Foraging postures are a potential communicative signal in female bonobos

Elisa Demuru1,2*, François Pellegrino1, Dan Dediu1 & Florence Levréro2

Body postures are essential in animal behavioural repertoires and their communicative role has been assessed in a wide array of taxa and contexts. Some body postures function as amplifiers, a class of signals that increase the detection likelihood of other signals. While foraging on the ground, bonobos (Pan paniscus) can adopt different crouching postures exposing more or less of their genital area. To our knowledge, their potential functional role in the sociosexual life of bonobos has not been assessed yet. Here we show, by analysing more than 2,400 foraging events in 21 captive bonobos, that mature females adopt a rear-exposing posture (forelimb-crouch) and do so significantly more often when their anogenital region is swollen than during the non-swollen phase. In contrast, mature males almost completely avoid this posture. Moreover, this strong difference results from a diverging ontogeny between males and females since immature males and females adopt the forelimb-crouch at similar frequencies. Our findings suggest that the forelimb-crouch posture may play a communicative role of amplification by enhancing the visibility of female sexual swellings, a conspicuous signal that is very attractive for both males and females. Given the high social relevance of this sexual signal, our study emphasizes that postural signalling in primates probably deserves more attention, even outside of reproductive contexts.

Body postures are an essential part of behavioural repertoires in animals and since Darwin's pioneering work on The Expression of the Emotions in Man and Animals researchers have been interested in their communicative role in a wide array of taxa and behavioural contexts. Some body postures have been interpreted as amplifiers, a class of signals that increase the detection likelihood of the information conveyed by other pre-existing signals associated with the signaller's quality. Amplifiers operate in conjunction with the signal they amplify, and although they do not transform it or change its quality (size, strength, colour, etc.), they do increase the probability that it will be perceived by potential receivers. Therefore, an amplifier is specifically selected as a conspicuousness-enhancing "extra signal component" resulting in the emergence of composite signals. A classic example of this type of signal has been revealed by Taylor and colleagues in the jumping spider of the species Plexippus paykulli, where males raise their bodies and point their abdomens downwards during interactions with rivals and potential mates. This posture exposes the abdominal pattern, a signal that makes the differences in abdominal width more visible. Other amplifiers have been documented in fish, reptiles, insects, and birds, especially in the context of male courtship.

While postures have long been mentioned as important in great ape communication, they have been overlooked in the recent surge of great ape gesture research and, to our knowledge, no study has ever considered their potential role as amplifier signals. Here, we aim to fill this gap by examining the role of two foraging postures in bonobos.

Bonobos present a particularly fascinating repertoire of social behaviours and communicative signals. Among these signals, the exaggerated sexual swelling of female bonobos is probably the most conspicuous. As in other primate species, bonobo females' anogenital region changes in size and turgidity along the menstrual cycle, becoming a highly noticeable signal during the phase of maximum swelling. However, in contrast with other primates, the maximum sexual swelling in bonobos is not a reliable indicator of ovulation; it has an extremely extended duration and is sexually attractive not only for males but also for females. More importantly, this signal is not strictly linked to the reproductive function, but plays an additional role of favouring
female socio-sexuality. A species-specific behavioural trait promoting female cohesion\textsuperscript{11,12} is genito-genital (GG) rubbing, in which two bonobo females embrace each-other face to face and rub their genitals together by moving them side to side\textsuperscript{13}. Considering the social significance of sexual swelling in this species, it is reasonable to hypothesize that any behaviour enhancing the perceptiveness of this signal should be positively selected.

