Gesture use in Consortship: wild chimpanzees' use of gesture for an 'evolutionarily urgent' purpose

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Introduction

Play has repeatedly been found the most prolific context for the use of gestural communication by great apes in captivity, where most study of great ape gesture has taken place (Liebal et al., 2004; Tomasello et al., 1994; Genty et al., 2009; Pika, 2003; Pika et al. 2005). In consequence, it

has been suggested that gestural communication is generally used for "less evolutionary urgent functions" (Tomasello & Call, 2007:5). But it is not clear which, if any, contexts experienced by captive apes would require communication about evolutionarily urgent functions; in other words, those that have been subject to strong selection pressures. In contrast, a wild chimpanzee patrolling its territorial boundaries, hunting, or initiating consortship behaviour, runs very real risks: up to and including their own death. Thus, they might be expected to employ communicative strategies that minimize these risks. In a secondary rainforest where visual lines of sight can be restricted, vocalization represents an effective means of communication; however, with all vocalizations there is a risk that the call may be overheard and the information employed by unintended recipients 'eavesdropping' – particularly where the individual calling can also be identified (Peake et al. 2002, Mennill et al. 2002). Unlike vocalizations, silent and contact gestures allow the signaller to communicate their intention without the risk of that message being 'overheard' by other parties. Unfortunately, its inherently secret nature means that to date there has been very little empirical analysis of consortship behaviour. Here we take advantage of a recent cluster of observations in the Sonso community to discuss the nature of consortships and the role of gestural communication within them in more detail.

Chimpanzee sexual strategies

Early work in this field emphasised male sexual strategy (Allen, 1981; Hasegawa & Hiraiwa-Hasegawa, 1983; Tutin, 1979; Tutin & McGrew, 1973); thus, sexual behaviour was defined in terms of male-male competition as either opportunistic (non-competitive mating, with free access to all males), or restrictive (access to the female is monopolised by a single male). Within the category of restrictive mating, we can discriminate two patterns of behaviour: *possessiveness*: where sexual access to a female is monopolized by a single male while remaining within the group (also known as *mate-guarding)*; and *consortship*: where a single male monopolizes sexual access by escorting a female away from the group (Tutin, 1979). At Gombe, Tutin found that consortships were associated with a high probability of reproductive success (Tutin, 1979), although a genetic analysis of the Taï community suggests that this may vary between males (Boesch & Boesch-Achermann, 2000).

More recently, work on sexual strategy has emphasised the role of female choice in determining paternity (Pieta, 2008; Stumpf & Boesch, 2006; Emery Thompson et al., 2008; Boesch, 2009; Stumpf & Boesch, 2010). This is particularly true in the case of consortship, where the consorting male must avoid detection by other group males: even a brief scream from the female may bring other males to investigate, particularly if she is known to be in oestrus. Aggressive coercion by the male is often

68 observed in the initial stages of consortship (Goodall, 1986), apparently to
69 overcome reluctance on the part of the female; this has suggested that
70 promiscuity represents a more favourable strategy for female chimpanzees
71 (Muller et al., 2007). However, a recent study showed that aggressive male
72 coercion did not in fact act to decrease female resistance (Stumpf & Boesch,
73 2010); and Nishida (1997) describes females at Mahale responding with
74 "blunt refusal of male courtship." Co-operation on the part of the female
75 may then be critical to the success of a consortship. Tutin observed that
76 males who frequently engaged in grooming and sharing food with oestrus
77 females while they were with the group were more likely later to be
78 successful in leading females away from the group on consortship (Tutin,
79 1979); and Goodall describes the use of grooming in consortship to reduce
80 the anxiety of a reluctant female, making her easier to lead away (Goodall,
81 1986).
82
83 Consorting males must invest time and energy in removing the
84 female from the group. Lower-ranking individuals may have to initiate a
85 consortship several days before a female reaches peak fertility, as she is
86 then maximally capable of conception and likely to be surrounded by other,
87 more dominant would-be suitors. In addition to the time and energy
88 invested, consortships are also associated with increased risk. A consorting
89 male risks aggressive attack from males within the community, should they
90 discover his attempt to remove the female or when he tries to rejoin the

group after the absence while on consortship (Riss, unpublished cited in: Tutin, 1979). Yet, in attempting to avoid detection by their own group, consorting pairs are more likely to occupy peripheral areas of the community territory, increasing their chances of encountering neighbouring groups. Both male and female risk attack from individuals of neighbouring communities; Tutin cites intercommunity encounters as the highest source of risk for individuals already on consortship (Tutin, 1979). For the male this may present a direct risk to his life, as intercommunity encounters can result in lethal aggression (Goodall, 1986). Females, particularly those in oestrus, are less likely to be killed, but may be aggressively herded into the neighbour's community (Boesch, 2009). There they risk attack by the community females (Townsend et al., 2007), and any dependent offspring travelling with them may be killed (Suzuki, 1971; Reynolds, 2005; Townsend, et al., 2007).

