Exploring greetings and leave-takings: communication during arrivals and departures by chimpanzees of the Bossou community, Guinea

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Introduction

In species with fission-fusion social systems, over the course of a typical day an individual will leave and re-join others multiple times. The individuals they fission from or fuse together with vary, but across these interactions there remains a coherent community or social group. These social dynamics sound familiar because humans are a fission-fusion species. We often disperse from our living partners in the morning and re-join them later. In the meantime, we meet other people from within and outside of our different social groups. These comings and goings are often accompanied by ritualised communications – greetings and leave-takings – that play an important role in validating access to and managing continuity in social relationships (Goffman 1967). These rituals vary in form according to particular features of the people we meet and our relationship with them, such as: their familiarity, age, gender, social status, etc. as well with some contextual features such as the individual's role: indicating who is traveling and who remains, the length of time elapsed since the previous encounter, the distance between interactants, and the number of individuals present (Youssouf et al. 1976; Ferguson 1976; Morita 2011). Despite rich cultural variation in the form of these rituals across humans as a species, they often share common elements, especially in the form of non-linguistic signals. The use of greetings and leave-takings in the appropriate context seems to be a human universal, likely evolutionary ancient in humankind (Firth 1972).

Could greeting and leave-taking behaviour be evolutionary older and precede the emergence of the linguistic communication that characterizes our human lineage? Or be a widespread feature of highly-social fission-fusion animal species? To investigate these questions, we must look outside of the human species and explore patterns of similarity and distinction in the communication that occurs during fission and fusion events in other species, in particular primates. Many social species produce signals when approaching other individuals from within their social group (Sogabe and Yanagisawa 2007; Smith et al. 2011; Whitehead and Rendell 2014). In primates, signals produced when approaching or being approached by others in the same party (e.g., Smuts and Watanabe 1990; Fedurek et al. 2019) or when joining a party have been widely reported in various modalities (e.g., Aureli and Schaffner 2007; Scheumann et al. 2017). For example, some species use tactile signals such as “embraces” to reduce tension (spider monkeys: Aureli and Schaffner 2007), and vocal “greeting calls” are produced by many primate species when meeting (Cheney and Seyfarth 1992; Scheumann et al. 2017; Fedurek et al. 2019). Primates also combine signals of different modalities during encounters (Alfaro 2008; Luef and Pika 2019). For example, baboons use multi-modal combinations that include visual signals (such as facial expressions, e.g., ear-flattening, and gestures, e.g., crouching), audible signals (e.g., grunt vocalizations), and tactile signals that include contact with vulnerable body parts (e.g., genital touching; Smuts and Watanabe 1990; Whitham and Maestripieri 2003).

A number of studies have explored ‘greetings’ in one of our closest living relatives: chimpanzees (Laporte and Zuberbühler 2010; Luef and Pika 2017; Fedurek et al. 2021). Chimpanzees (*Pan troglodytes*) are highly social, living in large stable communities within which smaller parties and individuals interact with highly-fluid fission-fusion dynamics (Nishida 1968; Goodall 1986). They live in philopatric societies with a relatively strong hierarchy in which mature males typically outrank mature females (Goodall 1986; Newton-Fisher 2004). Chimpanzees form long-term alliances with both kin and non-kin group members, and these relationships have an important impact on individual fitness (Pusey et al. 1997; Wroblewski et al. 2009; Gilby et al. 2013). In these highly dynamic societies, individuals may not see others from within their social group for days, or even months. During time apart, interactions with and between others may have impacted relative rank or the strength of a social bond (Laporte and Zuberbühler 2010). Greetings offer the opportunity to clearly signal dyadic rank-relationships or social bonds after a separation, both within the dyad and to others in the vicinity (Luef and Pika 2019), and without the need for more costly strategies such as physical aggression (McGrew and Baehren 2016; Fedurek et al. 2021).

During chimpanzee fusion events, the most frequently observed and widely studied communicative behaviour is the *pant-grunt* vocalization, which varies along a gradient that includes *pants* up to *pant-barks,* and, occasionally, is combined into *pant-hoots* (Goodall 1986; Crockford and Boesch 2005; Laporte and Zuberbühler 2010; Fedurek et al. 2021). Pant-grunts are typically associated with showing subordination by a lower-ranking individual towards a higher-ranking individual (Bygott 1979; Laporte and Zuberbühler 2010). Between males their use is largely dictated by the dyadic relationship of the two individuals approaching each other (Fedurek et al. 2019); and changes in the direction of their use between mature males are used as a behavioural indication of changes in social relationship or rank (Newton-Fisher 2004; Neumann et al. 2011). However, particularly outside of male-male interactions, pant-grunts can be used more flexibly, and their production also depends on the size and composition of the audience (Laporte and Zuberbühler 2010). Reciprocal exchange of greetings within a dyad may include pants and pant-grunts, as well as other signals and behaviour, depending on the nature and strength of the social relationship or the presence of others near-by (Luef and Pika 2017, 2019).

Pant-grunts (like many signals) have typically been studied in isolation; however, chimpanzees, like humans and many other species (Acquistapace et al. 2011; Grafe et al. 2012; Genty 2019), exchange a wide variety of vocal, gestural, and other signals in their greetings. The use of gestures by chimpanzees when greeting is less well studied, but includes: *bobbing*, *crouching*, and *presenting* (De Waal 2007), or *nibble cheek*, *nibble ear*, and *embrace*, among others (see Luef and Pika 2017). Greetings incorporating gestures are more likely to elicit responses than vocal-only greetings (Luef and Pika 2017), but the impact of individual and socio-ecological features on the use of gestures and signal combinations during greetings remains unclear.

While the occurrence and importance of greetings across primate species is well established, there is no similar body of work on leave-taking outside of humans (McGrew and Baehren 2016). Even in the very well-studied chimpanzee, there are only anecdotal descriptions (De Waal 2016). A recent survey of researchers across 10 chimpanzee field-sites on the occurrence of any leave-taking behaviour preceding a fission concluded it was likely absent (McGrew and Baehren 2016; but cf Heesen et al. 2021). Given the ease with which greetings are detected in social species, the apparent absence of leave-taking outside of humans appears to represent a striking divergence. If leave-taking is absent outside of humans, it suggests that there was selection for this type of signalling in humans. A number of potential functions for leave-taking in humans have been suggested (for example: signalling inaccessibility, supportiveness, or summarising recent interaction; Knapp et al. 1973). Alternatively, the ability to take-leave may depend on other cognitive capacities, such as the ability to imagine (Saito et al. 2014) or plan for future interactions and events (Suddendorf and Corballis 2010), which may be specific to humans (but cf Janmaat et al. 2014). Nevertheless, without systematic exploration, their presence, or absence, in other primate species remains unclear.

A particular problem in studying both potential leave-taking and greeting in non-human species is in differentiating these from other communications produced in proximity to a fission or fusion event, for example: a failed solicitation to travel together prior to departure, or a request to groom on arrival. A recent study of chimpanzee and bonobo interactions described the use of signals in an 'exit phase', arguing that here both partners are signalling the mutual intention to stop the interaction, and compare this to taking leave (Heesen et al. 2021). The use of imperative requests to 'Stop behaviour' have been previously described in great ape gesturing (e.g. Genty et al. 2009; Hobaiter and Byrne 2014); but requests to terminate a specific behaviour followed by one individual leaving are not necessarily leave-taking, in the same way that requests to initiate a behaviour on arrival are not necessarily greeting. While context has been used as a proxy for meaning in many studies of non-human communication (Call and Tomasello 2007; Pollick and de Waal 2007), context and meaning do not necessarily map. A negation gesture that means 'Stop that' can be used across many behavioural contexts, but its meaning is highly specific (Hobaiter and Byrne 2014). The pant-grunt vocalizations that are frequently a focus in studies of chimpanzee 'greeting' are also used to signal submission towards higher-ranking individuals even where the signaller and recipient have been in the same party for an extended period (Laporte and Zuberbühler 2010; Fedurek et al. 2019), but potential greetings include the exchange of a wide-range of signals outside of those associated with dominance and submission (e.g. Luef and Pika 2017). One approach to differentiating signals that function as greetings or leave-taking from within the signals that are produced in the context of arrival or departure is to compare communication in these cases to that produced across other contexts. A large body of evidence for signals that appear specific to meeting or leaving other individuals would provide a stronger case for the presence of greetings or leave-taking within these contexts.

In this study we explore the apparent behavioural asymmetry related to potential greeting and leave-taking behaviour in chimpanzees. We take a systematic multimodal approach and describe the frequency and form of signals produced when fissioning from or fusing with other individuals, given the number of opportunities to do so. We then investigate how individual, dyadic, and group-level features shape communication during these events.

At the individual level we examined how social rank, level of threat, and relative position (as traveller or party member) influence the likelihood of communication occurring at a fission or fusion event. Emotional arousal has been argued to represent an underlying cause for the production of 'greeting' calls (Goodall 1986; Luef and Pika 2019; Fedurek et al. 2021), and we predicted communication would be more likely to occur when the level of potential threat of physical aggression is high. Previous studies on *pant-grunts* suggest that low ranking individuals are more likely to greet than higher ranking individuals, possibly to reduce the likelihood of receiving aggression when approaching others (Laporte and Zuberbühler 2010; Fedurek et al. 2019). As well as producing a higher number of calls, low-ranking individuals produce more complex calls in the presence of high-ranking individuals, possibly related to high levels of excitement and to the increasing chances of receiving aggression when a call is not produced (Luef and Pika 2019; Fedurek et al. 2021). As a result, low-ranking individuals may be more likely to communicate and may do so more often in events with a higher level of potential physical risk (threat). We further investigated the impact of the individual's relative position to the party (as traveller or party-member) on the probability of communication. In addition to signalling the nature of the relationship, greeting and leave-taking rituals may function to inform partners and the wider audience about an individual's decision to travel. Once the decision to travel is made, both the traveller and the party-member may communicate; however, the party-member may only become aware of the traveller's decision to travel after some behavioural indication of traveling, and for that reason, we predicted that travellers may be more likely to communicate.

At the dyadic level we looked at whether communication during a fission or fusion event was mediated by kinship. Kinship appears to influence cooperation and affiliation rates among wild chimpanzees (Gilby and Wrangham 2008; Langergraber et al. 2009). However, to our knowledge, the impact of kinship on communication during fission-fusion events has not been directly explored. Previous research shows that greetings are less likely to occur and are less elaborate between closely affiliated dyads (Luef and Pika 2019). Building on these findings, we predicted that kin-related individuals would be less likely to communicate. We further investigated if communication varied with the relative difference in social rank of the two individuals. *Pant-grunts* and vocal combinations are most often given by low-ranking individuals towards high-ranking individuals (Fedurek et al. 2019; Luef and Pika 2019). As greeting calls are often associated with visual signals linked to submission (Fedurek et al. 2021), we predicted that communication would be more likely to occur from lower-ranking individuals towards higher-ranking individuals.

At the group level, we examined the influence of the composition of the audience on the probability of communication occurring. Specifically, we investigated whether communication depended whether mature males were present, and on the total party size. The presence of the alpha male and an increasing number of bystanders, in particular mature males, appears to have an inhibitory effect on the probability of females producing *pant-grunts* (Laporte and Zuberbühler 2010). As a result, we predicted that communication would be less likely to occur in the presence of mature males and in larger parties.

Finally, we describe the types of signals produced, and explored the impact of social relationship on the channel of communication used (gestural, vocal, facial, multi-channel).

To summarize, the goal of our study was to understand how social features influence the probability of communication occurring and the types of signals used during fission or fusion events. For this purpose, we studied the opportunities to communicate during fissions and fusions and analysed the influence of social factors at different levels (individual, dyadic and group level).

Material and Methods

Study site and subjects

The dataset contains data from 22 wild chimpanzees (12 females and 10 males) during three field seasons (1993-1994, 2003-2004, and 2013-2014) at the long-term field site of Bossou, Guinea (7°39′N, 8°30′W). The Bossou chimpanzee community (*P.t. verus*) is quite unusual as chimpanzees are both habituated to humans and coexist both closely and largely peacefully alongside local human communities (Sugiyama and Koman

1979; Matsuzawa et al. 2011). We evaluated the scope for sampling bias in our study using the STRANGE framework (Webster and Rutz 2020; Rutz and Webster 2021). The community size ranged from 9-18 individuals, which is relatively small. Chimpanzee communities are more typically around 30-70 individuals (ranging from 7-144 with a median 42 in a recent comparison across 18 groups in three subspecies: *P.t.schweinfurthii, P.t.troglodytes, P.t.verus*; Wilson et al., 2014; although note that within these data the West African sub-species (*P.t.verus*) range is 7-43 with a median 34). Aspects of chimpanzee behaviour at any one time may be impacted by individual differences (for example, the identity of the alpha-male, the presence of particular kin and non-kin relationships, the group demography). The impact of individual differences may be particularly strong in Bossou, where, for example, there were only ever a maximum of three adult males. As a result, it may be challenging to disentangle the effects of age-class and rank. Similarly, the effects of kinship and social-bonding may be difficult to discriminate in Bossou, as there are very limited numbers of dyadic relationships, and smaller communities of chimpanzees and communities of the West African subspecies appear to be generally more cohesive (Lehmann and Boesch 2004). We addressed these biases in part by including data from three different periods (at 10-year intervals), allowing us to increase the number of individuals present in the data and the diversity of other socio-demographic factors.

