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Cite this article: Grampp M, Girard-Buttoz C, Samuni L, Tkaczynski PJ, Wittig RM, Crockford C. 2026 Coordination challenges shape signal complexity in chimpanzees (*Pan troglodytes verus*), but not in mangabeys (*Cercocebus atys atys*). *R. Soc. Open Sci.* **13**: 260401.
https://doi.org/10.1098/rsos.260401

Received: 2 January 2025
Accepted: 19 March 2026

Subject Category:
Organismal and evolutionary biology

Subject Areas:
behaviour

Keywords:
social approaches, fission–fusion dynamics, social bonding, coordination contexts, signal combinations, collective behaviour

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Supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8449013.

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Coordination challenges shape signal complexity in chimpanzees (*Pan troglodytes verus*), but not in mangabeys (*Cercocebus atys atys*)

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Increased coordination challenges, such as in the negotiation of group movement and activity, has been suggested to promote communicative complexity. This hypothesis, however, has rarely been tested within and between species, specifically in relation to signal combinations. We compared two primates, chimpanzees and mangabeys, living in the same dense forest habitat, but with varying degrees of fission–fusion dynamics. In both species, we examined whether spatial coordination challenges across daily contexts and social relationship strength impacted signalling complexity, considering combined signals as being more complex than single signals. As high-level fission–fusion dynamics increase coordination challenges, we additionally evaluated whether combined signalling predicted increased coordination (association) duration in chimpanzees. We found that greater coordination demands, i.e. during travelling, compared with feeding and resting, increased combined signalling production in chimpanzees only. In chimpanzees, coordination challenges were more influential in predicting combined signalling than relationship strength, with the latter being influential only during resting in both species. Finally, combined and socio-positive signal production predicted chimpanzee coordination duration. Our findings offer support that coordination challenges drive signal combination production, adding strength to the broader hypothesis that social complexity is a principal driver of the evolution of complex signalling.

1. Introduction

Behavioural coordination relates to similar or complementary behaviours made in adjustment to the behaviours of other individuals, in space and/or time [1]. Coordinated behaviours underpin animal gregariousness, allowing group cohesion maintenance, bond formation and cooperation, thereby mediating the cost–benefit ratio of group-living [1–5]. Across animal taxa, behavioural coordination is facilitated by the production of various cues and signals [3,6]. It allows collective movement [7–11] and cooperation between partners, including mutual grooming [12,13], co-feeding or food sharing [14,15], social cohesion during foraging [16], collective avoidance of predators [16–18], cooperative hunting [19,20], cooperative breeding [21], coalitionary aggression [22–24] and joint mate guarding or sexual coercion [25,26].

The social complexity hypothesis for the evolution of communication posits that the complexity of social systems selected for an expansion of communication complexity to maintain and negotiate social cohesion and relationships in complex social environments [27–29]. Complexity may increase with the number and diversity of components, and their organization or interactions, or uncertainty in the arrangement [27,30,31]. With respect to social systems, individuals living in societies where group members form temporary subgroups of variable size and composition (i.e. high-level fission–fusion dynamics), may experience an increased unpredictability in the social environment [32–34]. Concerning communicative systems, an increase in the number or diversity of signal units within a repertoire, or a signalling event probably represent an increased level of complexity [35–38]. As a part of the social complexity hypothesis, the behavioural coordination hypothesis posits that high coordination demands in a specific domain (e.g. cooperative breeding) may particularly favour selection for signal specificity, and thus larger signal repertoires within that domain [39]. Coordination contexts, such as cooperative breeding, hunting or predator avoidance represent high-stakes situations that require specific responses from receivers in each context. A generalized coordination signal may be insufficient to achieve this. As a result, several different signals, or modifications by combining signals, that elicit different partner responses, may be selected [20,40,41]. Here, we broaden the behavioural coordination hypothesis by predicting that coordination challenges may increase signal combinations. Signal combinations may help the efficacy of message transmission [42,43], disambiguate messages [44,45] or modulate meanings or functions together [17,40,41,46–49]. Signal combinations may trigger variation in the behaviours of signal receivers [17,48] and thus contribute to an expansion of communicative repertoires [16,50]. As a result, the production of signal combinations that contain different types of signals may be considered as more complex than the production of single signals or the repetition of signals [35]. This is the case whether different signals are from the same or different modalities, such as auditory or visual. Across species, social systems with high coordination challenges may increase communication demands [51] and select for high communicative complexity, such as expanded communicative repertoires [16,21,37,52,53], and a frequent use of signal combinations [16,21]. Within species, combined signals may be beneficial in high-stakes situations [36,45], such as contexts requiring high coordination [54–56]. However, only two studies, both in bonobos (*Pan paniscus*), suggest that the production of combined signals may directly promote coordination between partners compared with the production of single signals. In this species, two specific call combinations stimulated the probability to join or recruit partners from another subgroup compared with single signals or other combined signals [55,56].

We conducted both within- and between-species tests of the broadened behavioural coordination hypothesis by examining whether the production of combined signals increased with elevated coordination challenges across two sympatric species with different social systems: western chimpanzees (*Pan troglodytes verus*) and sooty mangabeys (*Cercocebus atys atys*). Both species live in the same physical environment, a tropical dense forest habitat, and are omnivorous and largely terrestrial. They both form differentiated social relationships in large multi-male, multi-female groups, with promiscuous mating and moderately steep dominance hierarchies [57], but have different kinship and association patterns. Within species, we focused on coordination challenges while maintaining social cohesion and social support, as this represents a critical problem in societies with differentiated relationships and strong fission–fusion dynamics [55,56,58–60], including in chimpanzees [23,61–63], given the high unpredictability in partner availability [32]. We operated under the assumption that different contexts result in different coordination challenges. Specifically, in both species, in comparison to resting, coordination challenges are expected to be higher in the context of (i) feeding, given the need for social tolerance during feeding competition [15,64,65], and (ii) travelling, given the patchy distribution of food resources and a low-visibility forest environment [11,54,61]. Further, we expected that coordination challenges may also increase during mediation of activity changes [11,55,56,65–67]. Finally, between species, as chimpanzees show strong fission–fusion dynamics and are highly selective in who they associate with [68,69], we evaluated whether chimpanzee combined signalling production directly affected dyadic coordination, i.e. association duration.

Behavioural coordination mediates joint actions and cooperation, which rely on various mechanisms, such as kin selection and reciprocity [70,71]. Therefore, coordination may be biased towards preferred partners within a group, leading to the formation of differentiated relationships and strong and enduring social bonds [22,72,73]. Individuals often seek to associate specifically with others with whom they regularly cooperate or share interests [58,74,75] and may develop communicative strategies to ensure spatial cohesion over time with them [3,59,61,76]. High levels of social tolerance and coordination may thus correlate with increased signalling frequency and flexibility across dyads [15,59,77,78]. Further, individuals may more often direct combined signals towards affiliates or allies than towards other partners within a group (call sequences [54], or combined visual and tactile signals [24]). Alternatively, high familiarity and predictability, and low rates of misunderstanding may lower the risk of conflict between bonded partners, leading to reduced need to use complex signals when interacting [79], such as the repetition of the same signals [80]. It is thus important to consider variation in relationship strength between partners while examining variation in coordination demands [12,81]. This may be particularly important for cross-species comparisons, as coordination needs and communication complexity may increase with the strength of social relationships, for instance contributing to an expansion of communicative repertoires [28], or an increased use of combined signals across species [37,82]. Considering the contrasting results of previous studies [24,54,79,80], we examined the link between relationship strength and signalling complexity across daily activities in both species. Both chimpanzees and mangabeys form strong and long-lasting social bonds [57], but chimpanzees live in patrilineal societies and cooperate extensively with non-kin group members [83,84], whereas mangabeys live in matrilineal societies with a stronger kin-based bias in cooperation [85,86]. Therefore, between species, we expected that situations posing greater coordination challenges may promote the production of combined signals more in chimpanzees as they need to negotiate coordination more frequently with non-kin compared with mangabeys [79].

Societies with strong fission–fusion dynamics regularly form temporary subgroups and provide the option to split, which can help to reduce social conflicts [87,88], but generate uncertainty in partner availability [33,34]. As a result, the negotiation of cohesion [10,15,55,56,60,66], and support with specific partners [7,89], to achieve joint actions [20,73,90] and collective movements [61,67], may represent greater coordination challenges in societies with strong fission–fusion dynamics, than in more cohesive groups, where partners always remain in the audible range. Especially, auditory signals play a crucial role in the mediation of coordination by allowing individuals to communicate to non-visible partners, within and across different subgroups [10,20,55,56,60,66,67,91,92]. During fusion, affiliative and greeting signals may increase with social uncertainty and the risk of conflict [93–95], but also be directed towards preferred group mates [24,96,97], ultimately reinforcing coordination. Thus, high fission–fusion dynamics coupled with differentiated relationships may have selected for high levels of social and communication complexity to maintain behavioural coordination and social relationships in a highly variable social environment [33,34,60,98], particularly for species living in low-visibility habitats, such as tropical forests [36,55]. Previous studies have shown that chimpanzees may be more selective in their association partners than mangabeys [68,69,99,100], highlighting the beneficial value to stay associated with close affiliates or allies in a highly flexible fission–fusion system. As a result of high uncertainty in partner availability, in chimpanzees, the maintenance of social cohesion, especially with social supporters, may be particularly challenging, and thus require complex signalling to effectively negotiate coordination between partners. While in societies with lower fission–fusion dynamics, such as those of mangabeys, social cohesion can be primarily directed towards the whole group, possibly requiring less complex signalling at the dyadic level. Previous studies in societies with high fission–fusion dynamics demonstrated that negotiating cohesion between individuals separated in different subgroups may elicit the production of combined signals [36,55,56]. As such, we investigated whether signal complexity may help to maintain cohesion and reduce the probability of separation within dyads of chimpanzees.