The potential role of gestural communication when on consortship

The decision to initiate a consortship may evidently depend on a number of factors including male rank, female co-operation, and risks associated with intercommunity encounters. However, once the decision has been made, in all cases there is significant pressure on a consorting male to communicate his initial intention to the female in a discreet manner, and for both the male and female to avoid detection once in consortship. For

these reasons, use of gestural rather than visual communication may represent an effective strategy. Chimpanzees not only regularly use gesture to communicate their desires, but they intentionally alter the modality of their gestures with respect to other individuals' state of attention (Tomasello & Call, 2007; Genty et al., 2009; Liebal et al., 2004; Pika et al., 2003; Hobaiter & Byrne, under review). We hypothesised that, because of the need to limit the communication to a specific recipient, gestural communication - particularly silent and contact based gestures - would be favoured in the consortship context. Thanks to a recent peak in consortship behaviour within the Sonso community, we are able to report that high levels of gestural communication did indeed occur during these consortships, and we describe the nature of the interactions.

Method

Procedure

Observations of consortship behaviour were recorded on an ad-hoc basis during systematic data collection for a project on chimpanzee gestural communication among the wild Sonso chimpanzee community in the Budongo forest, Uganda at the Budongo Conservation Field Station (BCFS) (Hobaiter & Byrne, under review). Observations were made during 18-

137 months of observation, split into 3-periods between October 2007 and
138 August 2009. All examples of consortship behaviour (as defined below)
139 were recorded on miniDV using a Sony Handycam (DCR–HC-55).
140
141 *Long-term data collection*
142
143 In addition to direct observations we interrogated the 6 highly-
144 experienced, chimpanzee field-assistants (two of whom have worked with
145 the Sonso community for 20-years), in order to establish a long-term record
146 of consortship frequency. We also consulted the BCFS events book, kept on
147 site for the purpose of collating unusual or rare observations. Field-
148 assistants record the frequency and duration of aggressive behaviour ad
149 libitum onto handheld Workabout-Pro computers; these are collated in the
150 projects long-term records (Zuberbühler & Reynolds, 2005).
151
152 *Defining sexual behaviour*
153
154 We follow Tutin (1979), in defining *consortship* as: "where a single
155 adult male escorts a female away from the group and maintains exclusive
156 copulatory access to her" (Tutin, 1979). We define a consortship as
157 successful when the female was isolated from the group and the pair
158 remained absent for a minimum of 48-hours.
159

Defining gestures

We define gestures as discrete, mechanically-ineffective physical movements of the body observed during periods of intentional communication. Thus, each case of gesture had to be accompanied by an indication of intentional use. We considered gestures accompanied by one or more of the following to involve intentional communication:

Audience-checking: the signaller shows signs of being aware of the potential recipients and their state of attention, e.g. turning to look at the recipient before gesturing.

Response-waiting: After gesturing the signaller pauses for >1sec and maintains some visual contact.

Persistence: the production of further gestures after response-waiting.

Where a string of gestures, separated by <1sec, was followed by response-waiting, we assigned the intentional aspect to each gesture within the string.

Structure of the gestural communication

We define the following structures within gesturing:

Single gesture: a single gesture followed by a pause of >1sec of response-waiting.

Rapid sequence: multiple gestures without intermittent pauses of >1sec.

Bout: multiple single gestures and/or rapid sequences produced in succession with intermittent pauses of >1sec and/or non-gestural behavioural responses from the recipient.

Function of the gestural communication

Function was defined by the behavioural response that led to the end of the communication attempt (as per. Genty et al. 2009). Function was measured at the level of the bout: we considered all single gestures and rapid sequences within a bout to be produced for the same function.

