on great ape repertoires [36,43,44], close-range repertoire similarity between and within social groups (social environment) and settings (environmental parameter; [15] was assessed by calculating Dice coefficients (D_c; Dice 1945) for each pair of individuals following the formula:

$$Dc = \frac{2 \times N}{R1 + R2}$$

where *N* is the number of signals two individuals have in common, and *R1* and *R2* are the total repertoire sizes of the first and the second individual, respectively. Dice coefficients were averaged for each dyad category (i.e. within and between groups or settings) to assess (1) whether individuals of the same group (e.g. A-A and B-B pairings) or setting (e.g. zoo-zoo and wild-wild pairings) shared more signals than individuals from different groups (e.g. A-B pairings) or settings (e.g. zoo-wild pairings), and (2) whether repertoire overlap differed among specific groups or settings (e.g. whether individuals within group A shared more signals than individuals within group B).

Matrix permutation tests (*N* = 1000 permutations) were used to evaluate whether repertoire overlap differed among groups and settings more than expected by chance while accounting for the non-independence of dyadic comparisons. For each permutation, group or setting labels were randomly reassigned across individuals while the Dice coefficient matrix itself remained unchanged. Mean Dice coefficients were then recalculated for the corresponding dyad categories [43].

For comparisons between within- and between-category dyads, the test statistic was the difference between the corresponding mean Dice coefficients [36]. For comparisons among multiple groups or settings, the test statistic was an ANOVA-like weighted between-group sum of squares calculated from the group-specific mean Dice coefficients, weighted by the number of dyads contributing to each group mean. Observed statistics were compared to their permutation distributions to obtain two-sided *p*-values.

To evaluate the robustness of results to unequal sampling effort among individuals, additional rarefaction analyses were performed. For signal repertoire analyses, repertoires were repeatedly subsampled to a standardized subset of 50 observations per individual. For multicomponent repertoire analyses, equivalent rarefactions were conducted using thresholds of $N = 10$ observations per individual. Individuals with fewer observations than the respective threshold were excluded prior to subsampling. For each of the two rarefaction thresholds, 100 independent subsampling replicates were generated. Permutation tests were repeated for each replicate, and the robustness of results was summarized using the mean and standard deviation of effect sizes across replicates and the proportion of replicates yielding significant results.

3. Results

Of the 96 predefined signals, 69 were observed in the dataset: 34 limb gestures, 16 bodily gestures, 13 vocalizations, 6 facial signals, and 406 combinations were expressed by the study subjects.

a) *Sources of variation in close-range repertoire size*

Repertoire size (the number of different signals produced by an individual) varied greatly between the observed individuals, ranging from 6 to 30 signals and from 4 to 40 combinations (Figs. S2 and S3).

The sources of variation in individual repertoire size were analysed using linear models, controlling for individual variables (sex and age) and sampling effort, while testing the effects of setting, and social complexity variables (number of social goals expressed by an individual, number of males in the group, number of interaction partners). Overall, the full models including the key test predictors fitted the data better than the null models (signal repertoire: $\chi^2 = 25.745$, $p < 0.001$, $df = 5$; multicomponent repertoire: $\chi^2 = 47.152$, $p < 0.001$, $df = 5$). This indicates that the test predictors explained a significant amount of variation over and above that explained by the control variable of sampling effort, which, as expected, was positively associated with repertoire size (signal repertoire: 0.373 ± 0.052, p < 0.001; multicomponent repertoire: 0.422 ± 0.082, p < 0.001). The number of social goals towards which individuals signalled had a significant positive effect on both individual signal (Fig. 1a; estimate ± s.e.m. = 0.047 ± 0.012, p < 0.001) and multicomponent repertoires (Fig. 1b; 0.136 ± 0.020, p < 0.001) sizes. Specifically, both measures of repertoire size increased with greater sampling effort and with an increased number of expressed social goals (Figs. 1a, b). None of the other tested parameters (age, sex, setting, number of interaction partners and number of adult males) had a significant effect on signal or multicomponent repertoire size, although males tended to have smaller multicomponent repertoires than females (-0.148 ± 0.083, p = 0.080; see electronic supplementary material, Tab. S4, for detailed information on the model outputs).