We defined 'signals' as communicative acts thought to transmit information to others, whether intentionally or unintentionally. We only included signals previously described for each species [38,101–104]. We focused on signalling production during tolerant or affiliative dyadic approaches. Social approaches provide a good context to explore our questions given they entail a clear signaller and receiver in a dyadic interaction, that can be compared across dyads and species. We defined signals during social approaches as those produced when one individual approached another one within 2 m. A number of studies highlighted that social approaches may play a key role in the negotiation of coordination and cooperation across social animals [24,80,82,101,105–107]. Chimpanzees and sooty mangabeys may adapt their signalling modality depending on attentional states of receivers [108,109], indicating cognitive abilities necessary for mutual responsiveness [110], and produce combined signals during approaches [80,95]. In chimpanzees, signalling may facilitate coordination, such as joint actions and cooperation [12,18,20,23,111]. Mangabeys may also emit signals to promote coordination, such as prior to infant handling or grooming [101,112]. However, for both species, it remains unclear whether coordination challenges also promote the use of combined signals.

Chimpanzees coordinate their activities in a wider range of contexts relative to mangabeys, both at the dyadic and group levels, for example during mutual grooming [113], food sharing, cooperative hunting [71,72] and critically for territorial defence [73,90], which may in turn select for information sharing and communication complexity in this species [18,21]. With these species differences in philopatry, coordination and communicative behaviours in mind, we examined the effects of coordination challenges and relationship strength on signalling complexity during approaches within each species and compared standardized results between them.

We first examined whether high coordination challenges during feeding and travelling contexts (compared with resting) promoted the use of combined signals in both species. We predicted that this effect will be more pronounced in chimpanzees because of the risk of separation due to their high-level fission–fusion dynamics. We also considered the effect of the relationship strength between partners on signalling complexity. Here, relationship strength may influence coordination needs and have different implications on signal complexity across species due to species-specific dynamics in partner preferences and relationship formation. We then focused our analysis on chimpanzees, to assess whether combined signals during approaches predicted the subsequent duration of dyadic association (i.e. within the same party). Previous studies suggested that chimpanzees may show greater selectivity in association partners due to stronger fission–fusion dynamics than mangabeys [69,99,100]. Therefore, prior to these analyses on signal use, preliminary models were conducted in both species to examine whether approach rates, thus signalling opportunities, were primarily biased towards bonded partners more in chimpanzees than in mangabeys.

2. Methods

2.1. Data collection

2.1.1. Study site and subjects

We conducted this study in the Taï National Park (5°52′ N, 7°20′ E, Ivory Coast) at the Taï Chimpanzee Project (TCP, [95,114]). Subjects were male and female adult and sub-adult chimpanzees (greater than 9 years old, $n = 38$) in two neighbouring social groups (East and South) and mangabeys (greater than 2 years old, $n = 26$) in one group, which ranges approximately 5 km away from the South group chimpanzees, within the same forest patch [85,95,115]. Considering the difficulty to continuously film a focal individual in a dense forest habitat, M.G. collected data using observational methods. Specifically, M.G. conducted half-day focal follows [116] using the Cybertracker software (https://cybertracker.org/) on a smartphone device. The focal individual was selected with a pseudo-random order, with a priority given to less observed individuals (chimpanzees: mean ± s.d. = 41 ± 9, mangabeys: 33 ± 7 h per individual, electronic supplementary material, §1.1). M.G. recorded continuously the focal activity (including resting, travelling, feeding, foraging and grooming), all social interactions involving the focal subject, including social approaches within a 2 m radius of the focal, and the group (for mangabeys) or subgroup composition (for chimpanzees, see details in electronic supplementary material, §1.2). Data used in this study is a subset of the data used in [95].

2.1.2. Signalling during approaches

Data on signalling during social approaches were used to evaluate our hypothesis and questions. During a focal follow, M.G. collected data on all approaches (within 2 m, a distance allowing for full visual and auditory contact between partners) occurring between the focal individual and adult or sub-adult partners, noting their identities and the signals emitted by the first signaller. The focal subject may be either the individual initiating or receiving the approach and/or the signal during the approach. Considered signals occurred during the approach and within 10 s from the approach (see electronic supplementary material, figure S2 for a visual summary). The directionality of signals was estimated depending on the head orientation and the direction of movement during the approach.

We included two communicative acts in both species that could be social cues rather than signals during approaches (i.e. informative traits that may not been under selection for facilitating transmission of this information, as defined in [117]). Distinguishing social cues from signals may not always be straightforward, as social cues may also be used by receivers and result in a certain outcome [44,118]. These two communicative acts were: 'withdrawing/moving aside' within 2 m in both species (see electronic supplementary material, table S2), because this behaviour may act as a submissive signal by acknowledging dominance and reducing the costs of social conflict for both the signaller and receiver; and 'peering' in mangabeys, as in chimpanzees it has been previously considered as a signal [103]. M.G. noted each signal type emitted, but not repetitions of the same signal type. In the analysis, we only used signal types that were conspicuous, based on repertoires established in previous studies in both species [38,101–104]. We considered that the production of combined signal types (emitted with less than 1 s between them) during an approach may represent greater signalling complexity than single signal production or the repetition of the same signal [95], as it contains several elements [27] and has the potential to refine or change the meaning of the message [17,45,48].

Signal categories included visual signals (in chimpanzees: arm raise; and in both species: head movements, standstill displays, withdrawing, bowing/crouching, peering, present body and genitals, extend limb and throw arm [102,103,119]); auditory signals (vocalizations, in chimpanzees: bark, hoo, pant-grunts, pants, pant-hoots, whimper, pant-screams or barks [38,94]; mangabeys: twitter, growl, copulation call [101]; both species: grunt and scream; in chimpanzees only: non-vocal sounds (lip smacking, raspberry blowing, teeth clacking) [120]), and multisensory signals (body and arm gestures using body parts, objects, or ground to make sound, e.g. shaking a branch, see electronic supplementary material, §1.3, table S2 for further details).

2.1.3. Reliability tests

To ensure the reliability of the data collected by M.G., we conducted inter-observer and inter-method tests. Specifically, to ensure the reliability of data on signalling complexity during approaches, we calculated Cohen's Kappa coefficients (κ) that considers the possibility of the agreement occurring by chance [121]. Cohen's Kappa coefficients between 0.61 and 0.8 indicate substantial agreement, and between 0.8 and 1 near perfect agreement between the observers. To this end, while collecting data on Cybertracker, M.G. also recorded videos of approaches in both species during the study period. These videos were later coded by M.G., to estimate the reliability of data on signalling complexity during approaches collected *in situ* versus from videos ($\kappa > 0.8$). Some additional videos were also used to estimate the reliability of data on signalling complexity between M.G. and one other experienced observer in each species ($\kappa > 0.8$). From these videos, the reliability of data on the occurrence of socio-positive signalling between M.G. and one other experienced observer in each species was also evaluated ($\kappa > 0.9$). Finally, given a large and graded vocal system in chimpanzees, we also estimated the reliability of data on the probability to emit a single versus combined vocal signals with only listening versus both inspecting call spectrogram and listening between M.G. and another experienced researcher ($\kappa > 0.7$, further details in electronic supplementary material, §1.4).

2.2. Social relationship parameters

To estimate social relationship strength, we calculated a dynamic dyadic grooming index (DDGI) similar to the dynamic dyadic sociality index (DDSI) updated daily [72,115,122]. We used long-term grooming data, allowing a burn-in period preceding the study period. We estimated the day-to-day rank relationship between partners, using dynamically calculated dominance hierarchies based on long-term data on supplants in mangabeys and pant-grunts in chimpanzees [115,123], applying a modification [115] of the Elo-rating method [124] developed by Foerster *et al.* [125] (details in electronic supplementary material, §2 and [115,126]).

2.3. Statistical analyses

2.3.1. Selection of approaches

In all models, we focused on all signals emitted during approaches except for those accompanied by aggressive behaviour from the signaller towards the receiver, as aggression may trigger dyadic dispersion and break coordination (i.e. chase, charge, hold, bite, hit, jump on, or pull, or when the receiver fled as a response to the signaller behaviour). We estimated relationship strength based on grooming data, therefore, we also excluded approaches related to grooming contexts (i.e. before and during grooming bouts). We excluded approaches during socially uncertain contexts (fusions and post-conflict contexts), as social uncertainty may increase signal complexity during these approaches [94,95]. We wanted to investigate signalling complexity specifically related to coordination challenges during resting, feeding and travelling contexts, therefore, we also removed approaches during and up to 30 min after intergroup encounters, as these events may increase coordination needs in themselves [127] and were not numerous enough in the dataset to be controlled for in our analysis. In all models, except preliminary models on approach rates, we removed cases when individuals produced a single multisensory signal during approaches, as the production of several perception modalities may encode different functions or meanings, triggering different outcomes [44,81]. We took this decision to ensure that single signals indeed represent less complex signals than combined signals and because of low sample sizes in both species (see sample sizes of excluded approaches in electronic supplementary material, table S7).