While foraging on the ground, bonobos routinely pick up food directly with the mouth adopting two different postures: full-crouch, in which elbows and hindlimbs are flexed, and forelimb-crouch, in which the elbows are flexed but the knees are not (\textsuperscript{14} and Fig. 1). In contrast with the full-crouch posture, the forelimb-crouch posture has the peculiarity of exposing the anogenital area, but this postural behaviour has never been investigated as a potential communicative signal. Both postures typically coexist in each individual's repertoire and, to the best of our knowledge, it is still unknown whether social or ecological factors influence these postural behaviours. In this observational study focussing on the emitter's perspective, we provide a thorough analysis of the occurrence of forelimb-crouch and full-crouch in bonobos by putting these two body postures in relation with individual features, such as age, gender, and reproductive and hierarchical status. Knowing the importance of socio-sexual behaviours in bonobo society, our hypothesis is that the foraging posture, by enhancing the visibility of the anogenital swelling, could play a communicative role in the social and reproductive preferences of bonobos and match the definition of amplifier\textsuperscript{3,4}, which is still sparsely documented in the animal kingdom. We thus predict that the rear-exposing forelimb-crouch posture is not equally adopted among individuals. More specifically, we predict that adult females adopt this posture more frequently than adult males and immature subjects, and that this posture is preferred when the sexual swelling is in the maximum phase.

Materials and methods

Data acquisition and coding. Data collection was performed at the primate park La Vallée des Singes (France) in June–August 2012, June–July 2014, and April–June 2018, on a total of 21 captive-born bonobos (see supplementary information for group composition). These bonobos lived in a stable social group housed in an enclosure with both an indoor (about 500 m\textsuperscript{2}) and outdoor facility (8,500 m\textsuperscript{2}). Observations were performed when the animals were in the outside enclosure, consisting of a wooded island surrounded by water canals. Data collection was performed from the moment they left the inside enclosure in the morning (9:00) to the moment they were given access again to the inside enclosure to spend the night (18:30). Before letting the bonobos out, zoo keepers scattered a mixture of seeds and grains on the ground as a form of environmental enrichment. This is the type of food that mostly elicited forelimb- and full-crouching. During the day, the bonobos were fed at 11:30, 14:30, 15:45, 17:00, and 18:00, mainly with roughly chopped vegetables that bonobos eat while sitting or walking. Water was provided ad libitum.

Data collection was observational, complied with the park research charter and had been previously approved by the zoological curator of La Vallée des Singes. Data were collected through continuous video-recordings (~380 h) by applying Focus Group sampling\textsuperscript{15}, with no specific behaviour being targeted. The analysis encompassed events consisting of bonobos foraging on the ground by picking up small food items (seeds and grains) directly with the mouth. An event began when the bonobo started picking up food from the ground with its mouth by adopting either the full-crouch (i.e., elbows and knees are flexed) or the forelimb-crouch (i.e., elbows are flexed but the knees are not) posture and lasted until the individual lifted its mouth from the ground for at least 3 s, or if it switched directly from one posture to the other; this rarely occurred (only 7 times out of 2,403 recorded events). For each event, its duration, the individual identity and the body posture (full-crouch or forelimb-crouch\textsuperscript{14}, Fig. 1) were coded by the first author as primary coder. A second researcher, unaware of the aim of the study, independently coded around 25% of randomly chosen events (N = 642) of the total events (N = 2,403). We performed a Cohen's Kappa analysis that showed almost perfect agreement (98.92% agreement; Cohen's kappa: 0.98). Aggressive conflicts were recorded by the All Occurrences sampling\textsuperscript{15} method. For each
year, and for the mature subjects only, hierarchy was assessed by entering conflicts into a winner/loser socio-
matrix, and the rank was estimated by Normalized David’s Scores (NDS)\(^1\). For each year we created hierarchy
classes by listing the individual NDS in decreasing order and by categorizing an individual as high ranking (their
NDS is in the upper quartile), low ranking (NDS in the lower quartile), and medium ranking (all the others) (see
supplementary information for group composition). For each adult female, changes in size, firmness and colora-
tion of the sexual swelling were assessed by the keepers as part of their daily routine since the establishment of
the La Vallée des Singes bonobo group in 2009. The bonobo keepers code changes in sexual swelling firmness
and size following Furuichi’s method\(^1\) and distinguish three phases: minimum, intermediate and maximum.
The intermediate phase encompasses both increasing (i.e., from minimum to maximum) and decreasing swelling
size (i.e., from maximum to minimum) and, therefore, it does not represent a homogenous category. We decided
to keep the intermediate phase in the analyses to provide a general overview of the phenomenon. The keepers
were unaware of the aim of the study.