Success of the gestural communication

We considered persistence in communication to imply the failure of earlier gestures. Where a response appeared to satisfy the gestural communication, the single gesture or rapid sequence immediately preceding it was considered to be *successful*. Where the recipient produced a behavioural response that did not satisfy the signaller, but was congruent with a subsequent behaviour that did, we considered the gesture or rapid sequence to be *partially successful*. For example: a signaller gestures in a rapid sequence towards an inattentive recipient, the recipient looks round and moves towards the signaller but stops short of reaching them, the signaller gestures with another rapid sequence and the recipient then moves to play

with the signaller, the signaller then stops gesturing. Both rapid sequences in the bout would be considered to have the function of requesting play; the second sequence would be considered completely successful, the first sequence would be considered partially successful.

Gesture modality

We categorized gestures according to their potential mode of reception as signals, as *silent, audible* or *contact*. In the dense secondary rainforest many movements may result in a sound being produced; however, we treated gestures as audible only when they were made audible by their intrinsic features, i.e. that they would be audible in every case, irrespective of where or when they were produced.

Long and short-distance audible gestures

In rainforests, the complicated acoustic environment leads to increased degradation and attenuation of acoustic signals (Wiley, 1991). Mitani et al. (1999) found that the pant-hoot calls of different chimpanzee populations varied in a manner that maximized signal transmission with variation in the habitat acoustics. In dense, secondary rainforest such as that found at Budongo, the degradation of acoustic signals would be particularly high. Studies of chimpanzee vocal behaviour typically distinguish between

short and long-distance chimpanzee vocal behaviour (e.g. pant-grunt vs. pant-hoot, see: Van Lawick-Goodall, 1972; Crockford & Boesch, 2005), and we suggest that it is possible to distinguish audible gestures in the same way.

Although clearly audible, *Object-move* and *Object-shake* gestures appear to be limited in terms of their audible range. For example: when the highly experienced head field-assistant was trying to locate a consorting male whom we observed to repeatedly produce *Object-shake* gestures, he failed to do so until less than 100m away, despite awareness of the approximate location. In addition to the short range over which they can be heard, the audible component of these gestures comes from the rattling of leaves and foliage, something that can be caused by other large forest mammals such as bush-pigs (or field-researchers); and as such they are not immediately acoustically identifiable as chimpanzee gestural communication.

In contrast, certain gestures are audible over much greater distances, and are purely associated with chimpanzee communication. These are the *Drum-object* or *Stomp-on-object* gestures. When the object in question is one of the large tree buttresses regularly found throughout the forest, and regularly employed by the chimpanzees for drumming and stomping actions, the gestures produce a distinctive deep boom that is audible to

humans over 500m away. In many cases, individual idiosyncrasies allow us to identify not only the location but also the identity of the drumming chimpanzee: a highly effective long-distance signal (Clark Arcadi et al. 1998). Several observations of solitary male chimpanzees repeatedly drumming and then waiting until there is a response from a party of chimpanzees before moving directly to them, suggests that the chimpanzees themselves are aware of the long-distance quality of these communications. Furthermore observations of the immediate change in behaviour, when the drum of an individual from a neighbouring group is heard, strongly suggest that chimpanzees are also capable of distinguishing individuals in this manner: an observation supported by similar reports from chimpanzees in the Taï forest (Boesch & Boesch-Achermann, 2000).

Specific analyses

Data were converted to means for each individual, to remove any effect of pseudo-replication from the use of focal behaviour sampling. Only individual means calculated from 5 or more separate cases were included in any analyses. Analyses were carried out in SPSS v11, with $\alpha=0.05$ required for significance. Means are given ± Standard Deviation, throughout. Data were all examined for appropriateness for parametric statistics and where necessary transformations applied and the data re-tested. Where transformations were applied the results are clearly labelled; where no

appropriate transformations were possible non-parametric alternatives were used. Statistical tests are two-tailed.

Results

Consortship behaviour in Sonso chimpanzees

Consortship behaviour was rarely observed, with only 10 events reported in the past 10-years. During 266 days of observation between October 2007 and August 2009 we observed 4 cases of consortship behaviour in the Sonso community involving 2 males and 3 females, and were able to record over 2-hours of video footage (total 2h24m37s: includes 17m30s kindly donated by other researchers).