2.3.2. Preliminary models. The link between approach rates and relationship strength in both species

Chimpanzees and mangabeys have different patterns of relationships and social cohesion [57,100]; therefore, we fitted preliminary models to test whether approach rates are more likely to reflect relationship strength in chimpanzees than mangabeys because of stronger coordination demands to maintain relationships in a fission–fusion system. Each data point represents the sum of approaches per focal observation bout and per dyad (dyad combinations per focal follow bout: n = 5077 in mangabeys, n = 3332 in chimpanzees; dyads: n = 313 in mangabeys, n = 343 in chimpanzees). To account for varying opportunities for interaction, we included offset terms reflecting either the time individuals spent in the same group (for mangabeys) or subgroup composition (for chimpanzees, further details in electronic supplementary material, §3.1).

2.3.3. Models 1 and 2. Does signalling complexity during approaches differ according to social relationship strength and across coordination contexts?

We examined whether variation in signalling complexity reflected variation in coordination challenges, specifically increasing (i) from resting to feeding and travelling activities, (ii) immediately before an activity change (i.e. when the approach time was less than 2 min before an activity change), and depending on (iii) the social relationship strength with a partner (DDGI). We hypothesized that given a more dynamic social environment, with unpredictable partner availability, and a greater need to coordinate with non-kin, chimpanzees may face greater coordination challenges, and thus show a greater increase of signalling complexity in these contexts than mangabeys.

We chose a multinomial mixed-effect model structure to examine the variation in signalling complexity during approaches within a single analysis (model 1 in chimpanzees, model 2 in mangabeys). For each approach event, the response variable had three possible categorical values: no signal, single or combined signals (approaches: mangabeys: n = 4002; chimpanzees: n = 2265; dyads: mangabeys: n = 296, chimpanzees: n = 319). We ran each model twice per species, considering either 'no signal' or 'single signal' as the reference level, to evaluate the magnitude of change in the probability of emitting combined signals compared with the change in the probability of emitting no signal and single signals across contexts: (i) activity (rest, feed, travel) and (ii) activity change (yes/no), included as two-way interactions with the grooming index (DDGI). This type of model and error structure allowed us to examine the associations of our key predictors with the changes in the probability of each level of the response variable, particularly on the probability of emitting combined signals during approaches.

We tested the DDGI as a fixed effect, both as linear and quadratic terms. Signalling complexity may increase linearly with bond strength. Although, for partners with intermediate DDGI, coordination may still be advantageous but less predictable, presenting a higher challenge and more signalling than with strongly bonded dyads. Therefore, signalling complexity may follow an inverted U-shaped curve depending on DDGI, during contexts with high coordination challenges.

Foraging was defined as visually or manually searching for food prior to feeding [128]. However, in mangabeys, individuals usually travel slowly while foraging on the ground, therefore we considered that social cohesion challenges may also increase in these contexts, compared with stationary feeding. For information, we also ran model 2 in mangabeys with foraging included in feeding contexts instead of travelling, like in chimpanzees, which did not provide different results in terms of combined signalling production (electronic supplementary material, §4.3).

2.3.4. Model 3. Does signalling complexity during approaches predict dyadic association duration in chimpanzees?

As chimpanzee groups exhibit high-level fission–fusion dynamics, we could test whether the level of signalling complexity during approaches positively affected dyadic coordination, specifically the following dyadic association duration, estimated as the dyadic dispersion latency after the first approach following the start of a half-day focal follow.

We determined the duration of dyadic association post-approach(es) as the time from the approach until either the focal individual or the partner left the party (dispersion events: n = 1139, approaches: n = 1717, dyads: n = 307). If multiple approaches occurred, we calculated the duration from the first approach after the start of the focal follow until dispersion (electronic supplementary material, figure S4a). We considered only dyadic associations when the average duration of periods without visibility of the focal individual was less than 6.5 min. This corresponds to a 5% probability of missing an approach for a given dyad during the out-of-sight time given a rate of 0.46 approaches per dyad and per hour in chimpanzees (see electronic supplementary material, figure S4b). When dyads remained associated until the end of the focal follow, we could not determine the true duration of association, these datapoints were thus 'censored observations' (n = 331). To model with precision durations of dyadic associations, censored datapoints were included in the analysis along with uncensored ones (i.e. known association times) by using a survival model with a Weibull error structure [129] (see electronic supplementary material, figure S5). Signalling complexity during approach(es) prior to dispersion was the test predictor (categorical variable: no approach with signal, at least one approach with the production of a single signal, at least one approach with the production of combined signals).

We controlled for the number of approaches occurring in the dyad during the interval as this may increase signalling probability, and thus association duration. Variation in association duration pre-approach may also influence the duration post-approach, thus we included a control variable for the duration from the recorded start of association until the first approach (see electronic supplementary material, figure S6, which showed no clear difference depending on signalling complexity). However, in some cases, our survival analysis may underestimate the dyadic time spent in association, as some dyads may have been together prior to the start of the focal follows. We controlled for average party (subgroup) size at the time of approaches (relative to group size), as individuals may be more likely to use combined signals in large parties where more third-party social events can happen [95], and large parties may last for shorter durations.

We checked the prerequisite of proportionality of hazard ratios over time (function *cox.zph*, package 'survival' [130], electronic supplementary material, figure S7). Variables for signalling, sex combination and number of approaches showed time-dependent beta coefficients. Varying effects of the variable for signalling complexity across time could be explained by the variation of the implications of divergent strategies underpinning signalling during approaches. Coordination and conflict prevention strategies may stimulate signalling complexity, but have opposite effects on the duration of association. We implemented these variables into the shape formula (logit link function) allowing non-proportional hazard ratios [129]. We also created a variable reflecting the occurrence of at least one approach with clear 'socio-positive' signalling before dispersion (i.e. including only hoos, grunts, pants, loud scratches, peering, extending arm and presenting body part [131]), thus excluding submissive or more ambiguous signals that may primarily relate to conflict prevention [94,107].

2.3.5. General analytical procedure

Data preparation and analyses were conducted in R 4.1.2 [132] using the RStudio interface [133], and 'brms' package (Bayesian estimation [134], electronic supplementary material, §3). Philopatry can influence communicative strategies depending on rank relationship and sex combination [112], thus we controlled for the rank difference or distance and sex combination. In all models, we included a random effect of 'dyad' identity, controlling for dyadic-level factors not explicitly accounted for in the DDGI or the dominance rank. We included a random effect intercept for a variable of 'group/day' identity in chimpanzees, and 'day' in mangabeys (one mangabey group). This allowed us to account for group-level factors potentially varying across time and influencing signalling patterns, and that are not explicitly accounted for in our fixed effects (e.g. food availability). This also allowed us to account for the possibility that the observer increased the likelihood of detecting signals during approaches over time due to her experience. In all models, except in model 3 because of divergent transitions, we included a maximal random slope structure with enough variance, allowing for accurate estimation of slopes (electronic supplementary material, §3.3). To account for possible variation across groups [135], we added group identity ('East' or 'South') as a fixed effect in all the models for chimpanzees.

Result plots were generated using the package 'ggplot2' [136], *conditional_effects* function of 'brms', and script from [129] for survival curves. We estimated model efficiency, namely to what extent fixed effects explained variation in response variables (i.e. by comparing predictive performance of the models including all variables versus only random effect terms; details in electronic supplementary material, §3.7). These tests indicated weak predictive performance of the preliminary models, and the model 2 in mangabeys, but strong predictive performance of the models 1 and 3 in chimpanzees. We considered that the direction of the effect was strongly supported by our data or showed uncertainty, when the 95% or 89% credible intervals (CrI) of estimates excluded 0, respectively. We reported $p+$ and $p-$ as the percentages of posterior distribution in support for the direction of an estimate (full tables in electronic supplementary material, §4.2). In models 1 and 2, to provide a visualization of the results, we considered three classes of DDGI defined according to arbitrary cut-offs: low: below median, intermediate (around the mean in both species): 3rd quartile and high: 4th quartile. In models 1 and 2, we used the 'brms' function *fitted* to extract and compare average estimates of each signalling level across contexts, allowing us to compute the relative percentages of increase or decrease between categories that we report in §3.

3. Results

3.1. Relationship strength explains variation in approach rates more consistently in chimpanzees than mangabeys

Average dyadic rates of approaches per hour were comparable between chimpanzees: average ± s.d., 0.46 ± 1.28) and mangabeys: (0.33 ± 1.11). Tested fixed effects (grooming and dominance rank relationship indices and sex combination) weakly explained within-species variations in dyadic approach rates (electronic supplementary material, table S9, figure S11). These results indicated that in chimpanzees, approach rates may generally increase with higher DDGI, but this relationship is less clear and may even decline as DDGI becomes larger (DDGI^2: −0.07, 95% CrI [−0.12, −0.02], $p- = 99.6\%$; DDGI: 0.21, 95% CrI [0.10, 0.33], $p+ = 100\%$). A similar but less clear pattern was found in mangabeys, with approach rates also following an inverted U-shaped pattern depending on relationship strength (DDGI^2: −0.03, 95% CrI [−0.06, −0.01], $p- = 99.5\%$; DDGI: 0.06, 95% CrI [−0.03, 0.16], $p+ = 90.7\%$).