In the first period (1993-1994), the community consisted of 18 individuals: 8 adults (males: 16+ years, females: 15+ years), 1 subadult (males: 10 to 15 years, females: 10 to 14 years), 3 juveniles (5 to 9 years), and 6 infants (0 to 4 years). In subsequent years, the overall community size decreased (n=15 in 2003-2004, and n=9 in 2013-2014) as individuals disappeared (including probable emigrations) or died, and no immigration occurred (see Table 1). Our data were highly representative of the Bossou community over the 20-year time period, including 22 of the 25 individuals present (Table 1).

Table 1 Characteristics of the study subjects, including ID, sex, age and rank during the three periods analysed in the current study. * subject was present in the community but did not contribute data (no observations available or age < 1 year)

ID	Sex	1993-1994		2003-2004		2013-2014	
		Age	**Rank**	**Age**	**Rank**	**Age**	**Rank**
Tua	M	43	Alpha	53	Gama	-	-
Kai	F	43	Alpha female	-	-	-	-
Nina	F	39	High-ranking F	-	-	-	-
Na	M	8	Immature – 1	-	-	-	-
Nto	F	0	Immature – 2*	-	-	-	-
Fana	F	37	High-ranking F	47	High-ranking F	57	High-ranking F
Foaf	M	13	Beta	23	Beta	33	Beta
Fotaiu	F	2	Immature – 2	12	Low-ranking F	-	-
Fanle	F	-	-	6	Immature – 1	16	Low-ranking F
Fokaiye	M	-	-	2	Immature – 2	-	-
Flanle	M	-	-	-	-	6	Immature – 1
Fanwa	M	-	-	-	-	2	Immature – 2
Jire	F	35	High-ranking F	45	High-ranking F	55	Alpha female
Juru	F	0	Immature – 2*	-	-	-	-
Jeje	M	-	-	6	Immature – 1	16	Alpha
Velu	F	34	High-ranking F	44	High-ranking F	54	High-ranking F
Vui	M	7	Immature – 1	-	-	-	-
Vuavua	F	2	Immature – 2	12	Low-ranking F	-	-
Veve	F	-	-	2	Immature – 2	-	-
Yo	F	32	High-ranking F	42	Alpha female	52	High-ranking F
Yolo	M	2	Immature –2	12	Alpha	-	-
Pama	F	26	High-ranking F	36	High-ranking F	46	-
Pili	F	6	Immature – 1	-	-	-	-
Poni	M	0	Immature – 2*	-	-	-	-
Peley	M	-	-	5	Immature – 1	15	-

Video data in the Bossou Archive were collected at two natural outdoor 'laboratories' that were originally established in the Bossou chimpanzee home-range to study their tool use: 'Bureau' located on the top of Mont Gban in the first two periods:

1993-1994 and 2003-2004; and 'Salon' located in the middle of Mont Ghein in the last period of data collection: 2013-2014 (Fig 1; Matsuzawa 1994, 2011; Biro et al. 2003). By crossing the roads between the two forests (Hockings et al. 2007), both sites were regularly used by the chimpanzees for cracking palm-nuts with stone tools. During the dry season the quantity of palm-nuts and water available in the outdoor laboratories were controlled by the research team (Inoue-Nakamura and Matsuzawa 1997; Sousa et al. 2009; Hayashi and Inoue-Nakamura 2011), so all data collection occurred during periods in which food resources were consistently available. The presence of a specific food resource, even where reliably available, may lead to increased arousal (Muller and Wrangham 2004; Kalan et al. 2015), which in turn may impact the way in which communication is expressed. However, high-pitched food-calls were rarely observed upon arrival to the outdoor laboratories, in contrasts to the chimpanzees' arrival at a high-value food resource, such as a large fruiting tree (Hayashi, personal communication). Moreover, nuts, which requires additional cracking skill, appear less preferred when fruit is available nearby. Consumption of nuts increases in dry season, which has lower fruit availability (Yamakoshi 1998), but some fruits remain available year round, and chimpanzees also crop-raid in the village for high calorie cultivars when other food resources are limited (Hockings et al. 2009). Competition between individuals may also be mitigated by individual preferences for particular tools (Carvalho et al. 2009), as well as the reliable availability of nuts (Inoue-Nakamura and Matsuzawa 1997). The Bossou chimpanzees spend extended periods of time at these locations, typically visiting once or more per day, and spending over a total of 20-30 hours each year (within the natural nut season, which lasts ~1-3 months; Biro et al. 2006; Sousa et al. 2009). As a result, in addition to tool using, the videos in the Bossou

Archive contain abundant data on the community's social interactions (e.g. Schofield et al. 2019). The area is flat and clear, so filming conditions are ideal, allowing continuous recording of all individuals arriving and leaving the party, their interactions, and the communicative signals produced.

Fig.1 A group of chimpanzees feeding in the outdoor laboratory, 'Salon' (photograph by Catherine Hobaiter)

Data coding

Data were coded into a bespoke Filemaker Pro database, which was set up so that each opportunity to communicate corresponded to a record (for full details on the variables coded see Online resources 1). We coded data on interactions that occurred immediately before a fission event (the last interaction before someone left the party) or after a fusion event (the first interaction after someone joined the party) between any two individuals. Where two individuals left the party (fission events) with less than 5min between their individual departures and traveling in the same direction, we considered them to be potentially travelling together (joint-travel) and distinguished these from other fusion events. Similarly, where two individuals joined the party by arriving from the same direction with less than 5min between their fusion events, we considered them to be in a potential joint-travel.

All interactions that occurred immediately before a fission event were considered potential leave-takings, and those that occurred immediately after a fusion event were considered potential greetings. A signal's meaning or function (for example: as a greeting) does not necessarily map onto the context in which it is used (for example: on arrival). It is possible to produce communication in both arrival and departure contexts that are not greetings or leave-takings, for example: a failed request to ‘travel together’ immediately before fissioning would be difficult to distinguish from a leave-taking communication, and a request to ‘groom me’ immediately after arrival is not necessarily a greeting. As a result, we label the communication produced in these two contexts as *potential* greetings, and *potential* leave-takings. We compare the most common signals produced during each of these events to those produced in other contexts (for example: traveling, grooming, affiliation etc.) to determine whether we could identify signals specific to a fission or fusion context.

In addition to recording the communications that occurred, we assessed the opportunities to communicate for each fission and fusion. For example: in a fusion event where a single individual arrives to join a group (traveller) of three others (party-members) there are three potential opportunities for that individual to produce a potential greeting communication. We investigated each dyadic interaction from the perspective of the traveller as the focal, and from the perspective of the party-member as the focal. Within 393 video clips (28 days of observations across the 3 different periods) we recorded 253 fission and 215 fusion events (Table 2).

Table 2. Data available for analysis in each period of data collection: number of Clips, number of Days, Duration of video footage (in minutes), number of Fission events, number of Fusion events, and number of Opportunities to communicate during Fission and Fusion events.

Period	**# Clips**	**# Days**	**Duration** (min)	**Fissions**	**Fusions**	**Opp. in Fissions**	**Opp. in Fusions**
1993-1994	34	6	359	47	36	344	270
6am-10am	9	3	118	18	12	122	76
10am-2pm	22	5	153	19	15	116	118
2pm-6pm	5	3	88	10	9	106	76
2003-2004	147	11	1471	137	115	1064	934
6am-10am	59	8	551	68	61	432	486
10am-2pm	29	6	363	51	31	318	300
2pm-6pm	60	7	531	18	23	314	148

2013-2014	210	11	722	69	64	354	334
6am-10am	82	6	203	14	7	66	32
10am-2pm	57	5	219	36	33	114	190
2pm-6pm	72	6	300	19	24	172	112

Individual, Dyadic, and Group features

For each individual, we recorded their individual identity, relative position (traveller or party-member), the level of potential threat experienced, and social rank. Following Laporte and Zuberbühler (2010), we used the behavioural context prior to the interaction as a proxy for the level of potential threat interactions in that behavioural context typically represent, and grouped these into three categories. Low threat-level contexts: affiliation, grooming, social play; Neutral threat-level contexts: no visible social interaction such as feeding, resting, travelling, solitary play, moving in the trees, moving up/ down trees; and High threat-level contexts: agonism, display, displace or sexual contexts. Social ranks are typically classified using pant-grunt vocalizations (e.g., Newton-Fisher 2004; Fedurek et al. 2021); however, doing so here, where we explore the impact of social rank on the use of signals that include pant-grunts, would be circular. Instead, rank was classified by an experienced observer of these chimpanzees for each period, based on a suite of behaviour that included displacements and agonistic interactions as well as rank. While the assessment of rank in this way can be challenging in a typical-sized community, there were never more than three adult male chimpanzees, and adult female social rank is typically stable across the lifetime (Foerster et al. 2016). Male chimpanzees were classified as having a social rank of: Alpha, Beta, or Gamma on the basis of age and social interactions (such as *pant-grunts*). All mature male chimpanzees were considered to rank above all mature female chimpanzees. Mature female chimpanzees were categorised as having a social rank of: Alpha female, High-ranking (all other adult females), or Low-ranking (all subadult females). The distinction between Alpha female and High-ranking female was made on the basis of behavioural interactions, for example displacement at preferred feeding and nut cracking sites. All mature females were considered to rank above all immature individuals. We included all juveniles (male and female) in the social-rank category Immature-juvenile, and all infants (male and female) in the social-rank category Immature-infant. Individual rank was assigned per period, and the ranks were then scaled between 0-1 with Immature-infant individuals at the bottom of the scale (0) and Alpha male at the top of the scale (1).

For each dyad we considered kinship and rank relationships. Within kinship, only maternal bonds were considered so mother-infant, maternal-grandmother-infant, and maternal-sibling relationships were labelled as Kin, and all others as non-Kin. Data on the independence status of immature individuals were not available, thus mother-infant relationships include all mother-offspring pairs. Using the social rank categories described above, we then classed the focal individual as having one of: lower, same, or higher rank as their partner in the dyad. Finally, we recorded the group-size (number of individuals in the party) and the presence of males in the party (present, absent).

Signals

For each opportunity to communicate, we recorded whether any communicative signal was produced by the focal (yes, no). Where signals were produced, we distinguished gestures, vocalizations, facial expressions, and combinations of two or more of these channels (multi-channel). Gestures were defined (following Hobaiter and Byrne 2011) as a "discrete, mechanically ineffective physical movements of the body observed during periods of intentional communication" by the focal. These movements included movements of the whole body, limbs, and head, but not facial expressions or static body postures. In order to be considered a gesture, one of the following criteria for intentionality had to be observed in conjunction with the gesture: audience checking (the signaller shows signs of being visually aware of the potential recipients and their state of attention), response waiting (the signaller pauses at the end of the communication and maintains some visual contact) or, persistence or elaboration (the production of further gestures, after response waiting and in the absence of a response that in other cases is taken as satisfactory). Gestures were based on the classification used in Hobaiter and Byrne (2017) and contained a total of 93 types (see Online resources 2 for a full repertoire). The chimpanzee gestural repertoire includes gestures with only visual information (for example an arm-raise) and which are limited by lines of sight between the signaller and recipient; gestures that include tactile information, for which the signaller must be within reach of the recipient; and gestures that include auditory information – including signals that can be detected by out-of-sight individuals over medium distances (e.g. up to 100m; Hobaiter and Byrne 2012) and in the case of drumming at over a kilometre (Arcadi et al. 1998). Vocalizations were single (single element or a series of elements of the same call type) or combined calls (series of elements of different call types) emitted by the focal. Vocalizations all include both visual and acoustic information, and the chimpanzee repertoire varies from extremely soft calls such as pants and hoots (Crockford et al. 2018), to, again, those that can travel over a kilometre (Arcadi et al. 1998). Facial Expressions were recorded when focal produced a visual-silent signal facial display, and transmission of these are limited by lines of sight between the signaller and recipient. As movements of the face often occur along with vocalizations, in order to be considered as a facial expression they needed to be independent of any recent vocalization (at least 2 seconds separation). We included 12 vocalizations (adapted from Crockford and Boesch 2005) and 9 facial expressions (adapted from Parr et al. 2005) in the communicative repertoire (see Online resource 2 for repertoires). There is substantial grading across the categories in any vocal repertoire, so we followed previous literature in employing a broad definition of pant-grunts as pants with a voiced element, which includes acoustic variants that range from noisy pants to pant-barks.