1. 05.01.2008 Duane and Lola (45m50s video) unsuccessful
2. 20.01.2008 Duane and Zimba (53m15s) successful
3. 03.02.2008 Duane and Zimba (28m2s) successful
4. 04.10.2008 Nick and Nambi (17m30s) successful

Gestural communication in the consortship context

In the 18-month study of gesture in the Sonso community, consortships were recorded on only 4 of the 266 days of observation

297 (1.50%) but accounted for 412 of the 4397 gestures recorded (9.39%).
298 Critically, *gestures from consortships accounted for 62.18% of all adult*
299 *male gesture use* recorded during the study (393/632 gestures); with males
300 producing almost all of the gestures used in this context (n=412, males: 393,
301 females: 19). Gesturing was recorded both when the male and female were
302 still within the group, and also once the pair had moved away from the
303 group, but were still within the core area of the Sonso community.
304
305 *The consortship repertoire of gestures*
306
307 The complete Sonso gestural repertoire consists of 66 types of
308 gesture, used flexibly across 10 different contexts (Hobaiter & Byrne, under
309 review). Twenty-one of these gesture types were recorded during
310 *consortship*, 17 from males and only 4 from females (predominantly the
311 *Present-sexual* gesture, 16 of the 19 cases of female gesture). The most
312 frequently used gestures were the object related gestures: *Object-shake* (222
313 cases), and *Object-move* (41 cases), which together accounted for over 60%
314 of all gestural communication in this context. We observed no consortship-
315 specific gestures; however, the rare *Rump-rub* gestures were predominantly
316 produced within the consortship context (26/29 cases).
317
318 In *Rump-rub* the male signaller backs up to the recipient and pushes
319 his rump against them (usually their genitals or torso); this movement is

accompanied by a small but rapid, vertical up-and-down rubbing motion. *Rump-rubs* were often accompanied by a soft-pant vocalisation. 26 cases were recorded during consort behaviour. In other contexts (2 Agonistic, 1 Unknown) the gesture was used by a less dominant male to a more dominant male when apparently seeking affiliation or reassurance; however in the consortship context a dominant male directed the gesture to a lower-ranking female.

Gesture as discreet communication?

Perhaps surprisingly, audible gestures were extremely prevalent in consortship communications (334/412, 81.1%); even silent and contact gestures were accompanied by audible behaviours in a third of cases (26/78). Within male gestural communication 85.0% of gestures were audible gesture types (334/393, Duane: 321/379; Nick: 13/14); and 91.6% were either audible or accompanied by other audible behaviour (360/393, Duane: 347/379, Nick: 13/14). This actually represented an increase in the proportional use of audible gestures over use in other contexts, by both males (*Duane* consortship audible=321/379, non-consortship audible=7/17, Chi-square χ^2=21.67, df=1, p<0.0001. *Nick* consortship audible=13/14, non-consortship audible n=59/106; Chi-square χ^2=4.60, df=1, p=0.0319).

342 The prevalence of audible gestures was due to the prolific use of the
343 *Object-shake* and *Object-move* gestures described above; but critically these
344 are all short-distance audible gestures. In other contexts short-distance
345 audible gestures (*Object-shake* and *Object-move*) were used in the same
346 rapid sequence as long-distance audible gestures (*Drum-object* or *Multiple*
347 *stomp-on-object*) in a mean 6.7% of cases (19/285). However, despite the
348 prevalence of the short-distance *Object-shake* and *Object-move* gestures in
349 consortship communications, there were no cases of long-distance audible
350 gestures during consortships (0/211) (n=496, Chi-square: χ^2=14.06, df=1,
351 p=0.0002).
352
353 *The function of gestural communication in consortship*
354
355 Consortship communication included 127 separate bouts of
356 gesturing, 61 of which were successful and could therefore be used to define
357 function. Unsurprisingly, given the nature of consortship behaviour, the
358 overwhelming majority of the gestural communications produced by both
359 males had the apparent function that the female should 'follow' him
360 (Duane: 48/52 bouts, 92.3%; Nick: 5/6 bouts, 83.3%). Perhaps more
361 surprisingly, only a very low number of bouts (total 2: Lola 1; Duane 1)
362 were used for the function of acquiring 'sexual attention' (this function
363 includes both inspection and copulation). 'Leaf-clipping', a gesture that was
364 closely associated with the function of acquiring 'sexual attention' outside

of consortship (31 of 40 recorded cases), was never observed during consortship communication. Other recorded functions included: Affiliation, Direct attention, Move closer, Position and Stop behaviour (all single cases).