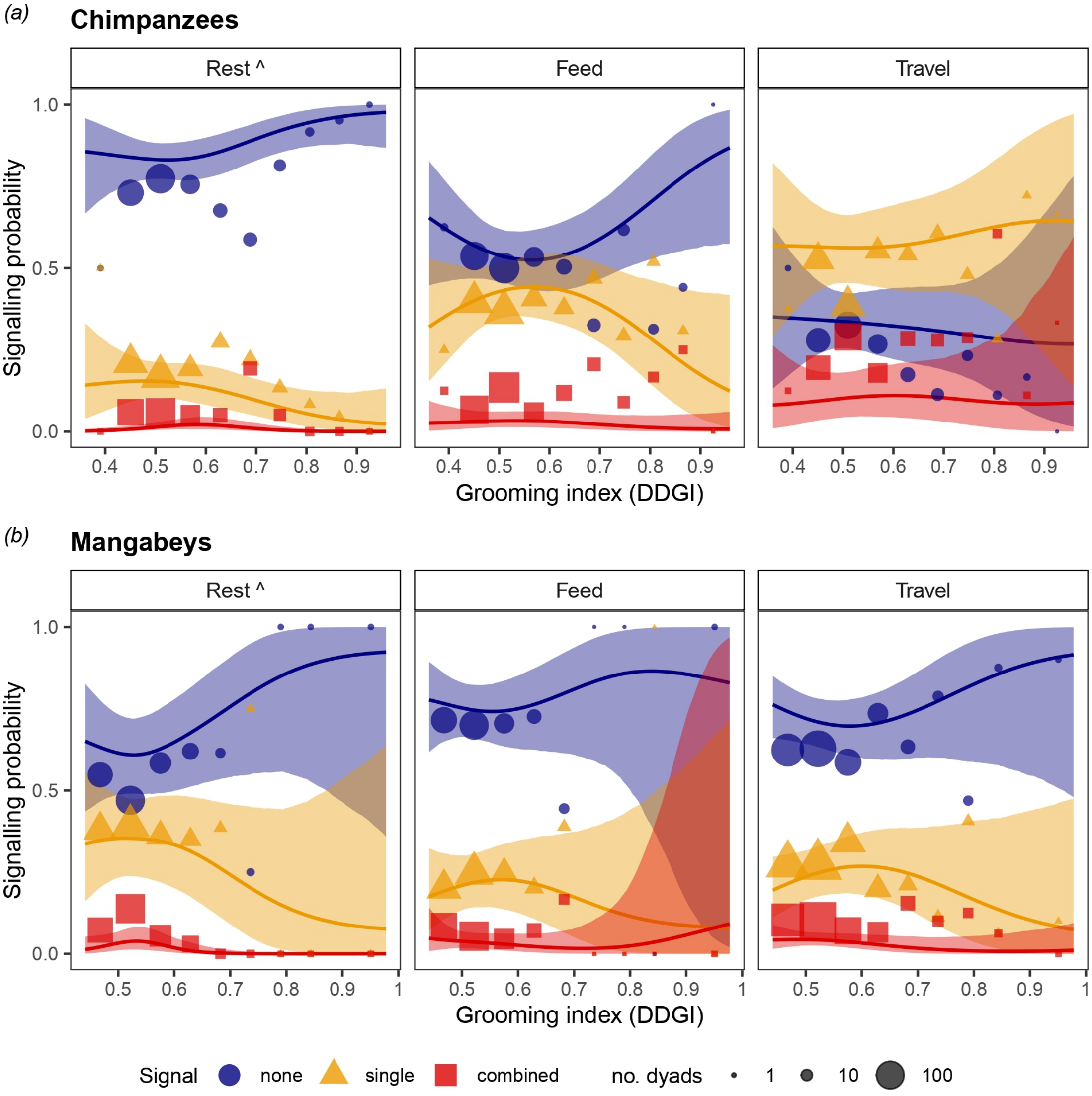

Figure 1. Does signalling complexity during approaches differ according to social relationship strength and across coordination contexts? Each panel illustrates the variation in signalling complexity (i.e. the probability of emitting no signal, single signal, combined signals) depending on relationship strength (DDGI) across contexts reflecting variable coordination challenges (in increasing order from rest to feed to travel) in chimpanzees (panels (*a*)) and mangabeys (panels (*b*)). Lines and shaded areas represent means and 95% CrI extracted from posterior distributions of the models 1 (for chimpanzees) and 2 (for mangabeys). Dots are average probabilities calculated from the raw data, with the size proportional to the number of dyads per DDGI value (10 categories) and per focal activity. ^: combined signalling probability varied quadratically depending on the DDGI during resting in both species (electronic supplementary material, figure S13 with log-transformed y-axis). In chimpanzees, but not in mangabeys, combined and single signalling probabilities increased during feeding and even more during travelling compared with resting. During travelling compared with resting, the probability of emitting combined signals increased to a larger extent than the probability of emitting single signals in chimpanzees.

3.2. Does signalling complexity during approaches differ according to social relationship strength and across coordination contexts?

In both species, we examined whether signalling complexity during approaches increases (i) in feeding and travelling compared with resting, (ii) prior to activity changes, and (iii) with social relationship strength with the partner, yet decreasing between partners with high and intermediate relationship strength, because of high common knowledge and familiarity [79]. We hypothesized that these coordination challenges may promote signalling complexity more in chimpanzees than in mangabeys, because of stronger fission–fusion dynamics, and thus higher unpredictability in partner availability, and a greater reliance on non-kin partners, potentially leading to a greater need for negotiation.

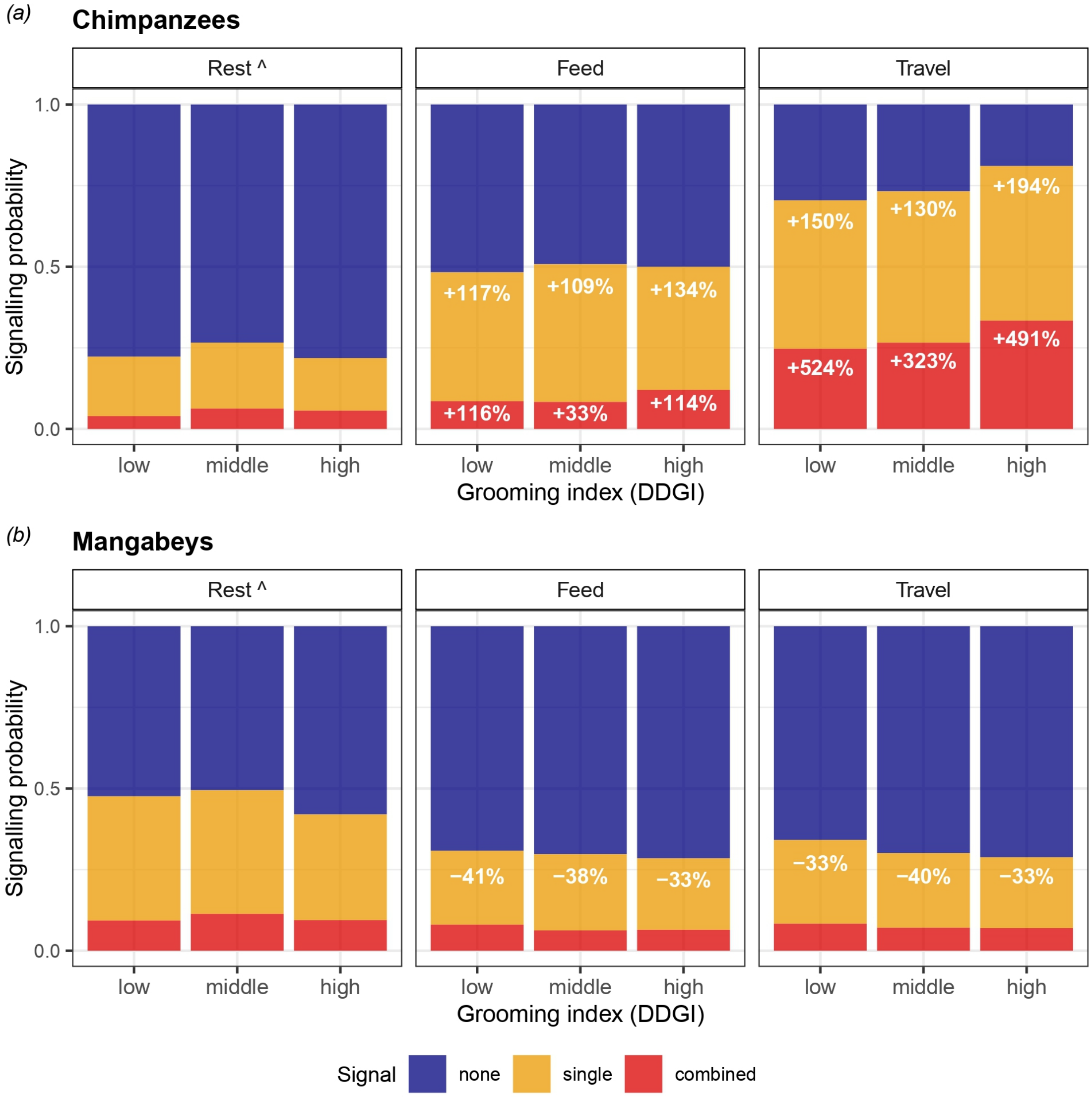

Figure 2. Signalling complexity depending on relationship strength across coordination contexts in chimpanzees (panels (*a*)) and mangabeys (panels (*b*)). Each bar represents the average signalling probability during approaches depending on the grooming index (DDGI, split in three classes: see in §2.3.5) and across contexts with variable coordination challenges (from lowest to highest: rest, feed and travel). Averages from the posterior distributions of the models 1 and 2, and conditional on the variables included in the models (table 1). ^: Combined signalling probability varied quadratically depending on the DDGI during resting in both species. In chimpanzees, but not in mangabeys, combined and single signalling probabilities increased during feeding and even more during travelling compared with resting. During travelling compared with resting, the probability of emitting combined signals increased to a larger extent than the probability of emitting single signals in chimpanzees.