Data reliability

Gestures, unlike vocal signals, show overlap in their physical form with non-communicative actions and non-intentional cues, and are discriminated by accompanying indications of their intentional use. In particular, we followed previous work in distinguishing the frequently used gesture type – Big Loud Scratch – from non-communicative scratches (scratching for hygiene or as a result of arousal; Goodall, 1968; Plooij, 1978; Pika and Mitani, 2009; Hobaiter and Byrne, 2011). We excluded all scratches that were small and/or rapid in movement (as being potentially associated with stress or displacement activity), or followed by any self-directed hygiene behaviour. We only considered scratches produced in an exaggerated manner (here a long, slow movement, with a clearly audible component) and that were accompanied by additional behavioural indications of intentional use: audience checking, response waiting, and/or persistence. We carefully checked all Big Loud Scratch candidate gestures for indications of intentional use and applied a very strict assessment for audience checking that excluded cases where visual checking by the signaller was potentially peripheral (in doing so we excluded an additional n = 12 potential Big Loud Scratch gestures).

We conducted inter-observer reliability between the primary coder (EDR) and another experienced coder (CH) on 5% of the dataset (142 opportunities to communicate within 23 events). Inter-observer reliability was conducted on the three core variables 1) whether a communication had occurred, 2) where there was communication which channel it was in, gestural, vocal, or combination, and 3) the signal types recorded in a communication. A good level of agreement was achieved on all three variables (Cohen's Kappa: communication K= 0.78, channel K=0.75, signal type K=0.71.

Statistical analysis

All models were implemented with R v4.0.2 (R Development Core Team & R Core Team, 2020) using the packages 'brms' and 'rstan' (Bürkner 2017; Stan Development Team 2020). The package 'brms' allows users to fit Bayesian generalized multivariate multilevel models using Stan. The package 'rstan' provides R functions to parse, compile test, estimate, and analyse Stan models. In all our analyses, one data point represented an opportunity for an individual to communicate within a dyad made up of the traveller (the individual fissioning from or fusing with the party) and the party-member. Each dyad was considered twice, once from the perspective of the traveller (and their opportunity to communicate) and once from the perspective of the party-member (and their opportunity to communicate). Before fitting models, we rescaled each numeric input to have mean of 0 and standard deviation of 1 to have comparable estimated coefficients (Schielzeth 2010). Multicollinearity between variables was assessed by Variance Inflation Factors (Field et al. 2012) using the R package 'car' (Fox and Weisberg 2019). We used weakly informative Cauchy-distributed priors on all logistic regression coefficients, each centred at 0 and with scale parameter 10 for the intercept and 2.5 for all other coefficients (Gelman et al. 2008). Posterior estimates were generated using the Hamiltonian Monte Carlo algorithm. We used 3000 iterations for two chains in the first two models and 7000 iterations for two chains in the third model. Chain convergence and influential cases were assessed by visual inspection of traceplots and Pareto Smoothed Importance Sampling plots (PSIS) respectively (Vehtari et al. 2019; McElreath 2020). For all models, we present the 95% credible interval.

Model 1: How does communication vary between fission and fusion events?

We tested whether individuals were more likely to communicate during fission or fusion events. To do so, we examined the influence of the type of event (fission or fusion) and whether or not these were associated with joint-travel on the likelihood of communication. From the 468 events and 3302 opportunities to communicate that were coded, we excluded from analysis opportunities in which we could not determine from the videos whether or not communication occurred due to limited visibility (1 fusion event and 105 opportunities to communicate). We included 467 fission or fusion events comprising 3197 opportunities to communicate (1749 during fissions and 1448 during fusions) were included for analysis. We fitted a Bayesian generalized linear multilevel model with a binomial response variable (communication occurred = yes or no). Where individuals fissioned or fused within 5 min of each other and travelled to/from the same direction they were marked as a possible joint-travel. Test predictors in this model included type of event (fission or fusion), possibility of joint travel (yes or no), and the interaction between both. We controlled for the period (1: 1993-1994, 2: 2003-2004, 3: 2013-2014) and for individual, dyadic, and group features. Individual features comprised focal position (traveller, party-member), focal rank (z-transformed), and level of threat experienced (low, neutral, high); dyadic features included kinship (kin, non-kin), and rank relationship (rank of the focal as: higher than, equal to, or lower than the partner); and group features included group size (z-transformed), and presence of males (yes, no). As random factors we included the identity of the focal, the identity of the partner, and the event number (given there was variation in the number of opportunities to communicate per event). We included a maximal random slope structure for the test predictors.

Model 2: Which social features affect the probability of communicating during fission and fusion events?

We were interested in understanding how social features impacted the probability of communication when individuals joined or left their conspecifics (fusion and fission events respectively) without being involved in any possible joint-travel. Excluding any events that might have been joint travels left a total of 202 fission or fusion events and 1221 opportunities to communicate. We again fitted a Bayesian generalized linear multilevel model with a binomial response variable (communication occurred = yes or no). As fixed effects we included the type of event (fission or fusion) and the social features: focal position, focal rank, level of threat experienced by the focal, kinship, rank relationship, presence of males, and group size. Because social features could have different impacts on potential greetings and leave-takings, we included the interaction between these features and the type of event. As random factors we included the identity of the focal, the identity of the partner, and the event number. Given the smaller dataset following the exclusion of possible joint-travels, we were unable to include a maximal random slope structure for the test predictors.

Model 3: What determines the channel of communication during fissions and fusions?

Individuals can communicate through gestures, vocalizations, facial expressions, or by combining these different channels of communication. Of the 221 communications in a fission or fusion event, we excluded 30 where we were not sure if signals in one or more channels occurred. We fitted a multinomial logistic regression, again using the 'brms' and 'rstan' packages, using each of the three signal channels plus their combination as a possible response (gestures, vocalizations, facial expressions, and multi-channel combinations). We tested if the type of event, level of threat experienced by the focal, kinship, and rank relationship influenced the channel chosen to communicate. We controlled for presence of males and group size as fixed effects. As a random effect we included the identity of the focal. Given the small sample size, we were unable to include a maximal random slope structure for the test predictors. We further restricted model complexity by excluding recipient and event number as random effects, as their inclusion increased the number of influential cases 50-fold. We interpret the outcome of this model with this limitation in mind.

Results

Communication occurred in 21% (n=54/253) of fission events and in 41% (n=88/215) of fusion events. Most events provided multiple opportunities to communicate, individuals communicated in 4% (n=75/1749) of opportunities during fissions, and in 11% (n=155/1448) of opportunities during fusions. Excluding possible joint travels, individuals communicated in 4% (n= 23/620) of opportunities during fissions and in 14% (n= 81/601) of opportunities during fusions.

Model 1: How does communication vary between fission and fusion events?

There was a main effect of the type of event (fission, fusion), and of apparently travelling together (joint-travel) on the likelihood of communication occurring (Table 3).

Table 3 Results for Model 1, testing when communication occurred across fissions and fusions taking into account possible joint travel. Factors in italics were controlled for. Posterior estimates and 95% credible interval for all fixed effects, and Odds Ratio for the estimates. Significant effects are reported in bold and control variables in italic.

	Estimate	Est.Error	Q5	Q95	Odds
Intercept	**-3.173**	**0.666**	**-4.517**	**-1.921**	**0.042**
Type of Event [Fission]	**0.825**	**0.574**	**-0.332**	**1.948**	**0.257**
Possibility of joint travel [Yes]	**0.825**	**0.574**	**-0.332**	**1.948**	**0.417**
Type of event* Possibility of joint travel	0.825	0.574	-0.332	1.948	2.282
Period [2]	*-0.309*	*0.415*	*-1.102*	*0.519*	*0.734*
Period [3]	*0.218*	*0.515*	*-0.749*	*1.263*	*1.243*
Level of threat [High]	*2.406*	*0.382*	*1.682*	*3.176*	*11.085*
Level of threat [Low]	*2.195*	*0.274*	*1.679*	*2.755*	*8.983*
Focal rank	*0.592*	*0.165*	*0.269*	*0.912*	*1.807*
Focal position [Traveller]	*0.320*	*0.208*	*-0.087*	*0.732*	*1.378*
Kinship [Kin]	*-0.215*	*0.300*	*-0.802*	*0.361*	*0.807*
Rank relation [Focal > Partner]	*-1.272*	*0.455*	*-2.164*	*-0.387*	*0.280*
Rank relation [Partner > Focal]	*0.078*	*0.432*	*-0.749*	*0.921*	*1.081*
Presence of males [Yes]	*-0.688*	*0.313*	*-1.310*	*-0.094*	*0.503*
Group size	*-0.947*	*0.188*	*-1.324*	*-0.593*	*0.388*

Individuals were less likely to communicate during fissions as compared to fusions (OR=0.257, Fig. 2a), and were less likely to communicate when apparently travelling together (OR=0.417, Fig. 2b). The full model explained a moderate portion of the variance in incidence of communication (R2=0.309).

Fig. 2 Impact of the type of event (a), and possibility of joint travel (b) on the likelihood of communication occurring in a fission or fusion event.

Model 2: Which social features affect the probability of communicating during fission-fusion events?

Several test predictors strongly influenced the probability of communication occurring during fission-fusion events (excluding potential joint-travels), but only low levels of threat had a differential impact on the likelihood of communication during fissions and fusions (Table 4). At low (but not neutral, or high) levels of threat individuals were 88% less likely to communicate in fissions as compared to fusions (OR=0.124, Fig. 3a). Focal rank impacted the likelihood of communication: one standard deviation increase in focal rank increased the odds of communicating during a fission-fusion event by a factor of 2.507 (Fig. 3b). There was weak evidence that kin-related individuals were less likely to communicate (OR=0.321, Fig. 3c). Communication was 88% less likely to occur towards lower ranking individuals (OR=0.120, Fig. 3d). Audience composition impacted the odds of communication: when males were present the odds of communication by the focal in a fission-fusion event decreased by 70% (OR=0.296, Fig. 3e); and one standard deviation increase in group size, decreased the odds of communication by the focal by 56% (OR=0.443, Fig. 3f). There was no evidence for the effect of focal position (as traveller or party member) on the likelihood of communication. The full model explained a moderate portion of the variance in incidence of communication (R2=0.397).

Table 4 Results for Model 2, testing which features affected the probability of communicating during fission or fusion events. Posterior estimates and 95% credible interval for all fixed effects, and Odds Ratio for the estimates. Significant effects are reported in bold and control variables in italic.

	Estimate	Est.Error	Q5	Q95	Odds
Intercept	**-4.296**	**1.049**	**-6.444**	**-2.344**	**0.014**
Period [2]	*0.644*	*0.686*	*-0.604*	*2.056*	*1.905*
Period [3]	*0.450*	*0.774*	*-0.984*	*2.046*	*1.568*
Type of Event [Fission]	0.952	1.020	-0.966	2.975	2.590
Level of threat [Low]	**3.794**	**0.545**	**2.813**	**4.940**	**44.450**
Level of threat [High]	**3.019**	**0.607**	**1.848**	**4.255**	**20.463**
Focal rank	**0.919**	**0.288**	**0.363**	**1.505**	**2.507**
Focal position [Traveller]	0.415	0.372	-0.313	1.143	1.515
Kinship [Kin]	**-1.137**	**0.597**	**-2.354**	**-0.017**	**0.321**
Rank relation [Partner>Focal]	0.733	0.705	-0.618	2.135	2.082
Rank relation [Focal>Partner]	**-2.121**	**0.806**	**-3.744**	**-0.576**	**0.120**
Presence of males [Yes]	**-1.219**	**0.528**	**-2.288**	**-0.190**	**0.296**
Group size	**-0.814**	**0.268**	**-1.39**	**-0.322**	**0.443**
Type of event * Level of threat [Low]	**-2.088**	**0.794**	**-3.716**	**-0.574**	**0.124**
Type of event * Level of threat [High]	-1.986	1.386	-5.025	0.469	0.137
Type of event * Focal rank	0.080	0.434	-0.766	0.956	1.084
Type of event * Focal position	-0.558	0.630	-1.770	0.667	0.573
Type of event * Kinship	-0.146	1.236	-2.965	2.047	0.864
Type of event * Rank relation [Partner > Focal]	**-1.633**	**0.915**	**-3.446**	**0.089**	**0.195**
Type of event * Rank relation [Focal > Partner]	-0.323	1.089	-2.509	1.757	0.724
Type of event * Presence of males	0.169	0.754	-1.303	1.647	1.184
Type of event * Group size	0.346	0.401	-0.446	1.121	1.414

Fig. 3 Impact of social features on the probability of communication in fission and fusion events. (a) levels of threat experienced during fission and fusion events, with neutral level of threat represented in grey, low level of threat represented in orange, and high level of threat represented in light blue, (b) z-transformed focal rank, (c) kinship, (d) rank relationship F=P

focal and partner have same rank; P>F: partner rank higher than focal; F>P: focal rank higher than partner, (e) presence of males, (f) and z-transformed party size.

Which signal types are used in fission or fusion events?

Within the 221 communications we recorded 383 signals: 102 signals (86 gestures, 13 vocalizations, 3 facial expressions) during 66 fissions, and 281 signals (178 gestures, 84 vocalizations, 19 facial expressions) during 153 fusions (see Online resource 2 for more detail). The most common signals produced during fissions were the *big loud scratch* gesture (n=36, 35%), followed by the *locomote: gallop* gesture (n=10, 10%), which together represented approximately half of the signals produced when an individual fissioned (Fig 4). The most common signals produced during fusions were the *pant-grunt* vocalization (n=51, 18%), followed by the *present-genitals backwards* gesture (n=25, 9%). Together with the *bipedal stance* gesture (n=15, 5%) and the *locomote: gallop* gesture (n=15, 5%), these 4 signals represent over 40% of the signals produced in fusions.