b) *Close-range repertoire overlaps between and within groups and settings*

The similarities in repertoire composition among the six social groups and the three settings (i.e. wild, zoo, and sanctuary) were then examined. To address this question, matrix permutation tests of Dice

coefficients were conducted to assess the repertoire similarity between two individuals from the same group or setting (e.g. both from group A or both from the wild setting), and between groups and settings (e.g. individuals from group A versus group B; zoo-housed individuals versus wild individuals) for both signal (Fig. 2) and multicomponent repertoires (Fig. 3).

For signal repertoires, the mean (± SD) Dice coefficient from 100 rarefactions for the comparison between groups was 0.477 ± 0.005, versus 0.564 ± 0.007 within groups (Fig. 2a), and 0.478 ± 0.006 between settings, versus 0.534 ± 0.005 within settings (Fig. 2b). For multicomponent repertoires, the mean (± SD) Dice coefficient from 100 rarefactions was 0.044 ± 0.004 between groups, 0.080 ± 0.007 within groups (Fig. 3a), 0.046 ± 0.004 between settings, and 0.067 ± 0.005 within settings (Fig. 3b).

For both measures of the repertoire, similarity was consistently greater within than between groups and settings. Across 100 rarefaction replicates, the within-versus-between comparison was significant in 100% of replicates for both signal repertoire analyses and in 100% and 99% of replicates for the two multicomponent repertoire analyses (permutation tests, $P < 0.05$), indicating that both signal and multicomponent repertoires were more similar among individuals from the same group or setting than among individuals from different groups or settings. Due to the exclusion of parts of the dataset, contrasts between specific groups were not sufficiently robust for reliable interpretation. Nevertheless, zoo-housed individuals shared the fewest signals (signal repertoire: 0.46–0.50; multicomponent repertoire: 0.032–0.063) whereas wild individuals shared the most (signal repertoire: 0.54–0.59; multicomponent repertoire: 0.06–0.11), with sanctuary-housed individuals generally showing intermediate levels of sharing (signal repertoire: 0.48–0.55; multicomponent repertoire: 0.046–0.086). The most reproducible contrast was for signal repertoires between zoo and wild settings (proportion $P < 0.05 = 0.54$; Tab. S5).

4. Discussion

The goal of this study was to investigate the impact of socio-environmental factors on the degree of complexity and between-individual variation in the communicative behaviour of adult chimpanzees. To this end, the size (i.e. the number of different signals and combinations expressed by individuals) and composition (measured as the number of signals shared among individuals within and across social groups and settings) of close range, dyadic communicative repertoires were examined as proxies of communicative complexity.

Important differences in both repertoire size and composition were identified. However, contrary to predictions, most socio-environmental parameters had no effect on variation in signal and multicomponent repertoire sizes. In contrast, mean signal and multicomponent repertoire similarity was generally greater between individuals belonging to the same setting or group than between those from different settings or groups, and in particular greater between wild individuals than between zoo-housed individuals. This apparent decoupling between socio-environmental variables and repertoire size contrasts with previous findings suggesting that gestural repertoire size increases with social and

environmental complexity, particularly in relation to social bonding and interaction patterns [46]. One possible interpretation is that, rather than affecting the overall size of individual repertoires, socio-environmental conditions primarily shape how repertoires are structured and shared within social units. Moreover, individuals had more signals in common with conspecifics from their own groups or setting than with others experiencing different socio-environmental conditions and challenges, in line with similar studies on orangutans communicative behaviour [36,44]. Such group-level convergence is consistent with evidence that primate communication systems are socially embedded and may be shaped by processes such as social interactional learning, interaction frequency, and network structure, leading to within-group homogeneity and between-group differentiation. This might mean that chimpanzees need a certain number of signals to cover the range of communicative situations they encounter, but that the specific signals used may be less constrained and are subject to variation. In this sense, repertoire size may reflect functional requirements, whereas repertoire composition remains flexible and responsive to local social dynamics, echoing broader debates on whether communicative systems are primarily constrained by innate capacities or shaped by usage and interaction [47,48].