3.2.1. Signalling complexity depends on activity, only in chimpanzees

In both species, approaches without any auditory or visual signalling (‘no signal’) were the most common across all activities, except during travelling in chimpanzees, where approaches with single signals, including an auditory or a visual signal, represented the predominant type of communication (figures 1 and 2).

In chimpanzees, the probability of emitting combined signals quintupled in travelling compared with resting (average probabilities from the posterior distributions of model 1, when scaled (DDGI) = 0, during travelling: $P(\text{combined}) = 0.27$, during resting: $P(\text{combined}) = 0.05$, combined versus no signal: $p+ = 100\%$; combined versus single signal: $p+ = 99.5\%$, table 1, figures 1*a* and 2*a* showing the increases in signal probabilities across three DDGI illustrative classes). Chimpanzees were also 87% more likely to emit combined signals in feeding (when scaled (DDGI) = 0: $P(\text{combined}) = 0.09$) compared with resting (combined versus no signal: $p+ = 99.9\%$; combined versus single signal: $p- = 59.7\%$), and three times

Table 1. Does signalling complexity during approaches differ according to social relationship strength and across coordination contexts? Two multinomial models (per species, panels (a) and (b)) illustrate the magnitude of change in (I) the probability of emitting single signals versus no signal, (II) the probability of emitting combined signals versus no signal, (III) the probability of emitting combined versus single signals. In (I) and (II), the models included 'no signal' as the reference level, in (III) the models included 'single' as the reference level, to evaluate whether the magnitude of change in the probability of emitting combined signals is higher than for single signals. Red and orange cells indicate estimates supported by 95% and 89%, respectively, of the posterior distribution from models 1 and 2. Bold: test predictors. Italics: control predictors. In brackets: reference level of a categorical variable. All continuous variables are z-transformed to a mean of 0 and standard deviation of 1.

response variable: signalling complexity during approaches (multinomial with 3 levels: no, single, combined signal)	**a) model 1: chimpanzees**		**b) model 2: mangabeys**	
	estimate	95%CI (lower, upper)	estimate	95%CI (lower, upper)
I) probability of emitting single signals versus no signal				
intercept	−2.39	(−3.06, −1.75)	−0.67	(−1.2, −0.15)
DDGI * activity (rest) feed	0.22	(−0.25, 0.67)	0.13	(−0.38, 0.63)
DDGI * activity (rest) travel	0.24	(−0.33, 0.82)	0.18	(−0.21, 0.59)
DDGI * activity change (no) yes	0.12	(−0.37, 0.6)	−0.16	(−0.58, 0.24)
DDGI ^2 * activity (rest) feed	0	(−0.26, 0.27)	−0.02	(−0.22, 0.19)
DDGI ^2 * activity (rest) travel	0.19	(−0.14, 0.53)	0.01	(−0.14, 0.18)
DDGI ^2 * activity change (no) yes	−0.15	(−0.44, 0.14)	0.13	(−0.01, 0.28)
focal activity (rest) feed	**1.57**	**(1.17, 1.97)**	**−0.66**	**(−1.08, −0.23)**
focal activity (rest) travel	**2.3**	**(1.79, 2.83)**	**−0.47**	**(−0.89, −0.03)**
activity change (no) yes (<120s)	**0.6**	**(0.09, 1.07)**	0	(−0.35, 0.34)
DDGI	−0.19	(−0.62, 0.24)	−0.04	(−0.45, 0.36)
DDGI ^2	−0.13	(−0.4, 0.12)	−0.1	(−0.26, 0.04)
dominance rank difference	*−0.55*	*(−0.95, −0.15)*	*−0.66*	*(−1.03, −0.29)*
group (east) south	*0.66*	*(0.05, 1.27)*	–	–
sex combination (female-female) female-male	*0.18*	*(−0.46, 0.82)*	*0.94*	*(0.27, 1.64)*
sex combination (female-female) male-female	*0.01*	*(−0.72, 0.74)*	*−1.03*	*(−1.84, −0.25)*
sex combination (female-female) male-male	*0.63*	*(−0.08, 1.32)*	*0.88*	*(−0.12, 1.87)*
II) Probability of emitting combined signals versus no signal				
intercept	−4.49	(−5.71, −3.38)	−2.7	(−3.72, −1.79)
DDGI * activity (rest) feed	−0.46	(−1.19, 0.25)	−0.2	(−1.03, 0.62)
DDGI * activity (rest) travel	−0.32	(−1.09, 0.45)	−0.02	(−0.7, 0.69)
DDGI * activity change (no) yes	−0.3	(−1.02, 0.41)	0.46	(−0.38, 1.34)
DDGI ^2 * activity (rest) feed	0.48	(−0.04, 1.02)	**0.69**	**(0.01, 1.44)**
DDGI ^2 * activity (rest) travel	**0.67**	**(0.14, 1.23)**	**0.67**	**(0.05, 1.4)**
DDGI ^2 * activity change (no) yes	0.08	(−0.35, 0.52)	−0.02	(−0.41, 0.34)
focal activity (rest) feed	**0.98**	**(0.36, 1.61)**	−0.34	(−1.08, 0.43)
focal activity (rest) travel	**2.68**	**(2.05, 3.33)**	−0.06	(−0.89, 0.89)
activity change (no) yes (<120s)	0.42	(−0.25, 1.07)	−0.87	(−1.98, 0.04)
DDGI	0.53	(−0.2, 1.3)	−0.18	(−0.91, 0.51)
DDGI^2	**−0.77**	**(−1.32, −0.27)**	**−0.79**	**(−1.54, −0.17)**
dominance rank difference	*−0.76*	*(−1.45, −0.05)*	*−0.89*	*(−1.37, −0.46)*
group (east) south	*−0.21*	*(−1.25, 0.82)*	–	–
sex combination (female-female) female-male	*0.93*	*(−0.28, 2.08)*	*−0.13*	*(−0.96, 0.69)*
sex combination (female-female) male-female	*0.58*	*(−0.62, 1.73)*	*−0.8*	*(−1.79, 0.12)*
sex combination (female-female) male-male	*1.43*	*(0.34, 2.45)*	*1.85*	*(0.76, 2.91)*
III) Probability of emitting combined signals versus single signals				
intercept	−2.57	(−3.58, −1.66)	−1.8	(−2.63, −1.08)
DDGI * activity (rest) feed	−0.46	(−1.21, 0.29)	−0.3	(−1.11, 0.52)
DDGI * activity (rest) travel	−0.32	(−1.07, 0.45)	−0.06	(−0.72, 0.62)
DDGI * activity change (no) yes	−0.32	(−0.98, 0.34)	0.48	(−0.36, 1.36)
DDGI ^2* activity (rest) feed	0.35	(−0.19, 0.91)	**0.77**	**(0.09, 1.51)**
DDGI ^2* activity (rest) travel	0.34	(−0.16, 0.89)	**0.72**	**(0.1, 1.43)**
DDGI ^2* activity change (no) yes	0.2	(−0.21, 0.61)	−0.11	(−0.46, 0.22)
focal activity (rest) feed	−0.08	(−0.71, 0.56)	0.09	(−0.62, 0.82)
focal activity (rest) travel	**0.83**	**(0.19, 1.49)**	0.24	(−0.47, 1.05)
activity change (no) yes (<120s)	−0.18	(−0.84, 0.46)	**−0.91**	**(−1.96, −0.04)**
DDGI	0.57	(−0.17, 1.33)	−0.12	(−0.79, 0.53)
DDGI^2	**−0.53**	**(−1.08, −0.01)**	**−0.77**	**(−1.49, −0.14)**
dominance rank difference	*−0.39*	*(−0.96, 0.17)*	*−0.24*	*(−0.58, 0.09)*
group (eeast) south	*−0.67*	*(−1.47, 0.13)*	–	–
sex combination (female-female) female-male	*0.95*	*(0.02, 1.86)*	*−0.44*	*(−0.98, 0.08)*
sex combination (female-female) male-female	*0.71*	*(−0.4, 1.79)*	*0.06*	*(−0.83, 0.9)*
sex combination (female-female) male-male	*1.16*	*(0.25, 1.99)*	*1.25*	*(0.33, 2.16)*