The function 'follow' was very rarely recorded outside of the Consortship context, and never from adult males. During the study it was recorded in only 8 other bouts, all in 'travelling'; and almost all were mother to offspring communications (6/8; also 1-case between two brothers, 1-case between two sub-adults).

Response-waiting in gestural communication on consortship

Response-waiting is an indication of intentional communication and as such was one of several criteria for intentionality within this analysis. However, response-waiting was not the only indication used, so its distribution might still vary within the overall data set. Indeed, both adult males employed response-waiting significantly more often following consortship communications compared with other contexts (*Duane* response-waiting: consortship=345/379, mean frequency=88.7%; other contexts: 5/17, mean frequency=29.4%, Chi-square χ^2=7.66, df=1, p=0.0057; *Nick* response-waiting: consortship=14/14, mean

frequency=100.0%; other contexts=40/89, mean frequency=44.9%, Chi-square χ^2=14.70, df=1, p=0.0001).

Success of male communications in consortships

Figure 1 illustrates the variation in frequency of success of gestural communications *from* males, within and outside of the consortship context, alongside the variation in frequency with which females provided a successful response *to* gestural communications, within and outside of the consortship context. In both cases, the level of any kind of success seems to be lower within consortships than at other times; this is particularly so when indexed by the rates of completely successful communication.

Figure 1 here

Full success. Duane experienced significantly lower success in consortship communication (successful gestural communications: consortship n=229, mean frequency=25.3%; other contexts n=16, mean frequency=75.0%. Fisher's exact test p<0.0001). There was no significant variation in the success of the alpha male Nick (successful gestural communications: consortship n=14, mean frequency=42.9%; other contexts n=68, mean frequency=58.8%. Fisher's exact test p=0.377.)

Partial success. Again the alpha male Nick experienced no variation in partial success between consortship and other communications; however Duane experienced a significant increase in partially successful communication. (*Duane* partially successful gestural communications: consortship n=229, mean frequency=33.6%; other contexts n=16, mean frequency=0.0%. Fisher's exact test p=0.004. *Nick* partially successful gestural communications: consortship n=14, mean frequency=14.3%; other contexts n=68, mean frequency=13.2%. Fisher's exact test p=1.000).

Female responsiveness to male gestural communication on consortship

The variation in rate of success and partial success experienced by the two consorting males may be due to a difference between the males (e.g. rank) or a difference between the females with whom they attempted consortship. Table 1 describes the variation in female responsiveness to gestural communication while on consortship when compared to that in other contexts.

The only significant change in behaviour was recorded from the female Zimba, with whom Duane consorted twice. She produced complete responses significantly less often when consorting, although her level of partial responses was then higher than usual, suggesting that her responses were often not outright refusals.

Table 1 here

Lola produced very low levels of successful responses when in consortship (less than a third of either of the other 2 females) but this was not significantly lower than her level of response outside of consortships; her level of partial responses was not increased, as observed in Zimba. Nambi also made no significant change in her behaviour, although her level of successful response was much higher than that of Lola, equivalent to that of Zimba.

Persistence in gestural communication on consortship

Sonso chimpanzees persist following the failure (n=41, mean frequency=48.02% ±20.43) and, in particular, the partial failure (n=23, mean frequency=71.31% ±15.97) of a gestural communication (Independent t-test: $t=4.76$, $df=62$, $p<0.0001$). When compared with communication in other contexts, persistence following total failure was significantly higher in consortship communication by Duane, and approached a significant increase in Nick (see Table 2). Persistence following partial success in consortship behaviour was high from both males, but the available data were limited and there was no significant variation between this and other contexts.

455

456 Table 2 here

457

458 *Vocalization during consortship*

459

460 *Male vocalization.* Neither male produced any loud vocalization while on
461 consortship. Duane was observed to produce soft-pants in connection with
462 the *Rump-rub* gesture, Nick was not observed to vocalize while on
463 consortship.

464

465 *Female vocalization.* Nambi was not observed to vocalize loudly when in
466 consortship with Nick. Lola and Zimba both produced loud vocalizations,
467 including 11 bouts of screaming (Zimba =6, Lola =5), in the early stages of
468 consortship; all of these were followed by (9) or produced during (2) an
469 aggressive attack from Duane. On the first consortship between Duane and
470 Zimba, screaming by Zimba resulted in the consorting pair being discovered
471 by a group of males. On this occasion all the newly arrived males were
472 subordinate to the consorting male Duane and after a brief period of rest he
473 escorted Zimba away again. The screaming from Lola is likely to have
474 contributed to the eventual location of the pair by a party containing the
475 alpha male, which resulted in the immediate termination of the consortship
476 as Duane was chased away. Zimba was frequently observed to produce a
477 soft-bark immediately following a bout of gestural communication from

Duane; she would then follow on shortly after. This appeared to satisfy Duane, who would only resume gesturing if she continued to then make no further move towards him.