Specifically, differences in repertoire sharing between individuals from the same versus different groups were stronger than those between individuals from the same versus different settings (Figs. 2,3). Consistent with this pattern, individuals exposed to similar social conditions (represented by social groups and their interaction structures) showed greater signal and multicomponent repertoire similarity than those sharing similar environmental conditions (represented by the setting affiliation; Fig. S4a,c), and the effect of group contrast was stronger than that of setting contrast (Fig. S4b,d). Together, these findings suggest that immediate social environments may play a more important role in shaping individual repertoires than broader environmental conditions associated with different settings. These findings have interesting implications for the social complexity hypothesis, which proposes that variation in social relationships and network structure can be a primary driver of communicative complexity.

Unfortunately, the data were not distributed evenly enough across social groups to further investigate whether some groups foster more repertoire overlap than others and to identify some specific social characteristics that might drive any such differences. However, we were able to identify some setting differences related to repertoire overlap. Repertoire overlap between individuals decreased with increasing degrees of captivity: wild individuals shared the most signals and zoo-housed individuals the least. It is unclear what drove this finding, as the settings differed both in terms of social and ecological variables. It is possible that available space, provisioning and food availability had a direct effect on repertoire composition. At the same time, captivity necessarily comes with a shift in social pressures, especially in species naturally expressing fission-fusion dynamics like chimpanzees do, and might also enhance the need for social tolerance, which is known to facilitate cooperation [49] and increase communicative complexity [5].

In line with the importance of social factors highlighted above, only the number of social goals expressed by the individuals had a significant positive effect on both signal and multicomponent

repertoire sizes. This suggests that variation in repertoire size is more closely tied to the diversity of communicative demands individuals face than to broader socio-ecological conditions per se. Even though chimpanzees associate signals and outcomes flexibly, some signals are more tightly linked to specific social goals (e.g. Hobaiter and Byrne 2014). As a consequence, individuals who express a greater variety of social goals require a greater diversity of communicative means to achieve them, namely more diverse and specific signal types. This supports the interpretation proposed above that repertoire size reflects functional requirements, whereas the specific composition of signals remains more flexible and shaped by social context and group-level dynamics.

No significant effect of individual-level parameters (age and sex) on repertoire size was found, despite substantial variation between individuals of the same groups. This is surprising, considering previous studies on multicomponent communication have shown that female chimpanzees rely more on multicomponent signalling than males [18], which might have suggested a higher diversity of signals in females. There was still a non-significant trend suggesting a similar sex effect on the size of multicomponent repertoires, in line with the literature, but no such trend was observed for the size of signal repertoires. Concurrently, recent findings on the same multimodal parameter also showed a strong effect of the sex of the recipient [50], suggesting differentiated risk associated with communicating with a male versus a female conspecific. Thus, the two sexes might express a similar number of different signals but adjust their combinatory use in response to external social challenges, further supporting the idea that social pressures outweigh environmental ones. Moreover, part of the effect of sex might be mediated by differences in social goals, as both the sex of the signaller and that of the recipient might impact signalling purposes. Nevertheless, there remain substantial differences in repertoire size between individuals of the same social group: a lot of variation still visible in Fig. 1 beyond the effects of sampling and social goal number, especially between 13–25 signals where several lower-sampled individuals have bigger repertoires than higher-sampled others. This seems to reflect intrinsic between-individual variation: individuals are not affected in the same way by the stress and complexity caused by social uncertainty and proximity.