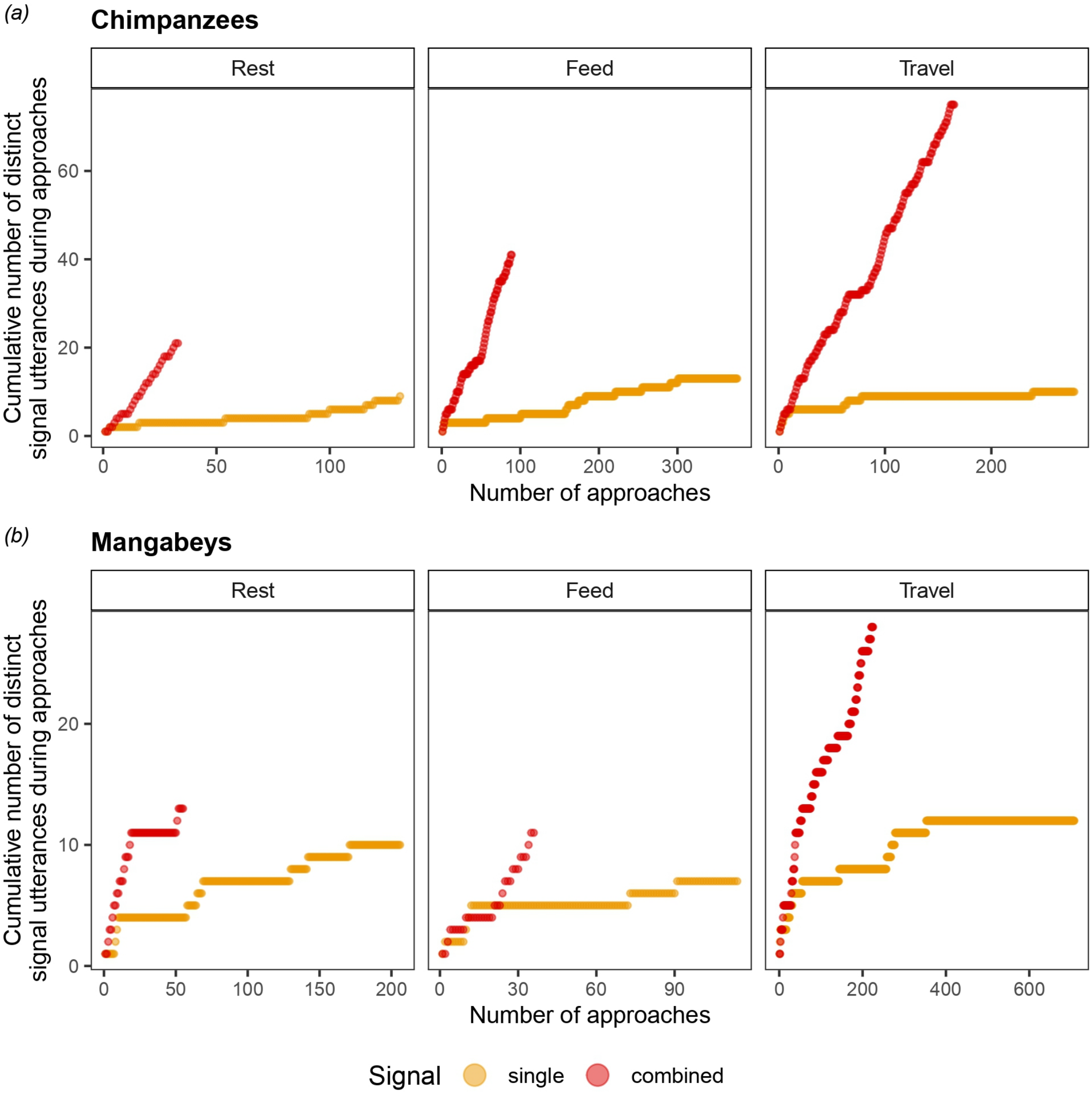

Figure 3. Cumulative number of distinct signal utterances during approaches across coordination contexts in chimpanzees (panels (*a*)) and mangabeys (panels (*b*)). Each point represents the cumulative number of distinct signal utterances during approaches considering single signals (in yellow) and combined signals (in red) and across contexts with variable coordination challenges (from lowest to highest: rest, feed and travel) in both species. The cumulative number of distinct signal utterances during approaches appears higher for combined than single signals, especially during travelling, and more clearly in chimpanzees than in mangabeys.

more likely to emit combined signals in travelling compared with feeding contexts (combined versus no signal: $p+ = 100\%$; combined versus single signal: $p+ = 100\%$). Before activity changes, chimpanzees were 26% more likely to produce single signals, but not clearly more likely to produce combined signals (single versus no signal: $p+ = 98.7\%$; combined versus no signal: $p+ = 88.7\%$).

In mangabeys, coordination contexts weakly explained the variation in signalling complexity across approaches (figures 1*b* and 2*b*, table 1, electronic supplementary material, §3.7). The probability of emitting combined signals did not clearly vary between approaches across travelling, feeding and resting contexts (figures 1*b* and 2*b*, $p-$ and $p+$ for all pairwise comparisons < 82%). However, mangabeys were 6% less likely to produce combined signals during approaches before activity changes compared with no change in activity (combined versus no signal: $p- = 96.7\%$; combined versus single signals: $p- = 98.0\%$).

Furthermore, the cumulative number of distinct signal utterances emitted during approaches appears higher for combined than single signals, especially during travelling, and more clearly in chimpanzees than in mangabeys (figure 3). While drawn from observational, rather than using video or audio data, we could not determine reliably the exact number of signals within sequences, but also do not expect observational bias across contexts or species, since the data were collected by the same observer in the same forest. We propose future studies to confirm this result.

3.2.2. Signalling complexity depends on relationship strength during resting in both species

In chimpanzees, during resting, combined signalling followed an inverted U-shaped pattern depending on the grooming relationship between partners (figure 1*a*, table 1, DDGI^2: versus no signal, *p*− = 99.9%; versus single signals: *p*− = 97.8%). When considering three classes of grooming relationships (low, intermediate and high; see in §2.3.5), chimpanzees were 58% and 11% more likely to emit combined signals towards partners with intermediate than low or high grooming index values, respectively (figure 2*a*). Compared with resting, signal complexity was neither markedly biased in favour of partners with intermediate grooming relationship in feeding nor travelling contexts (versus no signal, interaction DDGI^2 * travel: *p*+ = 99.5%; interaction DDGI^2 * feed: *p*+ = 96.2%; versus no signal: DDGI^2: feed: *p*− = 95.2%, travel: *p*− = 69.3%). Whether there was an activity change or not, signal complexity was similarly biased in favour of partners with intermediate grooming relationship (interaction DDGI ^2 * before activity change: versus no signal: *p*+ = 64.8%).

In mangabeys, during resting, combined signalling also followed an inverted U-shaped pattern depending on the grooming relationship between partners (figure 1*b*, table 1, DDGI^2: versus no signal: *p*− = 99.7%; versus single signals: *p*− = 99.6%). Again, considering three classes of grooming relationships (low, intermediate and high; see in §2.3.5), mangabeys were 22% and 21% more likely to emit combined signals towards partners with intermediate than low or high grooming index values, respectively (figure 2*b*). Compared with resting, signal complexity was neither markedly biased in favour of partners with intermediate relationship strength in travelling nor feeding contexts (versus no signal, interaction DDGI^2 * feed: *p*+ = 97.6%; interaction DDGI^2 * travel: *p*+ = 98.5%; versus no signal: DDGI^2, feed: *p*− = 68%, travel: *p*− = 91.4%). Whether there was an activity change or not, signal complexity was similarly biased in favour of partners with intermediate grooming relationship (interaction DDGI^2 * prior activity change: versus no signal: *p*− = 53.1%).

3.3. Signalling complexity predicts coordination (dyadic association duration) in chimpanzees

We examined whether signalling complexity during approaches directly predicted chimpanzee dyadic association duration, thus social cohesion. We assessed the association probability (‘survival’ probability) measured as the dyadic dispersion latency after the first approach following the start of a half-day focal follow.

The relation between signalling complexity during approaches and duration of association bouts changed with increasing durations (figure 4*a*, table 2). Specifically, at first association probability decreased faster for association bouts containing approaches with combined signals compared with no signal. Then, for relatively longer association durations, this pattern was reversed, with association bouts lasting longer when approaches contained combined signals compared with no signal. The negative estimate of combined signalling for the shape of the curve indicates that the steepness of the curve decreased even more with increasing dyadic association durations following approaches with combined signals compared with no signalling (*p*− = 99.2%). With marginally less support, this was also true for association episodes containing approaches with combined compared with only single signals (estimate for shape, combined versus single: *p*− = 96.6%).

The occurrence of socio-positive signalling during at least one approach always positively related to the duration of association (*p*+ = 99.3%, figure 4*b*). The number of approaches positively related to the duration of association (*p*+ = 100%). The duration of dyadic association was lower in South than East group (*p*− = 100%). A dyad was more likely to disperse as the party size increased (*p*− = 99.7%). With marginally less support, the probability to stay associated increased with the dyadic relationship strength (*p*+ = 98.2%), and was lower in mixed-sex than in female–female or male–male dyads (*p*− = 93.2%; *p*− = 87.6%).