Fig. 4 The signal types used most often during fissions (on the left) and fusions (on the right). The number of occurrences and definitions for all signals can be found in the Online resource 2. Signal types are accompanied by BonoboBOT 1.0. illustrations kindly provided by Kirsty E. Graham

Which channels of communication are used in fission or fusion events?

We recorded 191 communications in which we were able to record the presence or absence of signals in all three channels of communication. Gesture-only communications occurred most often (in 110 events) and these were similarly distributed across fissions and fusions (46 during fissions and 54 during fusions). Vocalization-only communications occurred less often (in 36 events) and were less likely to occur during fissions than fusions (6 during fissions and 30 during fusions). Facial-expression-only communication only occurred once (during a fusion). Multi-channel communication occurred in 44 events and was recorded more often during fusions (10 during fissions and 34 during fusions).

Across all social features of the interaction we explored, gesture-only communication was observed more often than communication in other channels or multi-channel communication (≥58% of communications; Fig. 5), with the exception of situations involving high levels of threat, in which individuals employed gestural, vocal, and multi-channel communication to a similar extent (36%, 36%, and 29% respectively).

Fig. 5 Proportion of communications produced in each channel across different social features at the individual, dyadic, and group level. Green bars represent facial expression-only communications; blue represent gesture-only; orange represent vocal-only, and pink represent multi-channel combinations. Rank relationship is categorised as F=P focal and partner have same rank; P>F: partner rank higher than focal; F>P: focal rank higher than partner.

Model 3: What impacts the channel of communication in fission or fusion events?

We included the 191 instances of communication in which we were able to record the presence or absence of signals in all three channels of communication. The channel of communication varied according to the type of event, the relative rank relationship within the dyad, and the presence of males (Table 5). Gesture was the most commonly employed channel of communication, and individuals used gesture more often during fissions, as compared to fusions (OR=5.667, Fig. 6a). Lower ranking individuals were less likely to use gestures, as compared to individuals with similar ranks, towards higher-ranking individuals (OR=0.105, Fig. 6b). Individuals were more likely to combine signals of different channels when experiencing low levels of threat when compared to neutral levels of threat (OR=4.808: Fig. 6c). Finally, there was no evidence that kinship influenced the signal channel used.

Table 5 Results for Model 3, testing which features influenced the channel of communication during arrivals and departures. Posterior estimates and 95% credible interval for all fixed effects, and Odds Ratio for the estimates. The Vocal modality was set as the reference level. Significant effects are reported in bold and control variables in italic.

	Estimate	Est.Error	l-95% CI	u-95% CI	Odds
Modality: Facial Expression					
Intercept	-9.938	10.432	-38.410	1.047	<0.001
Type of Event [Fission]	-2.169	6.845	-19.977	4.280	0.114
Level of threat [Low]	3.640	7.363	-2.544	22.069	38.085
Level of threat [High]	-2.197	6.221	-18.043	4.612	0.111
Kinship [Kin]	-2.286	6.314	-17.502	3.939	0.102
Rank relation [Partner > Focal]	-8.189	10.236	-33.566	0.250	<0.001
Rank relation [Focal > Partner]	-4.885	9.351	-26.225	2.265	0.008
Presence of males [Yes]	*2.811*	*6.530*	*-3.201*	*21.007*	*16.62*
Group size	*0.245*	*1.441*	*-2.666*	*3.064*	*1.278*
Modality: Gesture					
Intercept	**3.460**	**1.272**	**1.171**	**6.184**	**31.808**
Type of Event [Fission]	**1.735**	**0.684**	**0.469**	**3.180**	**5.667**
Level of threat [Low]	0.695	0.569	-0.399	1.823	2.003
Level of threat [High]	-0.371	0.658	-1.684	0.896	0.690
Kinship [Kin]	-0.336	0.728	-1.771	1.099	0.715
Rank relation [Partner > Focal]	**-2.252**	**1.060**	**-4.601**	**-0.378**	**0.105**
Rank relation [Focal > Partner]	-0.038	1.082	-2.343	1.986	0.963
Presence of males [Yes]	*-1.560*	*0.645*	*-2.894*	*-0.351*	*0.210*
Group size	*0.155*	*0.257*	*-0.348*	*0.659*	*1.168*
Modality: Multichannel					
Intercept	0.629	1.308	-1.865	3.363	1.876
Type of Event [Fission]	-0.038	0.804	-1.619	1.540	0.962
Level of threat [Low]	**1.570**	**0.649**	**0.354**	**2.885**	**4.808**
Level of threat [High]	0.572	0.72	-0.828	1.998	1.772
Kinship [Kin]	-0.374	0.764	-1.919	1.084	0.688
Rank relation [Partner > Focal]	-1.014	1.052	-3.288	0.906	0.363
Rank relation [Focal > Partner]	0.283	1.101	-1.951	2.407	1.327
Presence of males [Yes]	*-0.695*	*0.689*	*-2.084*	*0.615*	*0.499*
Group size	*0.123*	*0.255*	*-0.382*	*0.616*	*1.131*

Fig. 6 Impact of social features on the channel of communication used in fission and fusion events. (a) type of event, (b) rank relationship, and (c) level of threat; with facial expression, gestural, vocal and multi-channel events represented in green, blue, red, and pink respectively. Rank relationship is categorised as F=P focal and partner have same rank; P>F: partner rank higher than focal; F>P: focal rank higher than partner.

Discussion

We show that the occurrence and form of communication during fission and fusion events is mediated by social factors. Communication occurred in both contexts, but more than twice as often during fusions than during fissions. In addition, communication during these events was selective, with only a small portion of the number of opportunities to communicate acted on.

Chimpanzees were more likely to communicate to particular individuals. More communication occurred towards higher-ranking individuals and between non-kin individuals, and there was an inhibitory effect of the presence of bystanders (increased party size), particularly where these included males. As well as being more likely to be communicated to, higher-ranking individuals were themselves, in general, more likely to communicate than individuals of lower rank. Behavioural contexts that represented either high or low potential-threat levels resulted in higher levels of communication than neutral ones, although this pattern appeared driven by fusions; individuals experiencing low levels of potential threat were particularly unlikely to communicate during departures (fissions). In signal form, gesture-only communications were the most commonly employed and were similarly produced across both fissions and fusions. Gesture-only communication was less likely to be used when the communication partner was of higher rank, particularly during fissions. Vocal-only and multi-channel combinations were employed to a similar extent and relatively less often, but chimpanzees were more likely to combine signals from different channels when experiencing lower levels of potential threat.

Chimpanzees employed almost three times as many different gestural signal types as vocal signal types in these contexts. As a result, while vocalizations were in general recorded less often, *pant-grunt* vocalizations remained the most frequent signal type recorded in fusion events, more than twice as frequent as the next signal (the *present-genitals backwards* gesture). As communication during fusion events was more common than in fissions, and *pant-grunt* vocalizations are closely associated with social rank in chimpanzees (Bygott 1979; Laporte and Zuberbühler 2010), our findings that communication in these contexts was more likely to be produced towards higher-ranking individuals may have been driven, in part, by the prevalence of *pant-grunts.*

Our findings largely support those previously described in specific studies of chimpanzee 'greetings'. For example, *pant-grunt* greetings are more likely to be given when approaching higher-ranking individuals (Laporte and Zuberbühler 2010; Luef and Pika 2017), and across contexts higher-ranking males tended to employ more gestures than other mature individuals (Hobaiter and Byrne 2017). However, the Bossou chimpanzee community is unusually small (2-3 adult males across our study periods), and rank in our study is largely described by sex and age, so an apparent rank effect may also have been driven by a tendency for younger individuals to be less likely to communicate in these contexts.

Our finding that individuals in potentially high threat situations (for example shortly before or after an aggressive attack, a display, or sexual behaviour), were more likely to communicate than those in apparently neutral situations (e.g. feeding or resting) is similar to the findings that greetings (Luef and Pika 2019) and more specifically *pant-grunt* vocalizations (Wittig and Boesch 2003; Fedurek et al. 2021) provide a relatively low-cost opportunity to mitigate the need to engage in physical contests by signalling the current status of dyadic rank-relationships (Newton-Fisher 2004; Fedurek et al. 2019). However, we also found that individuals were as likely to communicate during apparently very low threat interactions (for example, communication shortly before or after grooming or play), showing that chimpanzees are more likely to communicate when engaging in diverse social activities independently of their valence. This pattern of communication suggests that signalling the current status of the relationship shortly before or after a period of separation may be important in affiliative, as well as competitive, relationships. Signaling relationship status may be less important where these are kin-based. The small and cohesive nature of the community may make it difficult to discriminate social-bonds on the basis of kinship, from the strong non-kin social bonds that are a feature of chimpanzee behaviour (Crockford et al. 2013; Samuni et al. 2018) – perhaps particularly so in smaller communities (Lehmann and Boesch 2004). Despite this, we continue to find a small effect of kinship: maternal kin appear to be less likely to communicate during fissions and fusions, even once possible joint travels were controlled for. As well as functioning to reassert the (postive or hierachical) nature of chimpanzees' relationships, communication in these contexts may be particularly important in relationships in which the nature or quality of the pair-bond may vary: you choose whether or not to keep your friends, but not your family.

Being a traveller or a party-members did not affect the likelihood of communicating. In other words, these communications do not appear to be limited to signalling your intention to join or travel, and if communication in these contexts represents greetings or leave-takings, there is no clear pattern to who employs these – it is as likely to be the individual being left behind or being joined, as the individual who is leaving or joining. While the choice to arrive or depart is made by the individual travelling, both the traveller and party-member can make a choice to communicate in this context, and in doing so perhaps inform the other individual or wider audience of the nature of their relationship. Fedurek et al. (2019) reported a higher frequency of *pant-grunts* for individuals who were being approached within a party. However, the decision to approach already indicates a decision to engage with a specific individual. As we see from the relatively low proportion of opportunities to communicate in fusions (and very low proportion in fissions), chimpanzees are highly selective in who – among the individuals present – they communicate with in these contexts. This pattern could represent a choice to communicate with particular individuals, and/or a choice *not* to communicate with specific others. In other words, the decision to communicate may include both the relationship between the two individuals (potential signaller and recipient), and the relationship between these two individuals and others who are present. Supporting this hypothesis, we found that chimpanzees were less likely to communicate in the presence of larger numbers of other individuals, in particular where these included other males. Chimpanzee bystander effects are well documented (e.g., Slocombe and Zuberbuhler 2007; Townsend et al. 2008; Laporte and Zuberbühler 2010; Mielke et al. 2017), and greeting an individual in the presence of other higher-ranking individuals may, for example, lead to aggression (Online Resource 3; Fedurek et al. 2021) - a strong disincentive for greeting indiscriminately or based only on the nature of your relationship with the potential recipient.

Our findings support the broad pattern that shows little evidence for parting rituals in chimpanzees. While individuals were more likely to communicate during fusions, communication did occur during fissions; however, whether or not these communications represent ‘leave-taking’ to the chimpanzees using them remains unclear. As McGrew and Baehren's (2016) survey highlighted there is no agreed definition for leave-taking. If we base our expectations of function or form on human rituals, we will likely miss chimpanzee-specific uses; nevertheless, we need a definition that would allow us to distinguish leave-taking from other types of communication that might occur in fission events. We can say several things: if present, explicit signals of leave-taking appear to be rare. Fewer than 5% of opportunities to do so involved any communication during fissions, and none of the signals produced were specific to this context. As a result, we are very cautious about assigning the signals produced during departures as leave-taking. The most common signal, the *big loud scratch* gesture, which represented almost half of all the signals produced, is produced during requests to ‘Travel with me’ by adult chimpanzees (Hobaiter and Byrne 2014; Fröhlich et al. 2016; Wilke et al. 2017) and is used for the same function by orang-utans (Fröhlich et al. 2019), indicating that at least some of these communications were likely failed requests to travel. Similarly, it is difficult to distinguish interrupted communication. For example, if a juvenile invites another individual to play, but then sees their mother is leaving, they may interrupt the play interaction to follow their mother. Distinguishing this from them having said ‘good-bye’ to their play partner is difficult.

Importantly, we can make the same argument for the potential greeting signals produced during fusions – *pant-grunt* vocalizations and *present-genital* gestures are also made between individuals in other contexts (Hobaiter and Byrne 2011, 2014) – and pant-grunts in particular are used when two individuals approach each other, even where they are already in the same party (Fedurek et al. 2019). The unidirectional use of *pant-grunt* vocalizations between adult males, including when already within the same party, suggests that these signals function to indicate hierarchical relationships – which, as found in human greetings (Firth 1972), are often important to establish or reinforce when meeting. The physical similarity between chimpanzee gesture forms during arrivals and those produced in human greeting-rituals (e.g. *kiss, bow*) is at first compelling, but – to date – evidence for similarity in their meaning remains limited. Great ape signals, and in particular their gestures, are flexible in function and meaning (Hobaiter and Byrne 2014; Graham et al. 2018). The definition of the context of 'greeting' in chimpanzees varies between studies (for example fusions following separations of 5 min up to those of several hours), and there has been a tendency to employ wider context, rather than the specific exchange of behaviour, to define function in non-human primate communication (Call and Tomasello 2007; Ouattara et al. 2009; Laporte and Zuberbühler 2010; Luef and Pika 2017). Thus, we also urge greater caution in assuming that all signals given in a potential greeting context function as greetings.