In addition, across all groups and settings, individual repertoires showed moderate overlap for signal repertoires and very low overlap for multicomponent repertoires. Moreover, some dyads within the same group showed high overlap scores (0.7 and more), whereas others showed very low overlap (0.3 and less). This highlights that not only do individuals differ in repertoire size but also show considerable between-individual variation in repertoire composition that is not explained by socio-environmental differences. Further research should investigate whether the dyad characteristics influence repertoire overlap: individuals of similar age, rank or high levels of proximity might share more communicative signals than more dissimilar or less closely associated individuals (e.g. Whitham and Maestripieri 2003; Roberts et al. 2019; Luef and Pika 2019).

The control variable of sampling effort also had a substantial effect on both repertoire variables, with individuals with larger number of communicative acts having larger repertoires. Although data collection was designed to ensure comparable observation time per individual across locations, some individuals

signalled much more often or are more likely to be visible than others, leading to discrepancies in the total number of recorded communicative acts, which directly impacted the observed repertoires. Despite this, the test predictors explained significantly more variation than the sampling effort variable, as evidenced by the full-null model comparisons. Studies on communicative repertoires require a large amount of data, especially when an individual centred approach is applied, and equalizing sampling effort across individuals can be challenging. In future, controlling not only for observation time of each individual but also for the behavioural contexts in which they were observed would help minimize the impact of sampling issues on repertoire size and composition.

In sum, this study advances our understanding of primate communicative complexity in two main ways. First, it shows that the size and composition of close-range communicative repertoire of chimpanzees is shaped primarily by social circumstances. Second, it shows that individual repertoires vary in composition and in the combinatory use of signal types, highlighting the value of a multimodal approach to the study of communicative complexity. These two results shed interesting light onto the social complexity hypothesis for communicative complexity and suggest that a shift in the approach to communicative complexity from repertoire sizes to their composition may be greatly informative, at least at the individual level. Finally, it shows the benefits of investigating communicative repertoires at the individual level.

Declarations

Data accessibility

The datasets and R script that support the findings of this study have been deposited on GitHub: https://github.com/angelelombrey/ALombrey-rep-dice-Data-and-code.git

Competing interest

The authors declare no competing interests.

Funding

This research was supported by the Volkswagen Foundation (Freigeist Fellowship 9B138 awarded to MF) and the German Research Foundation (DFG FOR 2237: Words, Bones, Genes, Tools – Tracking Linguistic, Cultural and Biological Trajectories of the Human Past; PIs: Katerina Harvati and Gerhard Jäger).

Author contribution

MF and ALo designed the study. ALo and ALu collected and coded the data. CW and KS provided data on wild chimpanzees. ND coded the data. AL analysed the data with critical help from UK and MF. ALo and MF wrote the manuscript with inputs from ALu, CW, KS, and UK.

Acknowledgements

We thank Barbara Struve (Leintalzoo Schwaigern), Hanna Petschauer and Daniel Hanus (Zoo Leipzig, MPI-EVA), Edwin van Leeuwen, Katja Liebal and Thalita Simões Calvi (Chimfunshi Wildlife Orphanage Trust) as well as the research staff and zoo keepers for their helpful collaboration during this study. We are also grateful for the permission to carry out this research on the Kanyawara chimpanzee community and support from the directors of Kibale Chimpanzee Project. We thank the KCP field managers Maggie Kobusingye and Emily Otali and the KCP field assistants for their valuable assistance and support in the field. We particularly thank the entire “Pathways to Language” group for support and help in making this study possible.