Statistics. We used mixed-effects logistic regression as implemented by R’s\(^{18} \texttt{glmer()} \) function in the
\texttt{lme4} package, where the posture in each foraging event, coded as "down" (= full-crouch) or "up" (= forelimb-
crouch), is the dependent variable, and the subject and year collection are random effects. The interpretation of
the fixed effect slopes \(\beta\) is in terms of increasing (\(\beta > 0\)) or decreasing (\(\beta < 0\)) the probability of an "up" posture.
For the first model (all subjects), the fixed effects considered were sex (female vs male), age (in years), age_class
(immature vs mature), and duration (the natural logarithm of the feeding episode’s duration in seconds). For
the second model (mature females only), we considered as fixed effects age, swelling (a three-level ordered factor
"min" < "intermediate" < "max"), hierarchy (ordered factor: "high" > "intermediate" > "low") and duration (as above).
For both models, we first tested each potential predictor separately, and we only retained those resulting
in a significant improvement (at the liberal \(\alpha\)-level of 0.10) in predicting posture over the null model (including
only the intercept and the random effects); importantly, hierarchy was never retained, as it did not make a
significant contribution on its own; also, age and age_class were never simultaneously considered in the same
model. We then used model simplification of the full model including all these retained predictors (and their
interactions), iteratively removing the interactions and predictors that failed to make a significant (at \(\alpha\)-level
0.05) contribution on its own; also,\(p^*\) is the p-value of the whole linear and quadratic effects. Bold = significance at \(\alpha\)-level 0.05.

Results

We sampled 2,403 foraging events from video recordings of 21 bonobos and statistically modelled them, with
posture (forelimb-crouch or full-crouch) as the dependent variable (see “Materials and methods” and Table 1. See
also the dataset, descriptive data, and detailed statistical analyses provided in the supplementary information).
The statistical analysis shows a diverging ontogeny between males and females in their probability of forelimb-
crouching (Fig. 2a): forelimb-crouching seldom occurs in mature males compared to immature males (6.3% vs
30.2% of observed events respectively), whereas this posture is more often displayed in mature (58.9%) than
immature (40.3%) females. There is indeed a significant positive effect of being mature on the probability of

\begin{table}
\centering
\begin{tabular}{|c|c|c|c|c|c|}
\hline
Model & Predictor & Estimate & 95% CI & p & \(p^*\) \\
\hline
All individuals & Intercept & 0.13 & (−0.77, 1.02) & 0.78 & – \\
& Sex (M) & 0.63 & (−0.51, 1.76) & 0.28 & – \\
& Duration & −0.56 & (−0.68, −0.43) & <2.16 \times 10^{-16} & – \\
& Age_class (mature) & 1.03 & (0.08, 1.98) & 0.034 & – \\
& Sex (M) : duration & −0.72 & (−1.01, −0.42) & 1.99 \times 10^{-4} & 5.21 \times 10^{-7} \\
& Sex (M) : age_class (mature) & −2.31 & (−3.60, −1.02) & 0.0004 & 0.0016 \\
\hline
Mature females & Intercept & 1.51 & (0.59, 2.43) & 0.0013 & – \\
& Swelling (linear) & 1.26 & (0.89, 1.63) & 2.59 \times 10^{-4} & 2.73 \times 10^{-14} \\
& Swelling (quadratic) & −0.47 & (−0.86, −0.08) & 0.018 & – \\
& Duration & −0.55 & (−0.72, −0.39) & 9.69 \times 10^{-11} & – \\
\hline
\end{tabular}
\caption{Summary of statistical models, showing fit indices (marginal \(R^2\) and Akaike Information Criterion
\(AIC\)), the between-group variances for the random effects (\(\tau_{00}\) for subject and year_collection), and point
estimates, 95% confidence intervals and \(p\)-values of predictors and their interactions (if included). The
estimates and 95% CIs are in log odds of the position being “up”. For interactions in the “all individuals” model,
each \(p^*\) is the \(p\)-value of the whole interaction, while for the “mature females” model, \(p^*\) is the \(p\)-value of the
whole linear and quadratic effects. Bold = significance at \(\alpha\)-level 0.05.}
\end{table}
forelimb-crouching ($\beta = 1.03, p = 0.034$) and a significant interaction between sex and age class ($p = 0.0016$). Event duration is also influential, with most individuals showing a preference for full-crouching for longer durations ($\beta = -0.56, p < 2.16 \times 10^{-16}$), but with a higher probability of forelimb-crouch posture for females ($p = 1.99 \times 10^{-5}$).