4. Discussion

Our results show support for the hypothesis that challenges related to spatial coordination drive signalling complexity in chimpanzees, but not in mangabeys. As suggested in other studies on signal use in primates, single signals may be more frequently produced than combined signals across daily contexts [35,43,104]. However, combined signalling production increased more than single signalling production during travelling compared with resting or feeding in chimpanzees, but not in mangabeys. Thus, our results in chimpanzees suggest that the likelihood of emitting combined signals increases

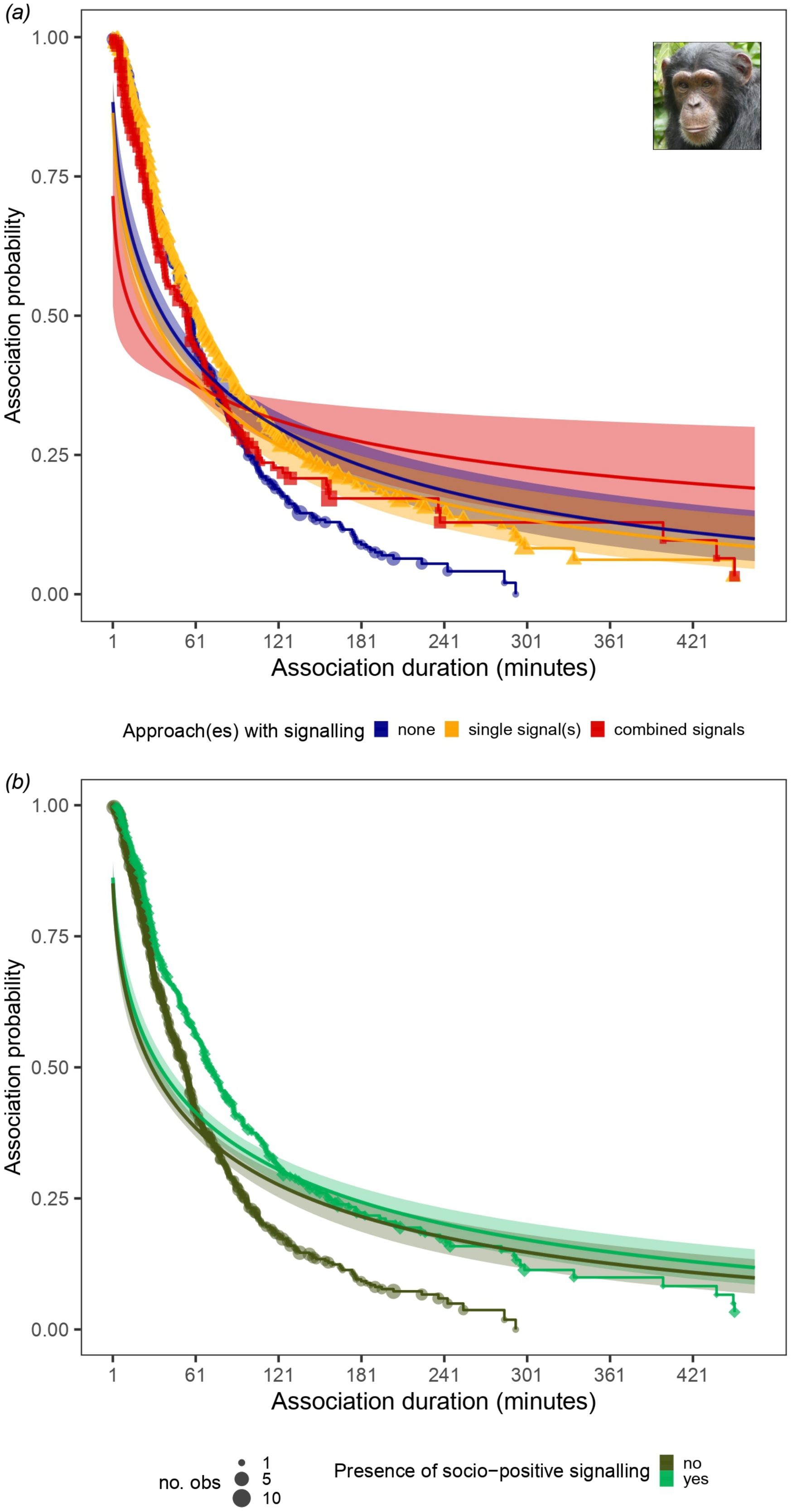

Figure 4. Survival analysis demonstrating how signalling complexity during approach(es) predicts association duration in chimpanzees. Kaplan–Meier survival curves depict the association probability post-approach depending on (*a*) signal use during approaches (none, one or more single signal(s), including combined signals); (*b*) at least one approach with 'socio-positive' signalling (yes/no). Observed survival curves with steps representing dispersion latencies and dots with the size proportional to the number of observations. Posterior survival curves and 95% CrI of the model 3: solid lines and shaded areas.

Table 2. Signalling complexity predicts dyadic association duration in chimpanzees. Red and orange cells indicate estimates whose directions are supported by 95% and 89%, respectively, of the posterior distribution of the model 3. Bold: test predictors. Italics: control predictors. In brackets: reference level of a categorical variable. All continuous variables are z-transformed to a mean of 0 and standard deviation of 1.

response: dyadic association duration (a negative estimate indicates that the variable is associated with lower association durations)	estimate	95% CI (lower, lower)
intercept	8.74	(8.56, 8.92)
signal use during approach(es) (none) single signal(s)	−0.19	(−0.39, 0.00)
signal use during approach(es) (none) combined signals	−0.20	(−0.39, 0.00)
Presence of 'socio-positive' signalling (no) yes	*0.24*	*(0.05, 0.43)*
number of approaches	*0.40*	*(0.29, 0.51)*
grooming index (DDGI)	*0.07*	*(0.00, 0.13)*
dominance rank distance	*−0.01*	*(−0.09, 0.07)*
group (east) south	*−0.51*	*(−0.7, −0.31)*
time before first approach	*0.02*	*(−0.04, 0.08)*
sex combination (female-female) female-male	*−0.17*	*(−0.33, 0.00)*
sex combination (female-female) male-male	*0.04*	*(−0.20, 0.29)*
% party/group size during first approach	*−0.09*	*(−0.16, −0.03)*
shape of the curve: variable relationship with association duration changes with time (a negative estimate indicates that dispersion probability decreases with time)		
intercept	0.51	(0.39, 0.64)
signal use during approach(es) (none) single signal(s)	−0.03	(−0.17, 0.12)
signal use during approach(es) (none) combined signals	**−0.22**	**(−0.41, −0.03)**
number of approaches	*0.02*	*(−0.07, 0.13)*
sex combination (female-female) female-male	*−0.02*	*(−0.16, 0.12)*
sex combination (female-female) male-male	*−0.15*	*(−0.35, 0.04)*

when dyadic coordination maintenance is challenging and separation risk is high. Chimpanzees display much higher degrees of fission–fusion dynamics than mangabeys, which can generate a more unpredictable and fluctuating social environment [32], especially during group movements. Since proximity maintenance with valuable partners probably represents a greater challenge in societies with strong, relative to weak, fission–fusion dynamics [55,56,58–61], chimpanzee association patterns may relate more to partner preferences and reflect cooperation patterns than in mangabeys [68,69,99,100]. We found that the use of combined and socio-positive signalling predicted the longest periods of spatially coordinated activity in chimpanzees, demonstrating the functional value of complex signals in maintaining spatial association, independent of relationship strength.

Dyadic grooming relationship strength predicted higher approach rates in chimpanzees than mangabeys. However, this pattern was weak, suggesting that close-range communication opportunities were not restricted to bonded partners in chimpanzees, despite strong fission–fusion dynamics. In both species, individuals were more likely to emit combined signals towards partners with intermediate relationship strength, but contrary to our expectations, this pattern was only clear during resting. Resting may involve lower coordination challenges compared with feeding and travelling, but probably still requires some coordination that may be mediated through signalling, especially in low-visibility environments [66].

4.1. Coordination challenges in relation to fission–fusion dynamics shape signalling complexity during approaches in chimpanzees

In chimpanzees, single and combined signal production during approaches was highest when travelling, compared with when feeding, then resting. Moreover, in chimpanzees the magnitude of change in combined signalling probability was higher than single signalling probability in travelling compared with resting or feeding. The likelihood of emitting single signals compared with no signalling, increased immediately before a change in activity in chimpanzees but not in mangabeys. These findings demonstrate that signals and in particular combined signals may facilitate dyadic coordination in chimpanzees, where coordination challenges during these contexts are higher than in mangabeys. In societies with fission–fusion dynamics, when risks of conflict and separation are high, such as during feeding and travelling, combined signals may serve to maintain or negotiate proximity and social support with specific partners [36,55,56], and/or a larger audience [137]. Combined signals may increase message efficacy [42–44], disambiguate messages [44,45] or convey additional meanings [17,40,41,46–49]. Increasing message efficacy may be advantageous in conditions of high social noise [54] and low visibility, such as in a forest environment [36]. Combined signals may be produced less frequently than single signals [35,43,104] but be particularly adaptive in high-stakes social contexts [36,44,45,94], such as when coordination needs or challenges are high [54–56]. Ultimately, signal combinations may be particularly prominent and frequently used in highly social species [40].

Here, in mangabeys, single signal production during approaches was highest when resting. Mangabeys showed less likelihood of producing combined signals compared with single signals or no signalling, before a change in activity. Given that groups of mangabeys are more cohesive than those of chimpanzees, contexts of feeding, foraging, travelling and changes in activity do not represent the same coordination challenge. Considering that mangabeys are less selective in their proximity partners than chimpanzees [68,69,99], spatial cohesion may rely more on indiscriminate coordination with nearest neighbours [138] and quorum decisions during movement [139] than social interactions and active negotiation via dyadic signalling. Signals during resting contexts, rather, may relate to motivation for direct social interaction with specific partners, such as socio-positive contacts.