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Figures

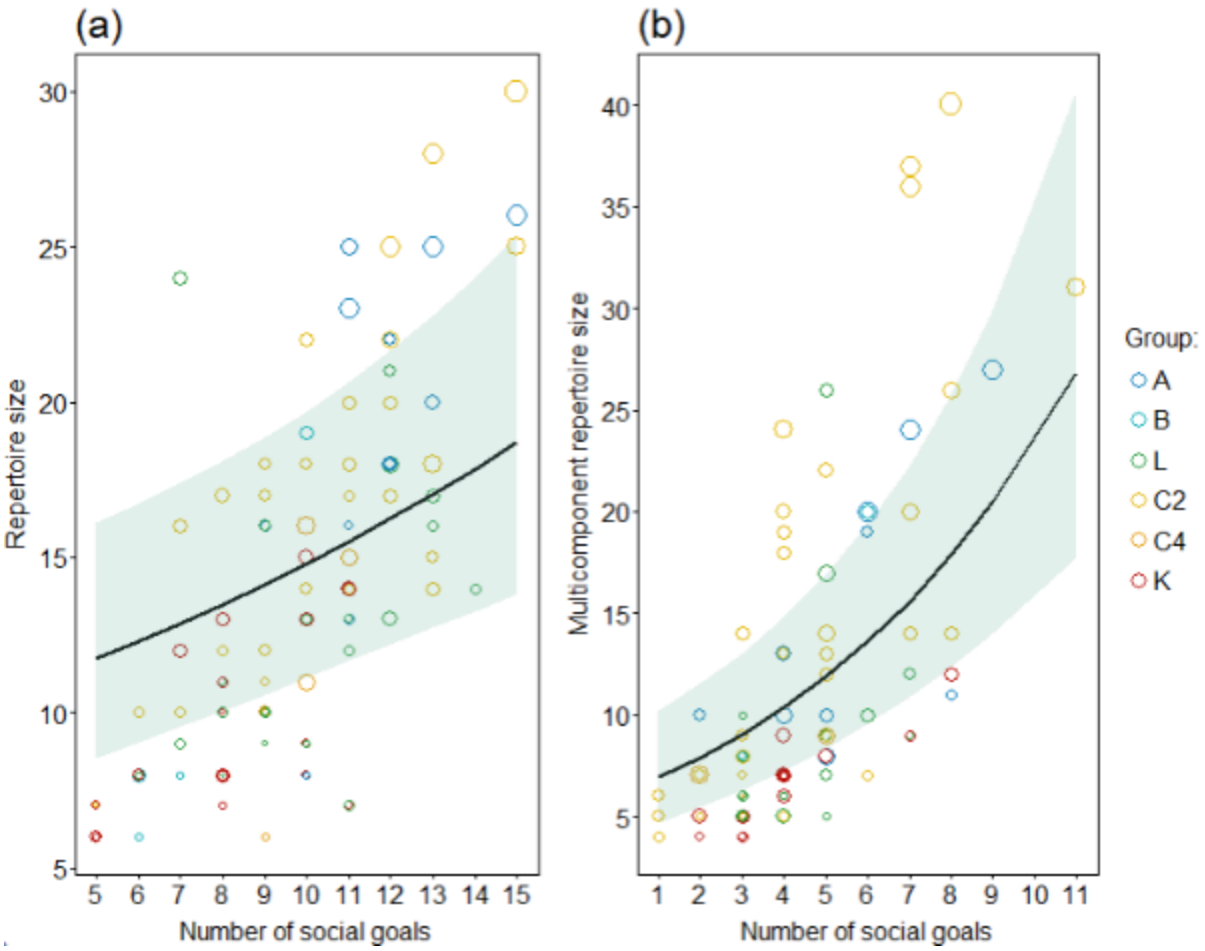


Figure 1

Individual repertoire (a) and multicomponent repertoire size (b) in relation to the number of expressed social goals. Circles represent individuals with area corresponding to sample size. The solid line represents the model predictions, and the green area represents the 95% confidence intervals.