The study of greeting and leave-taking highlights the constraints underlying the detection of meaning in non-human communication. The broader patterns of use provide a compelling case that communication during fusions serves to demonstrate the nature and strength of social bonds, and so – perhaps irrespective of specific meaning – functions similarly to human greetings. However, there is – so far – no similar case for the pattern of communication prior to fissions and leave-taking. If leave-taking is absent in chimpanzees, it may be because there is no similar social need for it. That may be because chimpanzees do not engage in the imaginative future-tracking required to promote the need for leave-taking: we do not say good-bye every time someone steps out of the room for a moment, only when we imagine or predict that we will not see them for a longer period. Similarly, for the individual leaving, the highly fission-fusion nature of their sociality may make it difficult to predict whether they will be absent for a longer period. It may be more effective to invest in a clear signal of the relationship on arrival, when the parameters of the need to communicate are more clearly defined (I have been away for X-time, the other individuals present are A,B,C, etc.). Finally, when a human leaves their immediate social party, doing so essentially prohibits social contact with them (without technology), while chimpanzees have at least two long-distance (>1km) regularly produced social signals: *pant-hoots* and *drums*, both of which appear to encode aspects of signaller identity and activity (Babiszewska et al. 2015; Fedurek et al. 2016; Fitzgerald et al. in revision), allowing them a possible means to 'touch base' with other individuals, even when split across parties.

If leave-taking is present in chimpanzees, it may be particularly rare in the Bossou community during the nut-cracking season. West African chimpanzees, and smaller communities of chimpanzees, are relatively cohesive (Sugiyama 2004; Lehmann and Boesch 2004) and most individuals meet most days. In addition, the presence of a valuable and consistently available food resource at the nut-cracking site during the dry season may further reduce any uncertainty about the likelihood of re-encountering another individual in the near-future. In contrast in the highly fission-fusion communities of East African chimpanzees, individuals – and in particularly the more rarely studied females – may not meet for weeks or months (Nishida 1968; Goodall 1986).

We show that chimpanzees are selective about their use of communication during fission and fusion events, which is mediated by both individual and social factors including rank, kinship, and audience size and composition. Our data largely support and extend the findings in studies of greeting in other chimpanzee communities. By taking a broad approach across opportunities to communicate and signal channels, we show the importance of considering the full range of signals employed in these contexts, as well as the specific individual and community level socio-ecological context of their use. Our use of systematic video-coding allows us to provide a thorough description across signalling channels, including subtle visual signals that can be missed or neglected. Further research is needed across different chimpanzee communities – in particularly on the highly fission-fusion East African females – and with larger datasets that allow us to better explore the infrequent use of communication during departures. For example: investigating the impact of how far apart individuals are (within or outside of the range of long-distance conspecific signals – such as pant-hoot calls or buttress drumming in chimpanzees) and for how long, as well as exploring changes in the behaviour of individuals before and after some-one arrives or leaves, could provide crucial new understanding of the function of communication in these contexts for fission-fusion species. We particularly highlight the methodological challenges in detecting signals that are functionally equivalent to leave-taking and we urge caution in interpreting communications during fusion events as functionally equivalent to greetings. While great ape communication, and in particular their gestures (Tomasello et al. 1985; Leavens and Hopkins 1998; Hobaiter and Byrne 2011), has been showed to be clearly intentional; there remains limited exploration of the sharing of different types of intentions outside of human communication. While a *big loud scratch* gesture may not function to signal ‘good-bye’, there is a distinction between the imperative ‘travel with me’ and the declarative ‘I’m leaving’. Exploring the intention sharing of other apes in greater detail may deepen our ability to detect the evolutionary origins of human leave-taking – and greeting – behaviour.

Declarations

Conflict of interest: The authors declare that they have no conflict of interest.

Data and Code Availability: Data, scripts, and online resources available in https://github.com/Wild-Minds/Bossou_HelloGoodbye

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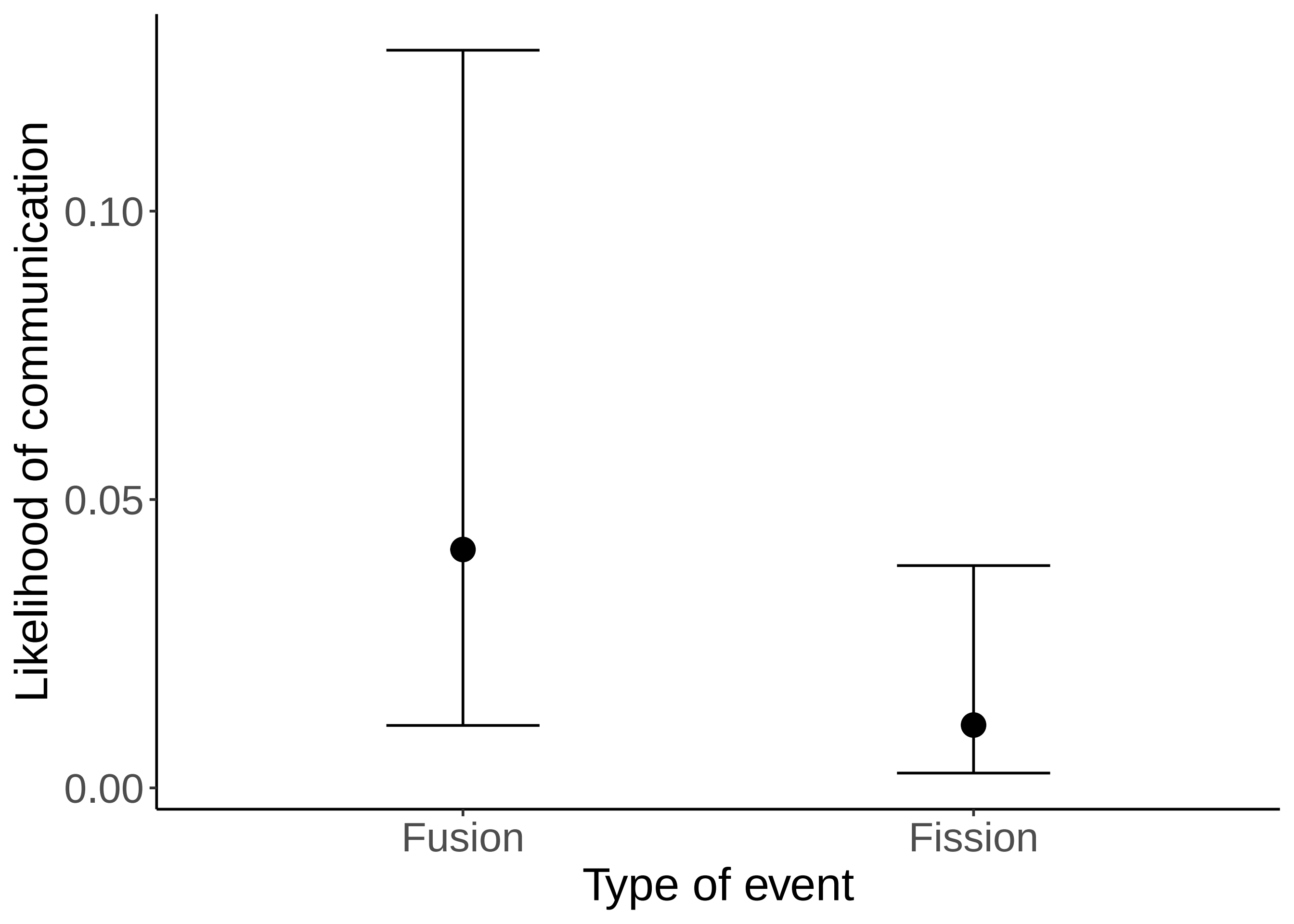
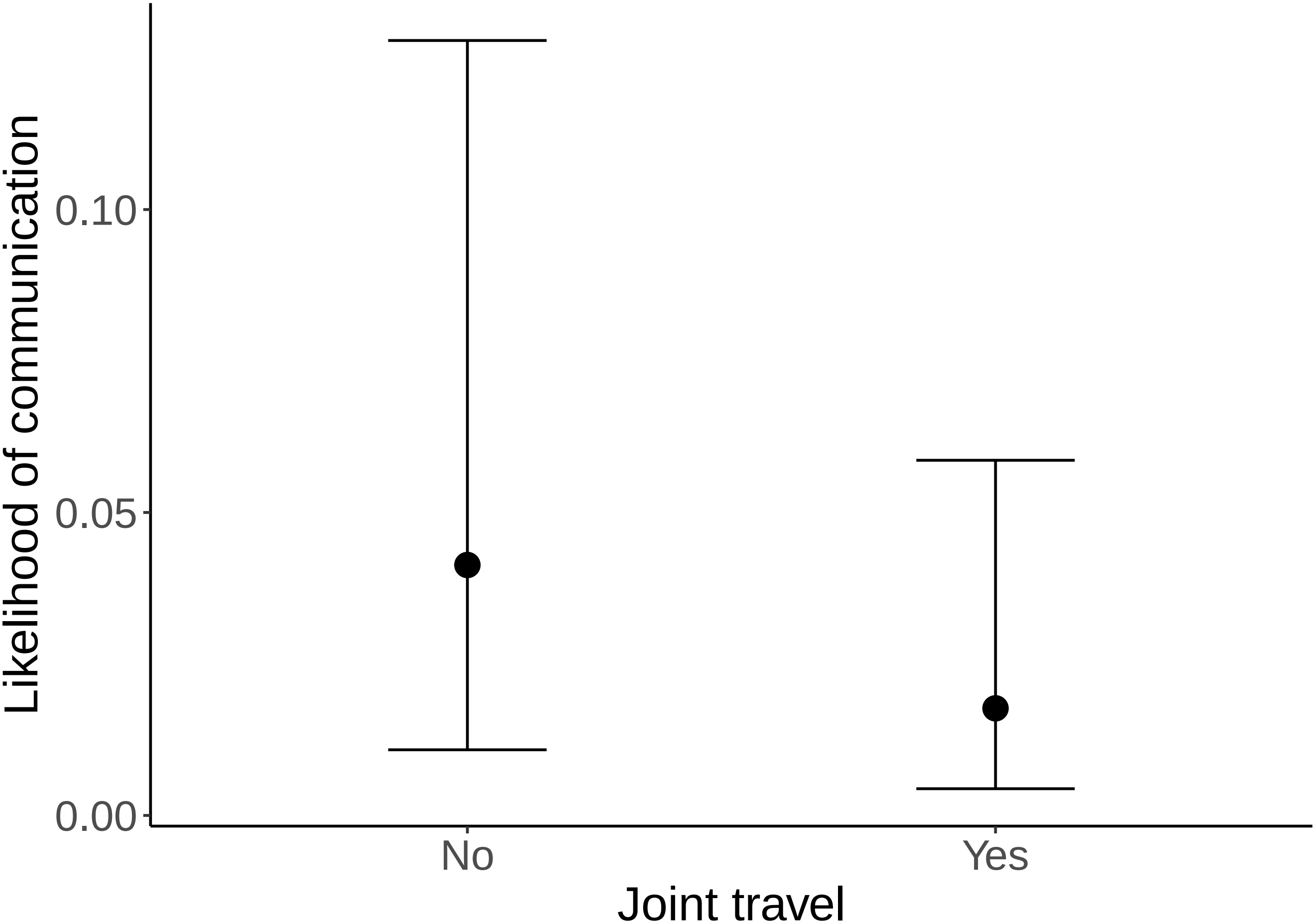
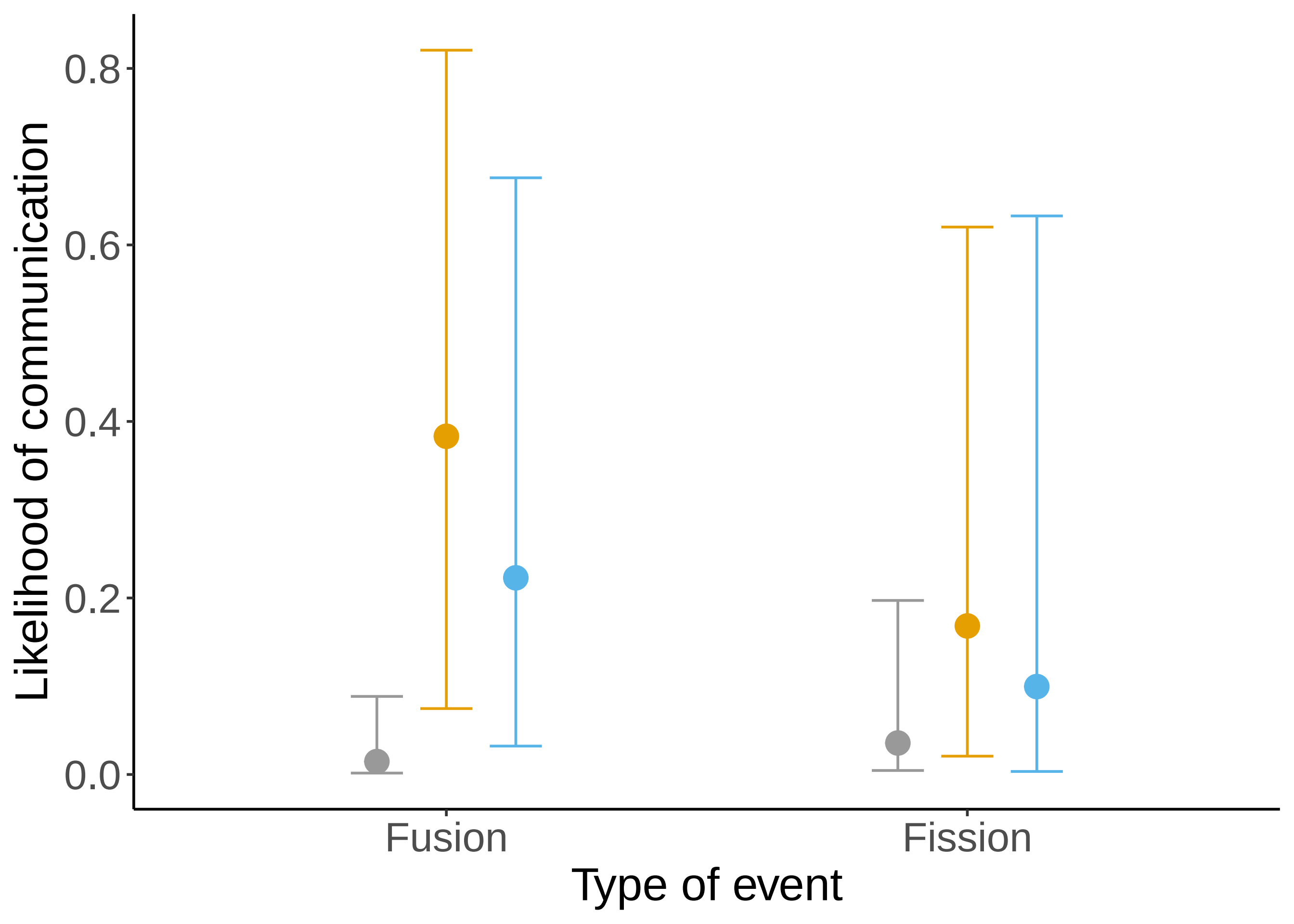
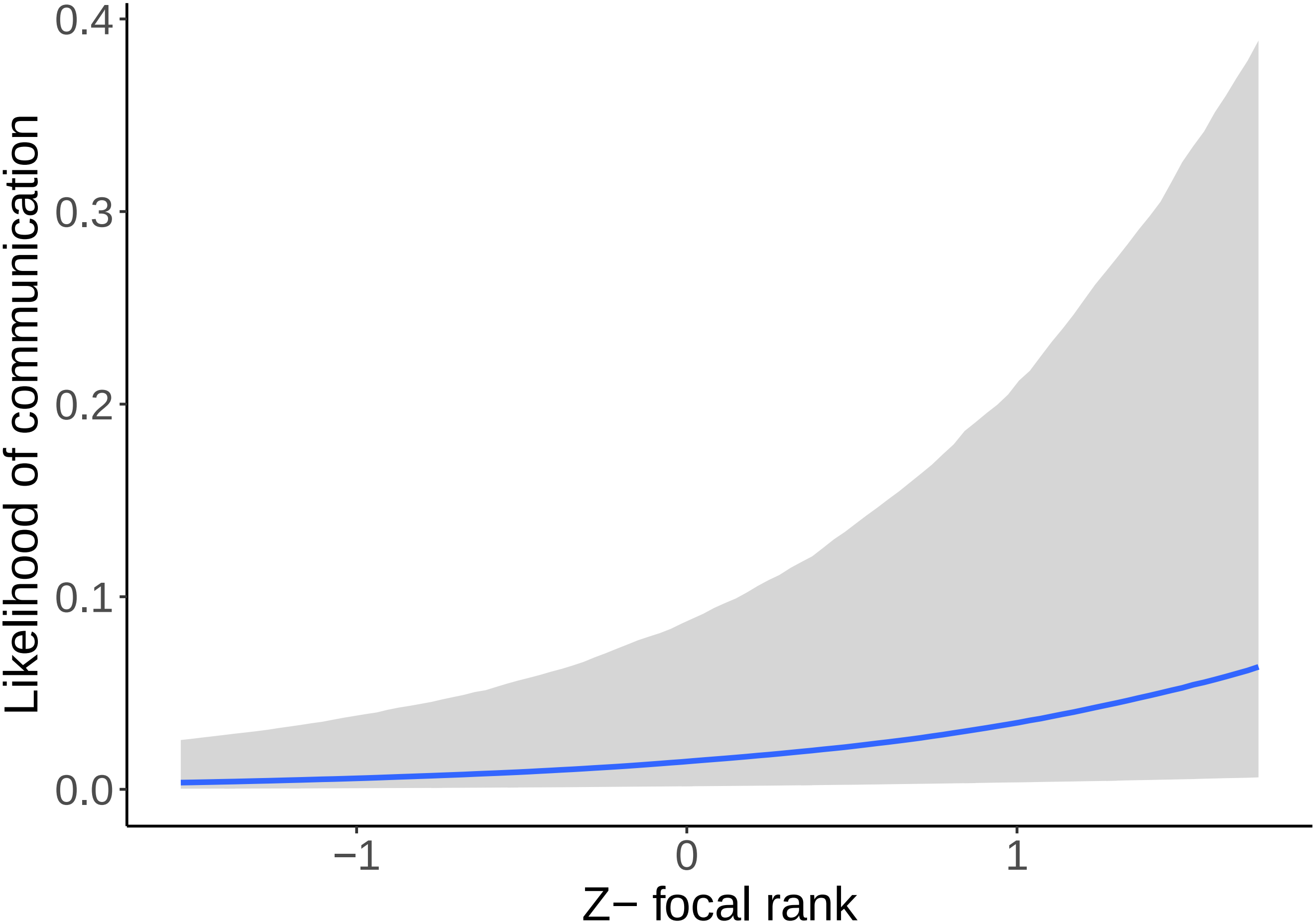