4.2. Signalling complexity predicts coordination during long associations in chimpanzees

A previous study demonstrated that signal production may trigger longer periods of resting in association with other chimpanzees [66]. Further, two other studies in bonobos examined how the use of two specific call combinations may coordinate inter-party movements [55,56]. Here, by using a 'survival' analysis to assess association duration, we found that in chimpanzees combined signalling during approaches predicted the longest periods of dyadic association. This was the case when considering all signals, whether socio-positive (e.g. 'hoo' and 'grunt') or not (e.g. 'bark'). These results underline the crucial role of combined signals in dyadic coordination in chimpanzees. This is particularly relevant given that chimpanzees cooperate both at the dyadic (agonistic support [62,69]) and the group levels (hunting [71], territorial defence [73,90]). As cooperation depends on coordination, signals that prolong coordination duration may also facilitate cooperation.

We also found that chimpanzees from East group associated on average for longer periods than chimpanzees from South group in line with a previous study, where males in East group showed more cooperative behaviours and higher average oxytocin levels than in South group [140]. Similarly, same-sex dyads associated for longer durations than mixed-sex dyads, consistent with a previous study [75], also potentially reflecting cooperation patterns in this population.

4.3. Signalling complexity during short associations in chimpanzees

The 'survival' analysis demonstrated a different pattern with respect to signalling complexity and cohesion for relatively short dyadic associations. Here, the production of non-socio-positive combined signals predicted shorter association periods (see electronic supplementary material, figures S14 and S15). Such signals may be inefficient at prolonging the association and designed rather to reduce message ambiguity and the risk of misunderstandings [44] and/or to mediate competitive or uncertain social interactions [36,94,95] with no goal to coordinate with the other. These different patterns, based on whether or not socio-positive signals were emitted, highlight that both coordination challenges and social uncertainty [95] represent two fundamental social drivers of signalling complexity in chimpanzees.

4.4. Social relationship strength affects signalling complexity during approaches in both species

Variation in relationship strength had a similar influence on signalling patterns during approaches in both species. Combined signals were relatively more often directed towards partners with intermediate relationship strength, but contrary to our expectations, only during resting. Socially close individuals share high familiarity, which encourages predictability and common knowledge, and therefore may reduce the signalling effort required to achieve coordination [79]. When feeding and travelling, combined signalling production was not clearly biased towards partners with an intermediate relationship strength. Given a greater coordination challenge in these contexts relative to resting, individuals may increase combined signalling even towards socially close individuals to sustain coordination and maintain existing bonds. Further, considering the common need for group-level coordination, individuals may also show less discrimination in their motivation to coordinate with other group members, extending a motivation to coordinate with socially distant partners.

4.5. Study limitations and future directions

Using focal observational rather than focal or ad libitum video data of approaches allowed us to use a large sample to examine with precision variation in focal activity and party composition. However, this data collection approach limits the detail with which one can examine signal combinations and signalling complexity. We opted for conspicuous signal categories that could be reliably coded live, as demonstrated by good inter-rater reliability scores, as in [95]. Future studies may examine other aspects of signalling complexity (e.g. signal diversity, [47,141]). By contrast to our previous study [95], we could not specifically examine the production of multisensory signals, which may also improve message efficacy [44,46], because of a limited sample size of multisensory single signals. We focused on signals during approaches, which gives a clear dyadic context, but does not address signalling emitted at greater distances. Future research examining whether complex signals outside of approach contexts relate to increased coordination challenges would be valuable. Future research may focus on signalling events immediately before fissions, although the determination and existence of these contexts, such as the occurence of 'leave-takings', remain unclear in chimpanzees [142]. To assess these ideas more broadly, further cross-species studies will be relevant to examine whether combined signals lead to different receiver behaviour compared with single signals [45,48], and whether contexts with high coordination challenges involve a greater number of distinct signal utterances, especially signal combinations, as our data suggest (figure 3, and electronic supplementary material, figure S16). Ultimately, variation in coordination challenges may explain variation in repertoire size and communicative complexity across contexts and species, particularly in relation to signal combinations. Especially in chimpanzees, and less so in mangabeys, the cumulative number of distinct signal utterances appears higher for combined than single signals, more clearly during travelling than during feeding or resting (figure 3).

Accounting for possible variation in signalling or association patterns across the two chimpanzee groups, allowed us here to determine generalizable effects of coordination contexts and signalling patterns. Nevertheless, future research in these species could further examine possible group differences in signalling patterns, and social structure and dynamics [135,137,143]. Fission–fusion dynamics have evolved independently several times across taxa [34], and may be underpinned by different social and coordination processes, which probably vary in complexity (e.g. inter-party movements [55,61,144]), for example depending on the degree of differentiation in relationships [34]. Therefore, further comparative studies across a wider range of groups and species are needed to examine how the presence of differentiated relationships combined with varying levels of fission–fusion dynamics may promote complex signalling.

5. Conclusions and study implications

Previous research has suggested that signalling probability (comparing any signal with no signal) may facilitate the coordination or collective behaviour of group members [6,12,20,66] and the maintenance of social bonds [24,54,59,97]. Further, pressures on coordination and cooperation may increase communication complexity within and across species [20,21,26,28,29,37,52,145], referred to as the behavioural coordination hypothesis for the evolution of communication [39]. A previous study in bonobos suggested that a key facet of complex communication, specifically the use of combined signals may be advantageous when coordination challenges increase between partners. However, deducing general patterns of combinatorial signal use from this study was not possible as it assessed a single social context (i.e. prior to fusions) and two related call combinations [55,56]. In addition, previous studies have suggested that signalling may be particularly valuable when individuals gain from maintaining coordination with specific group members and, furthermore, in societies with a highly unpredictable social environment [33,34,60,62,66]. Forming and maintaining differentiated relationships allows for social support which helps stress reduction [22,63] and provides fitness benefits [4,5], but may represent a critical challenge in species with highly variable social environments [55,56,58–61]. As a result, high-level fission–fusion dynamics creating unpredictability in partner availability [32], combined with differentiated relationships, are thought to increase the levels of social and communicative complexity within [94,97] and across species [34], although this hypothesis has not previously been directly tested.

In support of both hypotheses, we provide strong evidence that, within species, combined signals are more likely to be emitted in contexts that pose coordination challenges—travel rather than feed or rest. Between species, these effects were evident in chimpanzees, the species displaying strong fission–fusion dynamics, but not in mangabeys. In chimpanzees, coordination challenges were more influential in predicting combined signalling than relationship strength, with the latter being influential only during resting in both species. Also, combined and socio-positive signal production during approaches prolonged spatial coordination in chimpanzees, measured by dyadic association duration.

Developing robust empirical tests of theories relating to the evolution of complex signalling has proved challenging. Here, we demonstrate that combining within- and between-species analyses, which provide two independent axes of assessment, yields robust results. Critically, here we compare social contexts in which complex signals are produced [36,44,146], such as those with high coordination challenges [54–56,81], with contexts in which they are not produced, both within and between species [37,95,147]. This increases our understanding of the function and evolution of signalling complexity across species. Selection pressures that apply to most parts of daily life, rather than a single or narrow aspect of daily life, are likely to exert a greater impact on traits, here signalling complexity. For example, species that face not only coordination challenges but also social uncertainty, which is also demonstrated to promote combinatorial signalling [94,95], are likely to experience stronger selection pressure to express combinatorial signalling across contexts throughout daily life. Our findings offer compelling support for the hypothesis that high degrees of fission–fusion dynamics, combined with a variety of daily activities that benefit from coordination—and cooperation—with other group members, may have both contributed to the selection for expanded communication skills in the hominid lineage [21,34,98,148,149].

Ethics. Data collection protocol was observational and non-invasive, approved by the 'Ethikrat der Max-Planck-Gesellschaft', allowed by the 'Ministère de l'Enseignement supérieur', and from the 'Recherche scientifique' and 'Eaux et Forêts', and from the 'Office Ivoirien des Parcs et Réserves', in Ivory Coast.

Data accessibility. Data and Rcode are provided on Figshare [150].

Supplementary material is available online [151].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. M.G.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; C.G.-B.: conceptualization, methodology, writing—review and editing; L.S.: conceptualization, data curation, methodology, writing—review and editing; P.J.T.: conceptualization, data curation, methodology, supervision, writing—review and editing; R.M.W.: conceptualization, funding acquisition, methodology, project administration, resources, supervision, writing—review and editing; C.C.: conceptualization, funding acquisition, methodology, project administration, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This study was funded by the Hominoid Brain Connectomics Project through the Max Planck Society (M.IF.NEPF8103 and M.IF.EVAN8103) and European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme awarded to C.C. (grant agreement no. 679787).

Acknowledgements. We thank the Ministère de l'Enseignement supérieur et de la Recherche scientifique; des Eaux et Forêts en Côte d'Ivoire and the Office Ivoirien des Parcs et Réserves for allowing the study. We are grateful to the Centre Suisse de Recherches Scientifiques en Côte d'Ivoire for their support. We are indebted to the efforts of the late Christophe Boesch in the establishment and nurturing of the field site, and in aiding the survival of the western chimpanzee. We thank the staff, assistants and students from TCP, particularly A. Bründl, T. Bortolato, A. Le Floch, S. Kanieu, C. Kaye, K. Kolff and R. Sigmundson for their great help. We thank Dr. C. Hobaiter and Dr. L. Gygax for their guidance.

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