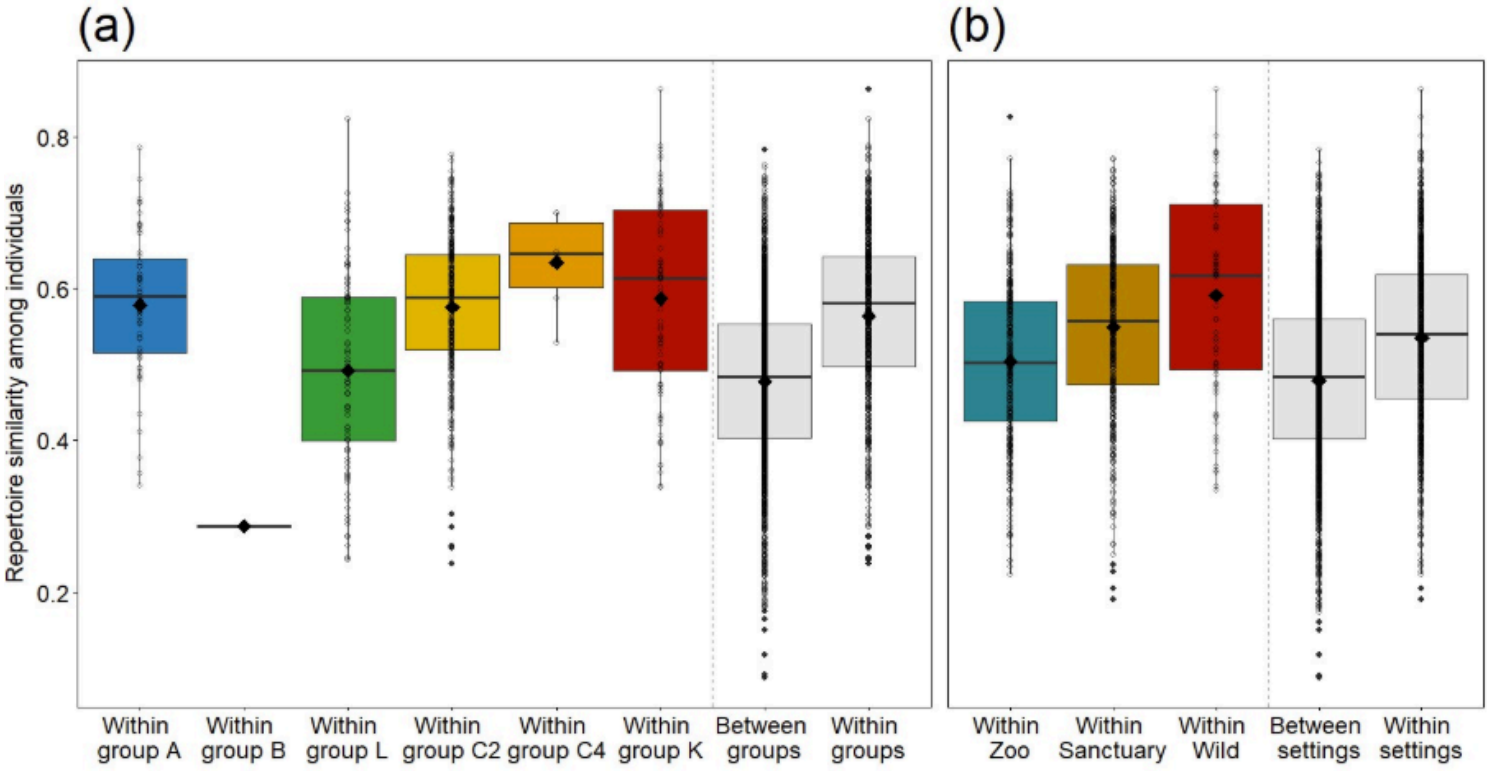


Figure 2

Signal repertoire similarity among individuals of the same and different social group (a) and setting (b), and within each social group and setting, quantified as Dice coefficients. Filled diamonds indicate group means, circles individual values, horizontal lines medians, boxes quartiles, vertical lines the 2.5% and 97.5% percentiles, and filled dots outliers.