Likelihood of communication
0.10
0.05
0.00
Fusion
Fission
Type of event

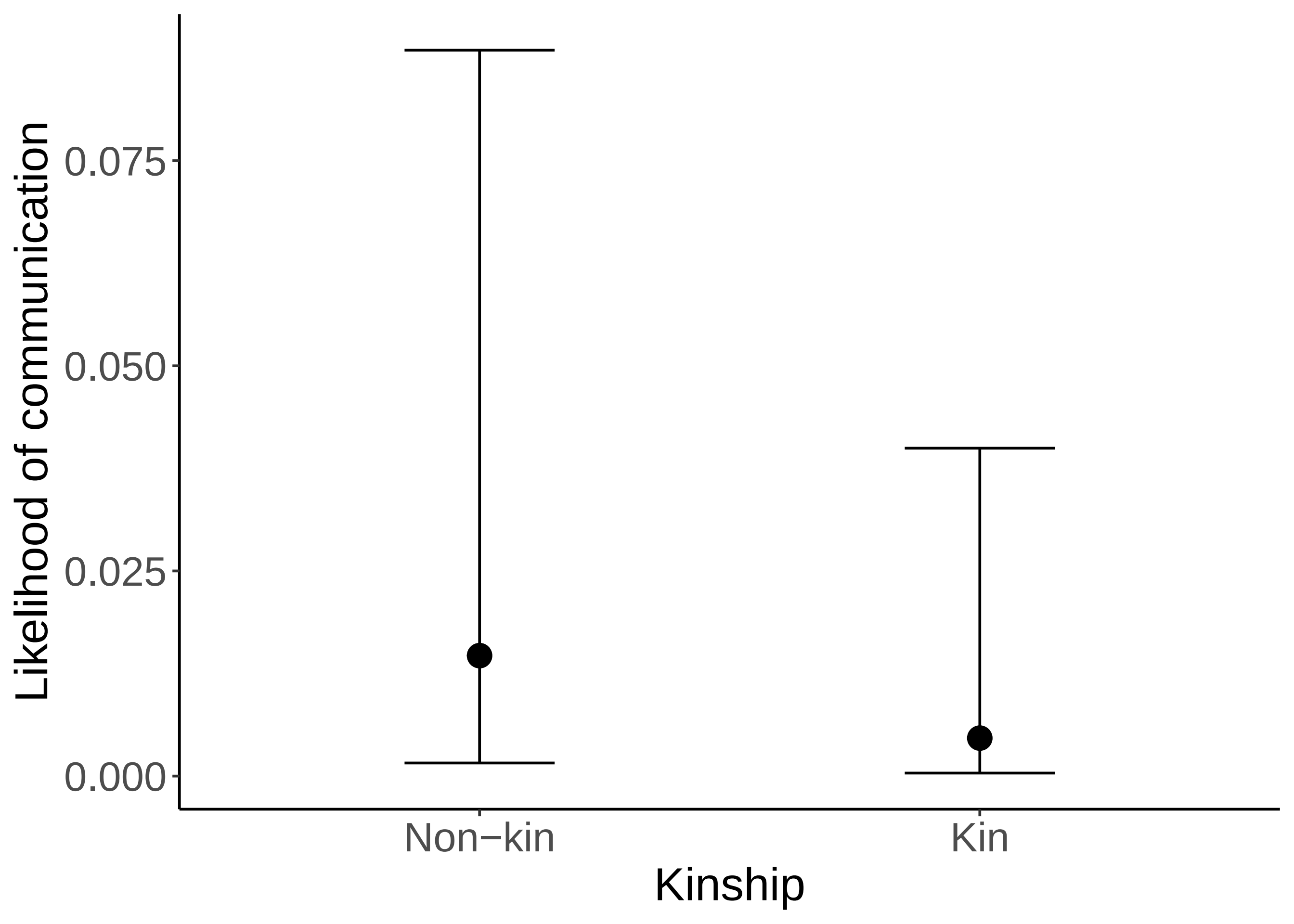

Likelihood of communication
0.10
0.05
0.00
No
Yes
Joint travel



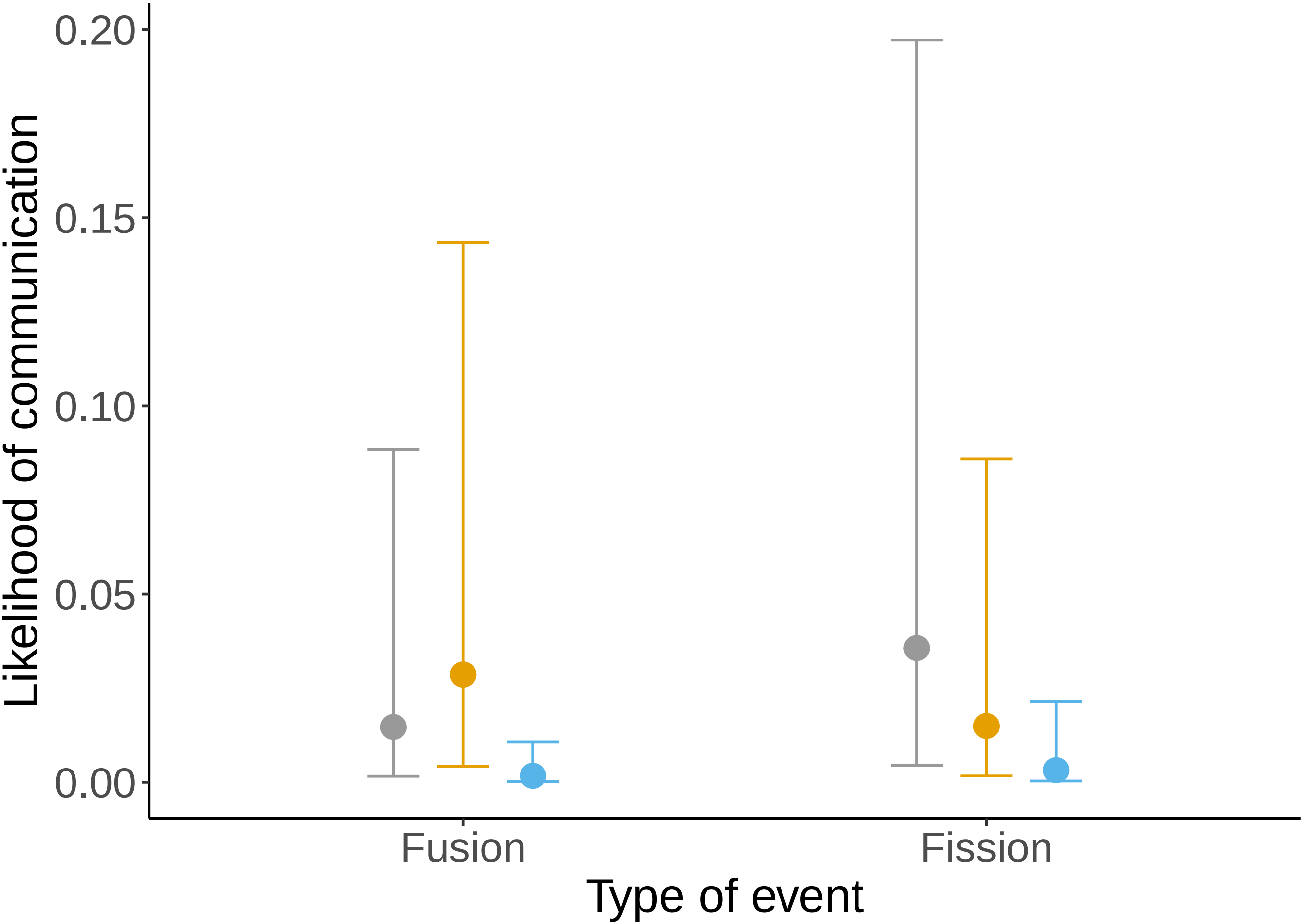
Likelihood of communication
0.0
0.2
0.4
0.6
0.8
Fusion
Fission
Type of event