The coercion of females on consortship

During the year 2008, a total of 178 physically aggressive attacks were recorded in the Sonso community. Sixty-three of these attacks were classed as high-intensity attack due to repeated physical contact (hitting, kicking, biting etc.) and/or a resultant physical injury. Twenty-five of the high-intensity attacks were directed to females during consortships (39.7% of high-intensity attacks on 1.1% of observation days).

The majority of the high-intensity physical attacks (17/25) followed a failure by the female to respond to the male's gestural communication, predominantly a request that the female follow him. Three high-intensity attacks followed an attempt by the female to communicate vocally with other group members, and a further 3 followed attempts by the female to move away from the male.

Duane groomed the female on all three consortships but to a varying degree. In his consortship with Lola he aggressively coerced her from the start, and grooming behaviour was negligible (two bouts both <10seconds). During the first consortship with Zimba he was discovered in the morning

grooming her in her sleeping nest. He groomed her briefly once when she climbed down, and then following a period of more aggressive coercion he started grooming her for longer periods (>5min). On the second consortship, the beginning was again marked by a brief period of aggressive coercion followed by long bouts of grooming (>10min) once they were away from the group. Nick was not observed to groom Nambi.

Discussion

Consortships represent an understudied area of chimpanzee behaviour. Irregular, infrequent, and inherently secret, they are particularly difficult to record. Nevertheless, they provide crucial insight into an unusual form of social relationship in chimpanzee behaviour: an isolated male-female pair. Consortships are rare in the Sonso community (on average ~1 per year: slightly higher than the rate reported at Mahale (Hasegawa & Hiraiwa-Hasegawa, 1983), but much lower than Taï (Boesch & Boesch-Achermann, 2000) or Gombe (Tutin, 1979)). However, despite the low frequency of consortship events, gestural communication was used prolifically within them, and indeed consortships represented the dominant context for gestural use by adult male chimpanzees. This enabled us to compare the gestural communication of individuals within the context of

consortship with that made in other contexts. Male chimpanzees produced almost all of the gestural communication within consortships; they used a range of 17 gesture types, predominantly to request that the female follow them away from the group. In order to maintain exclusive access to female at her point of peak fertility, it is necessary to remove her before she reaches this stage. It is thus logical that the immediate function of the male's communication is to take the female away with him, rather than to facilitate engagement in sexual behaviour. The apparent lack of interest in immediate sexual access is supported by the absence of 'leaf-clipping', which is commonly used by Sonso chimpanzees to request sexual attention. Almost all gestures with the function of obtaining sexual attention were produced by the females, and accounted for most female gestural communication in consortships.

Perhaps surprisingly, considering the pressure to avoid detection by other chimpanzees (either by other Sonso males, or other communities), the majority of gestures used in consortship were audible. Given the loss of investment and the physical risk, should other individuals become aware of the consorting male's intentions, the use of audible gestures seemed initially counterintuitive. In attempting to understand this, we developed the post-hoc hypothesis that, as with vocalizations, there may be different levels of 'audibility' within gestural communication. Audible gesturing while in consortship was restricted to relatively quiet audible gestures such as

546 *Object-shakes*. These gestures were not only limited in the range that their
547 sound would travel, but the audible component was an extremely discreet
548 one: rustling foliage. Furthermore, unlike a vocalization or high-amplitude
549 gesture such as a buttress-drum, these short-distance, low-amplitude
550 gestures do not reveal individual identity; reducing the risk to the male
551 signalling should another individual, particularly another more dominant
552 male, 'overhear' the message. In contrast, in consortships there was no use
553 of the long-distance drumming gestures that are immediately identifiable as
554 chimpanzee communication, and from which it is also possible to discern
555 individual identity (Arcadi et al. 1998). Thus, the gesturing still appeared to
556 provide a discreet means to communicate in the dense secondary-forest
557 environment. This use of short-distance audible communication in gesturing
558 mirrors the pattern of vocalisations produced during consortship behaviour.
559 Males were only observed to produce soft-pant vocalisations and we found
560 that, as McGinnis (1973) reported, loud vocalisations on the part of the
561 female resulted in the threat or use of physical violence by the male. This
562 supports the idea that consorting male chimpanzees are highly motivated to
563 employ discrete methods of communication.
564
565 In comparison to contexts such as play or grooming, sexual
566 behaviour - in particular risky sexual behaviour such as consortship -
567 represents an evolutionarily more urgent function. Although the scarcity of
568 the behaviour limited the number of events and individuals available for