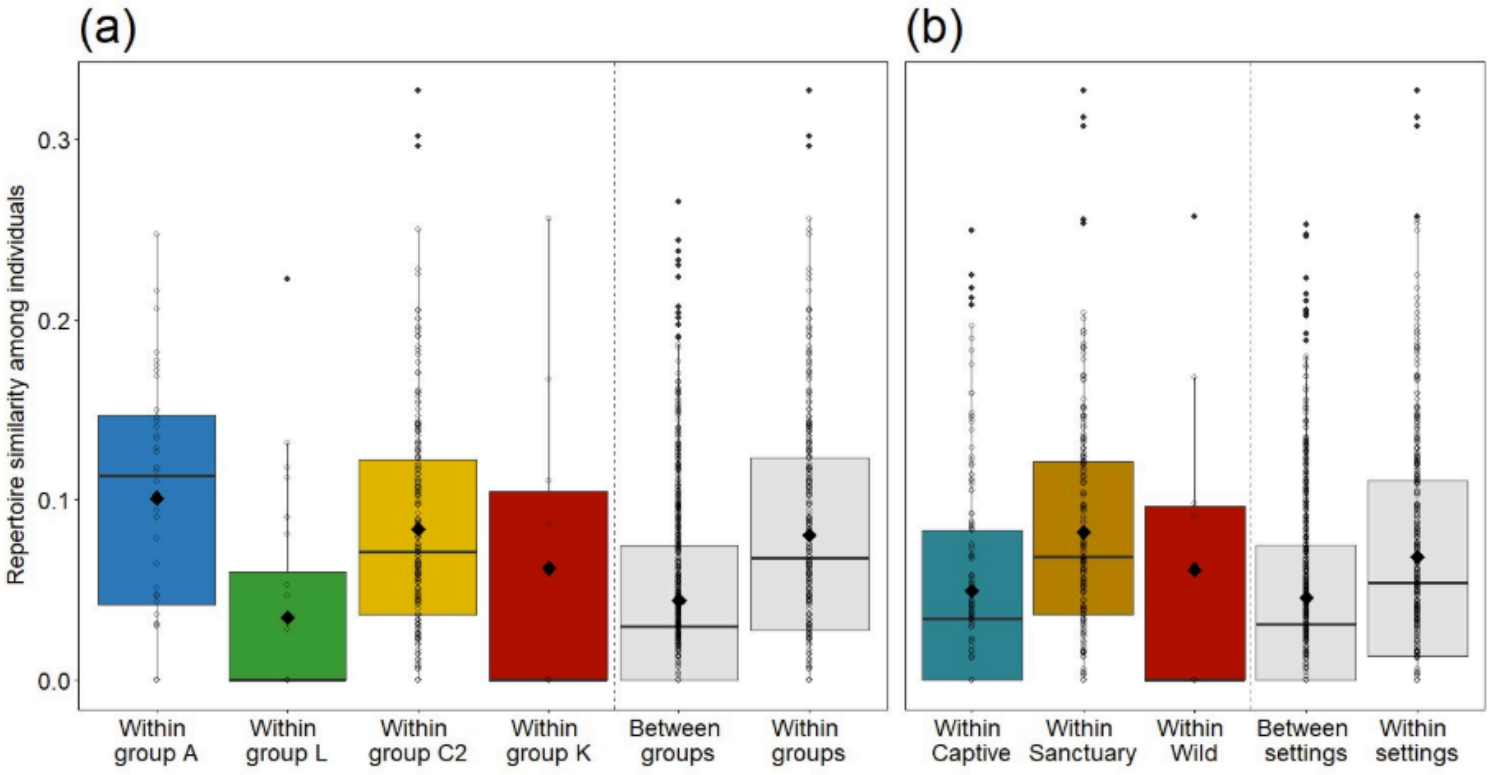


Figure 3

Multicomponent repertoire similarity among individuals of the same and different social group (a) and setting (b), and within each social group and setting, quantified as Dice coefficients. Filled diamonds indicate group means, circles individual values, horizontal lines medians, boxes quartiles, vertical lines the 2.5% and 97.5% percentiles, and filled dots outliers.

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