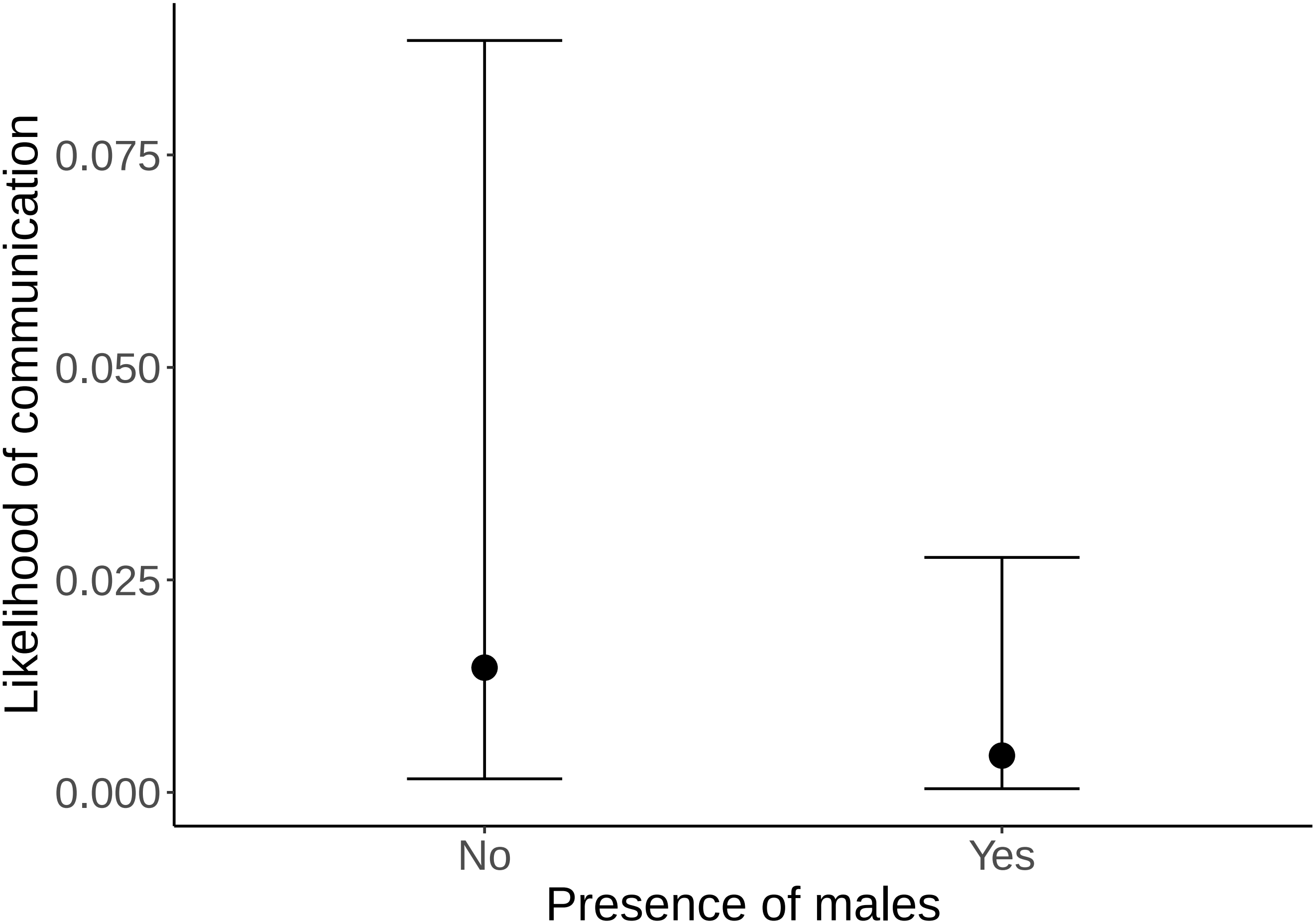
Likelihood of communication
0.4
0.3
0.2
0.1
0.0
−1
0
1
Z− focal rank



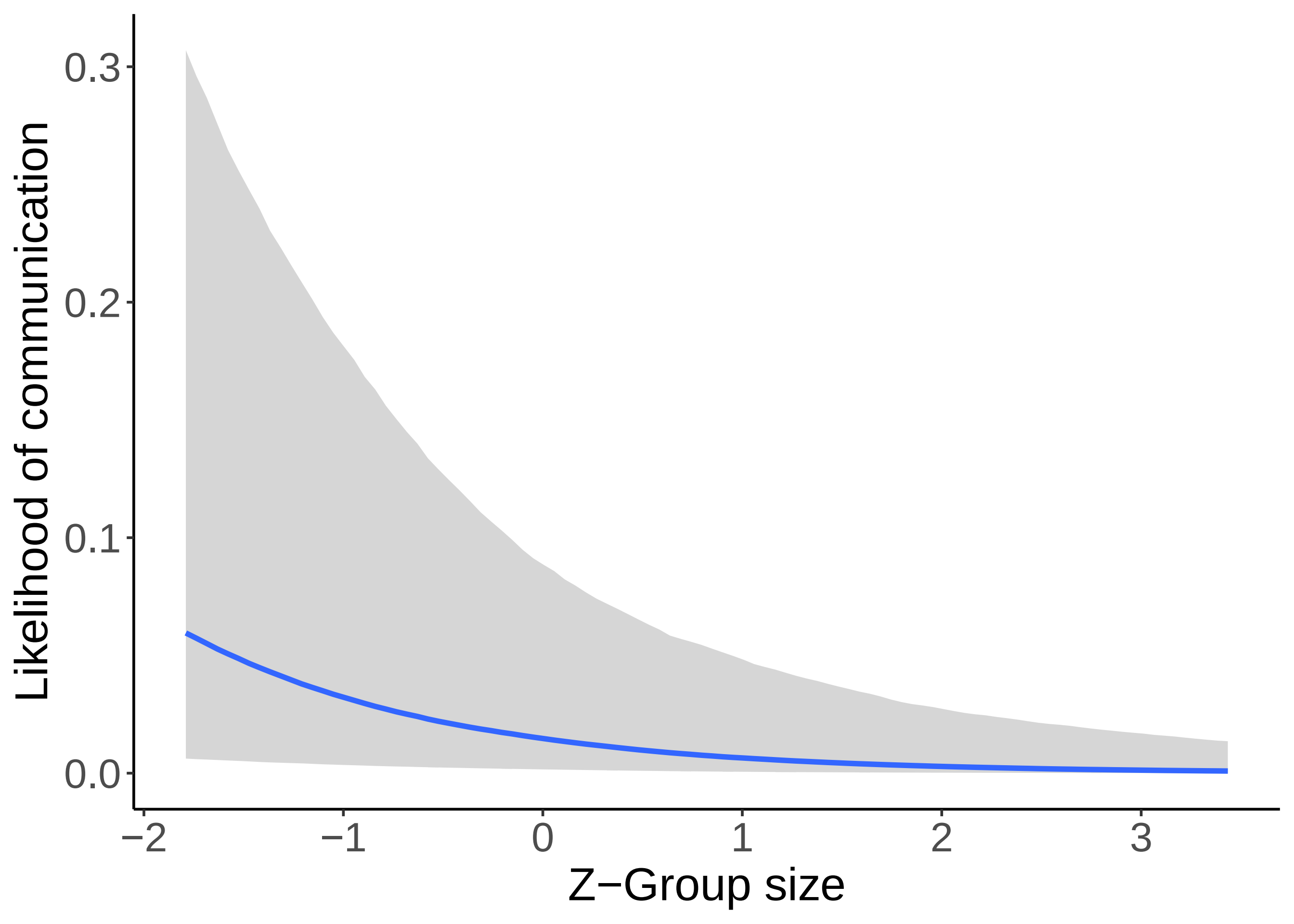
Likelihood of communication
0.075
0.050
0.025
0.000
Non−kin
Kin
Kinship



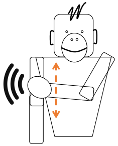
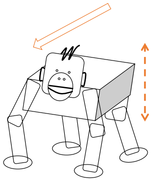
Likelihood of communication
0.20
0.15
0.10
0.05
0.00
Fusion
Fission
Type of event

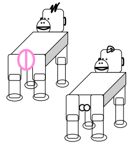
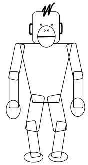
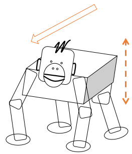


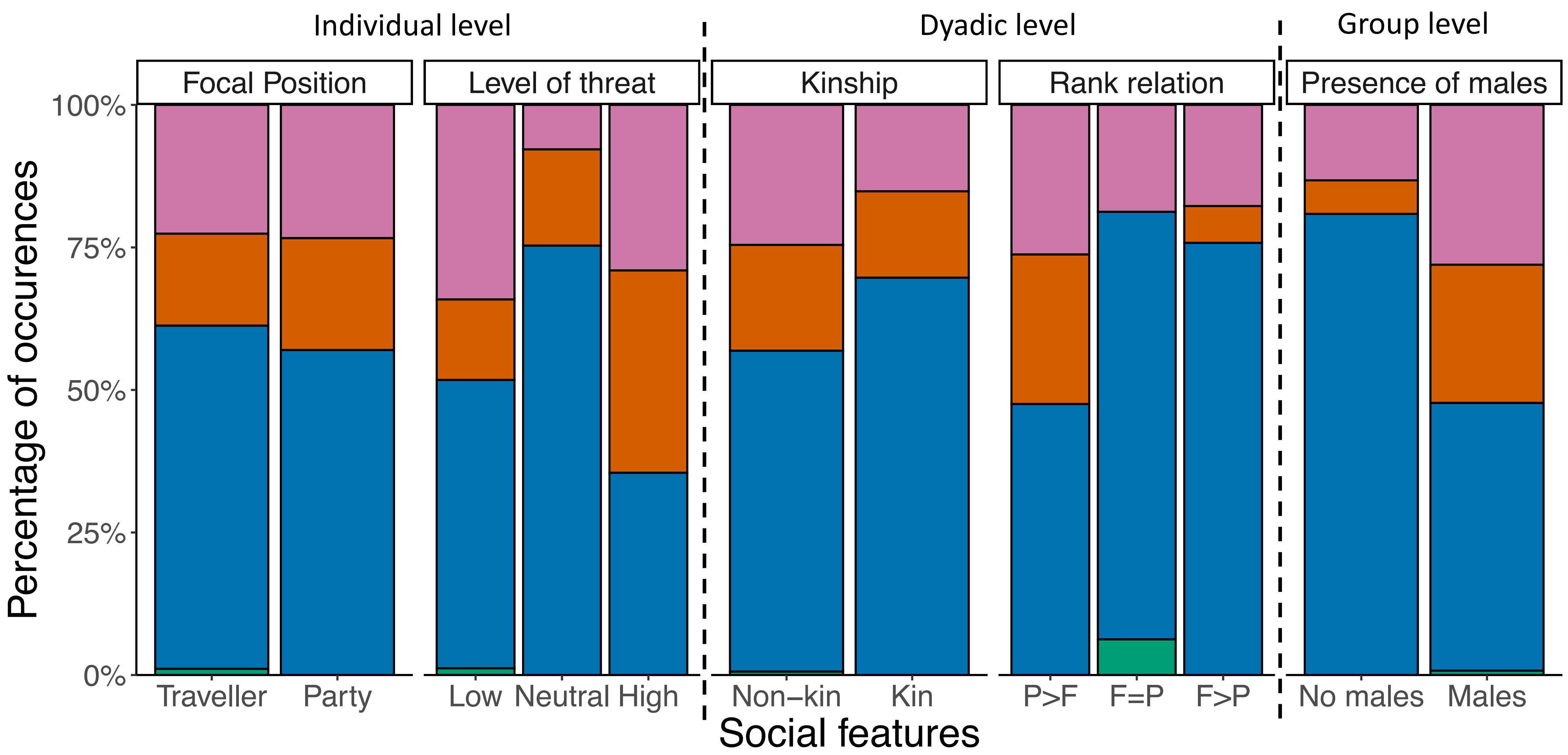
Likelihood of communication
0.075
0.050
0.025
0.000
No
Yes
Presence of males