569 analysis, the high levels of gesturing allowed us to compare the gestural
570 behaviour within consortships with that of the same individuals in other
571 contexts. Given the extremely large potential payoff of a successful
572 consortship, consortship communication may be considered to have a high
573 evolutionary value for the male. This increased value is reflected in
574 increased response-waiting, and (to an extent) increased persistence
575 following failed communications.
576
577 The motivation to succeed in a consortship, as evidenced by
578 unusually high levels of response-waiting when gesturing, can also be
579 judged by the level of aggressive coercion employed by consorting males.
580 While brief fights are not unusual in chimpanzee behaviour, prolonged
581 bouts of severe aggression are rare, particularly between males and females.
582 Extensive grooming of the female did occur on two successful consortships,
583 but only after the female started to follow freely and the pair had moved
584 away from the core Sonso territory. Thus, grooming appeared to function
585 less as a form of coercion and more as a means to re-establish the social
586 bond between the pair following the earlier aggression. This delay in
587 grooming makes the repeated use of the rare *Rump-rub* gesture at the
588 earlier, more aggressive, stage in the consortship particularly interesting.
589 *Rump-rub* was documented at Gombe as "rump-turning" (Goodall, 1968)
590 and in a captive group by Tutin & McGrew (1973) as "bump rump". At
591 Sonso the gesture is usually used outside of consortship, by a lower-ranking

individual towards a more dominant one, in requests for affiliation or reassurance. Given the use of aggressive coercion towards a still-reluctant female, it seems puzzling that the dominant male would at this stage choose to employ a gesture whose physical form (a low crouch with the genitals exposed) is classically submissive, and that is associated with a submissive role in other contexts. However, the soft-pant vocalisation that accompanied the gesture may give some clue as to his intention. This vocalisation is normally given to a trusted group member in contexts such as food excitement or the arrival of a friendly other. The apparent submission implied by the use of the *Rump-rub* gestures by the male may represent an attempt to reassure the female, while continuing to gesture and communicate his desire that she follow him. Goodall suggested that the use of grooming by a consorting male might relax the female and give "proof of his fundamentally friendly intent", making her easier to lead away (Goodall, 1986:402). However, grooming requires that both individuals are stationary for several minutes or more. While this may be appropriate once they have moved away from the main group, it could be extremely costly for the male to sit down while still 'under-the-nose' of the other community males, particularly if the female is still not entirely co-operative. Thus the rump-rub gesture may function as a 'quick-and-dirty' way of expressing the consorting male's essentially friendly intent: encouraging the female in the initial stages of consortship as she is being coerced into leaving the main

614 group; but without the need for time-consuming bouts of grooming while
615 the pair are still in the vicinity of other community males and risk discovery.
616
617 While on consortship, levels of female responsiveness to male
618 gestural communication were generally low. However, one female, Zimba,
619 although she infrequently responded with the desired 'follow', did, at least,
620 frequently produce behaviour that was congruent with following. In practice
621 this meant that although she did not follow the male she would turn to
622 attend to his communication, and approach a little way towards him. While
623 on consortship Zimba was accompanied by her two young sons who would
624 occasionally wander behind, so her partial responses may have represented
625 an attempt on her part to acknowledge Duane's communication while at the
626 same time giving her sons time to catch up. In doing so Zimba avoided the
627 complete refusals that were that were associated with aggressive coercion
628 such as high-intensity physical attacks.
629
630 The extensive gesturing by adult males in consortship differs
631 dramatically from the low frequency of adult male gesturing reported in
632 captivity, and represents the first description of gesture use in an
633 'evolutionary urgent' context. Gestural communication offers male
634 chimpanzees the opportunity to communicate their intentions to the female
635 they wish to engage in consortship, while minimising the risk of also
636 advertising these intentions to other community males. This finding

637 highlights the importance of studying behaviour in a natural population
638 where the full range of environmental and social contexts is available.
639
640
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651
652
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