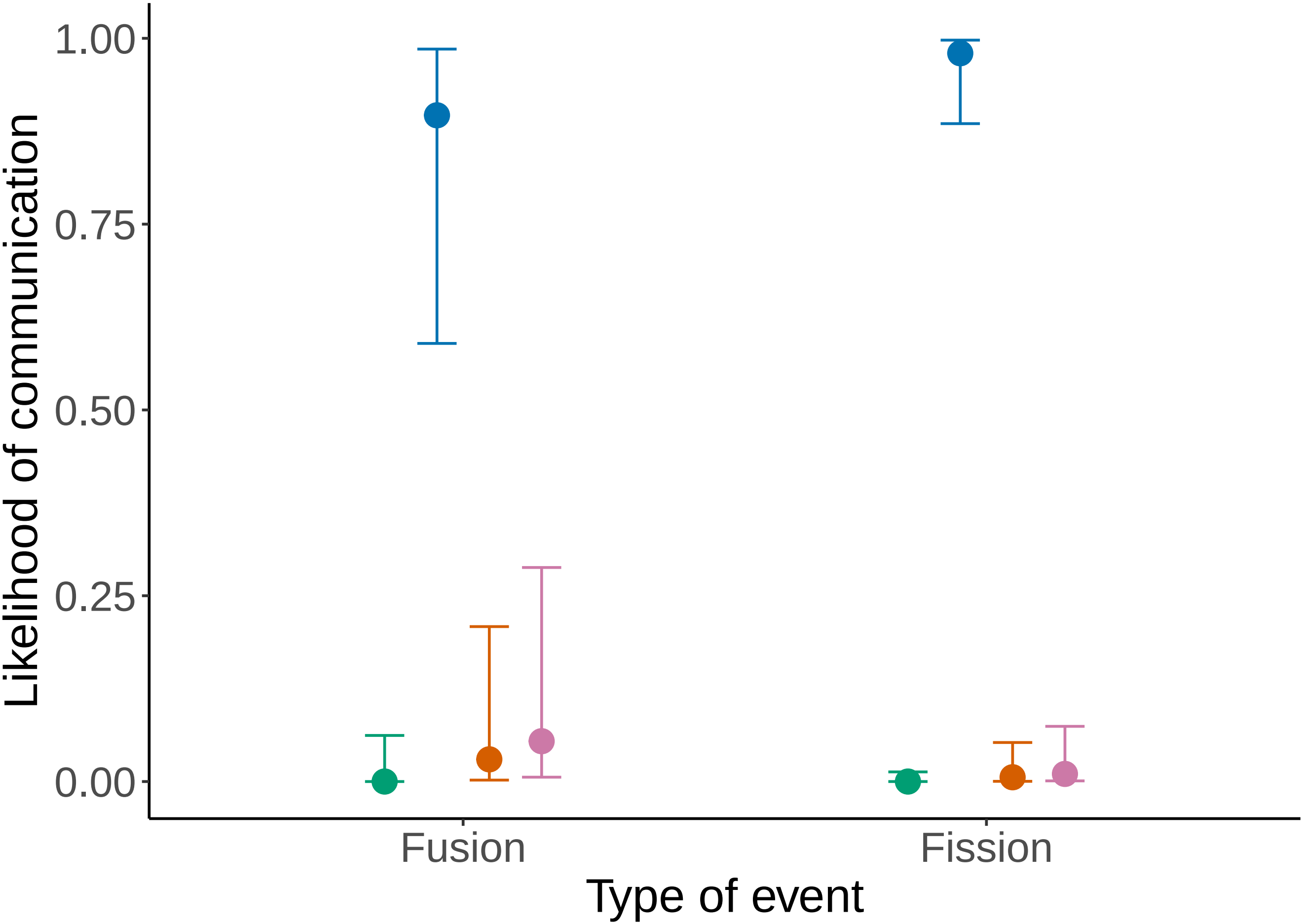


Likelihood of communication
0.3
0.2
0.1
0.0
−2
−1
0
1
2
3
Z−Group size

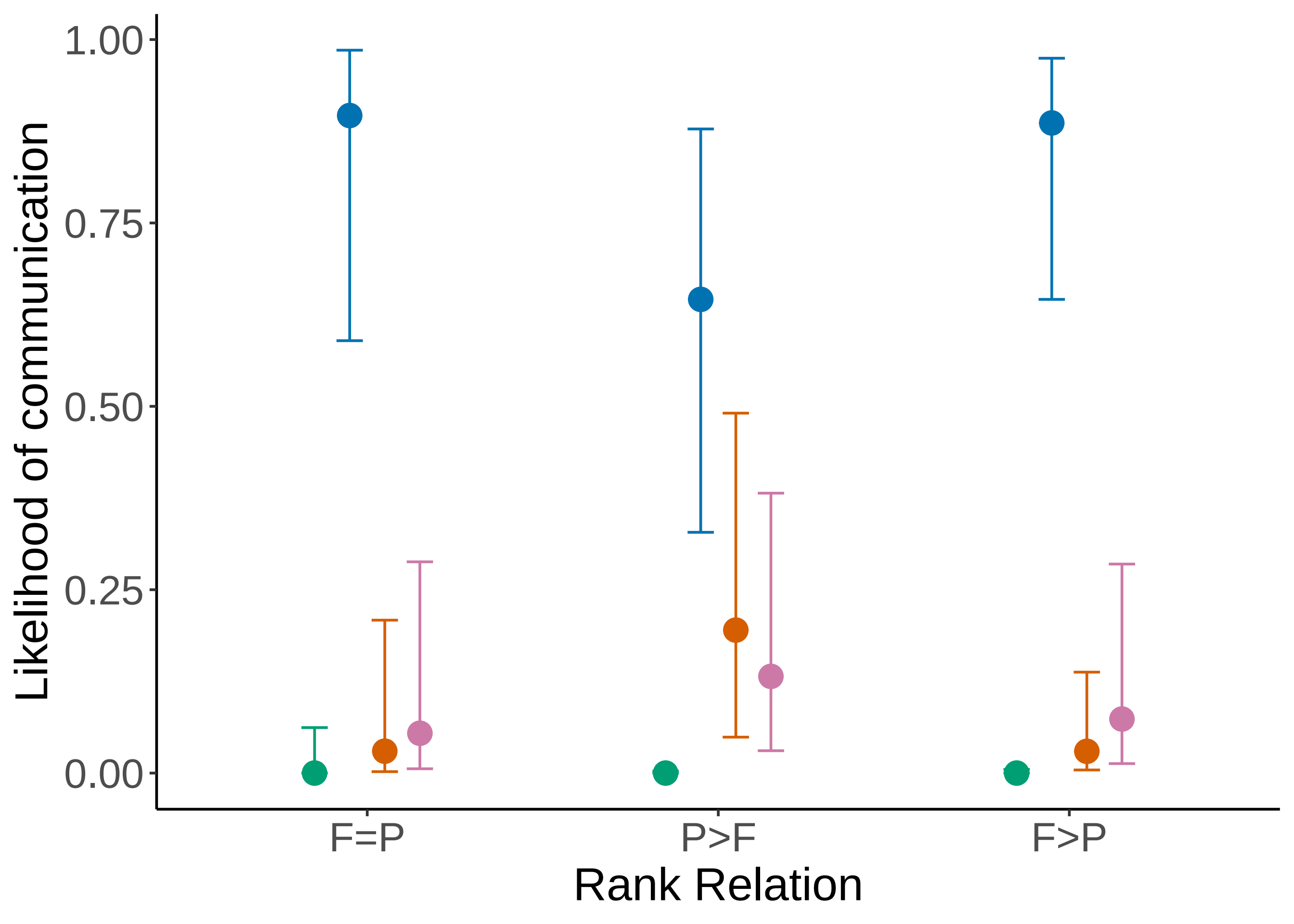
Fission		
Signal type	N (%)	Definition
Big loud scratch 	36 (34%)	Loud exaggerated scratching movement on signaler's body.
Locomote: gallop 	10 (10%)	An exaggerated running movement where the contact of signaler’s hands and feet is deliberately audible

Fusion		
Signal type	N (%)	Definition
Pant-grunt	51 (18%)	Series of grunts joined together by voiced inhaled elements, includes variants from noisy-pants to pant-bark.
Present genitals backwards 	25 (9%)	Signaler approaches recipient backward and deliberately exposes swelling or groin area to the recipient's attention
Bipedal stance 	15 (5%)	Signaler stands bipedally and holds position
Locomote: gallop 	15 (5%)	An exaggerated running movement where the contact of signaler’s hands and feet is deliberately audible

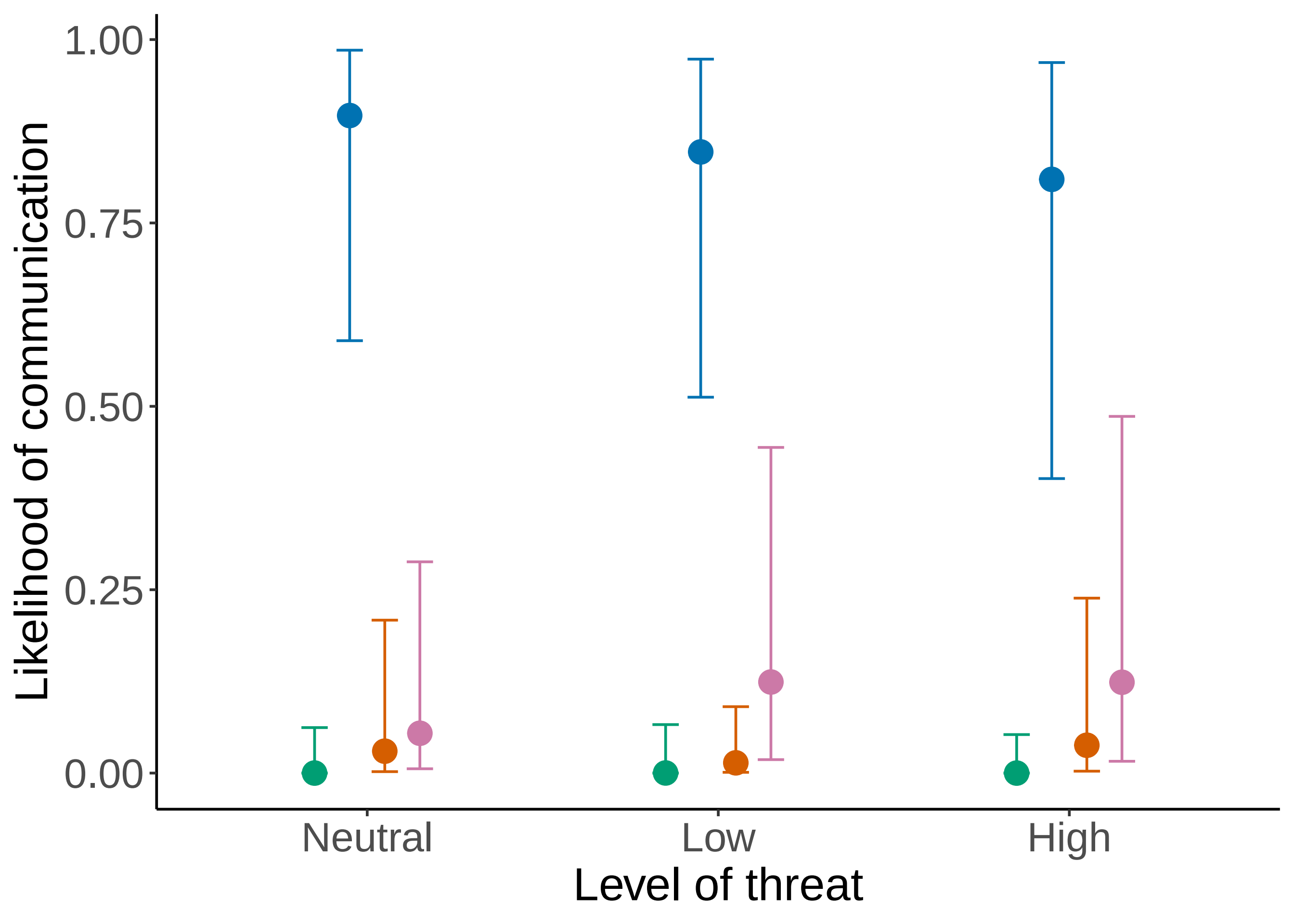

Individual level
Dyadic level
Group level
Focal Position
Level of threat
Kinship
Rank relation
Presence of males
100%
75%
50%
25%
0%
Percentage of occurences
Traveller
Party
Low
Neutral
High
Non−kin
Kin
P>F
F=P
F>P
No males
Males
Social features



Likelihood of communication
1.00
0.75
0.50
0.25
0.00
Fusion
Fission
Type of event



Likelihood of communication
1.00
0.75
0.50
0.25
0.00
F=P
P>F
F>P
Rank Relation



1.00
0.75
0.50
0.25
0.00
Likelihood of communication
Neutral
Low
High
Level of threat