Focusing on mature females (Fig. 2b), we found that while their posture is not affected by hierarchical rank ($p = 0.71$), it does change with swelling ($p = 2.73 \times 10^{-13}$): at intermediate and maximum swelling phases there is a higher probability of forelimb-crouching (69.0% and 66.3%) than at minimum swelling phase (49.6%), this relationship being non-linear (linear component: $\beta = 1.26, p = 2.59 \times 10^{-11}$, and quadratic component: $\beta = -0.47, p = 0.018$; Table 1). The negative effect of duration is confirmed in this second analysis ($\beta = -0.55, p = 9.69 \times 10^{-11}$).

Discussion
Our results show that whereas immature bonobos did not show any significant sex differences in positional preference, mature bonobos displayed strong preferences either to adopting the rear-exposing forelimb-crouch (females) or to avoiding it (males). For mature females, the changes in their postural behaviours through their sexual swelling cycle suggest a stronger preference for forelimb-crouching during the swelling phases (i.e., intermediate and maximum) over the non-swelling phase. In all cases, individuals engaging in foraging events longer than 12 s tended to adopt the full-crouch posture, which is compatible with the physiological cost of ingesting food with an upside-down digestive tract. These findings outline a general pattern with a random distribution between forelimb-crouching and full-crouching for immature subjects and for mature females in the minimal swelling phase. In contrast, the dichotomy observed between mature females in swollen phases and mature males strongly suggests a non-random sex-dependent cost–benefit ratio. The infrequency of forelimb-crouch in mature males may be driven by the need to reduce the risk of exposing the testicles, a body part often targeted during conflicts in the Pan species\(^{19,20}\). For mature females, the fact that dominance rank did not influence the probability of forelimb-crouch lets us reject the competing explanation that this posture might represent a hierarchy signal\(^{21}\).

Moreover, the fact that a general preference for full-crouching for longer foraging events was also observed in females during the maximum swelling phase rules out the competing explanation that this posture is adopted because the swelling hinders full-crouching.

Figure 2. Panels displaying the percent probability of forelimb-crouching and the log(duration) for three subgroups of subjects: (a) by sex for immatures and adults, and (b) by swelling phase for mature females.
environments than previously thought, and notably forest-savanna mosaic environments, and the efficient use of data in situ, it is currently difficult to assess the efficiency of such visual amplification. Although bonobos live in forests and savannas, the forelimb-crouch posture that highlights the genital parts and thus the sexual swelling stage of adult females. Because of the lack of data in situ, it is currently difficult to assess the efficiency of such visual amplification. Although bonobos live in forest habitats, these are of heterogeneous types. Whereas previous studies on wild bonobos have mainly been conducted in rich tropical rainforests, it has been recently confirmed that wild bonobos inhabit a wider range of environments than previously thought, and notably forest-savanna mosaic environments, and the efficient range in the visual channel thus varies among these forest habitat types. In line with the importance of visual communication in bonobos (e.g. gestures), a potential amplifier role of forelimb-crouching is thus possible and our unambiguous results in captivity are consistent with this hypothesis. However, we cannot conclude that captivity has favoured this behaviour since (i) the visibility between individuals is almost permanent and (ii) bonobos spend more time on the ground foraging than in the wild (F. Levréro’s personal communication). In addition, we suggest that the forelimb-crouch posture might be present in other primate species showing sexual swelling, where it might enhance this more reliable signal of fertility. More generally, by focussing on human’s closest living relatives our study bridges theoretical and empirical aspects and sheds light on postural signalling as a potential neglected dimension of the evolutionary pathways leading to improved communication efficiency in animals, including humans.

Data availability
Dataset is provided in the supplementary information as well as the Rmarkdown script and html output of the statistical analyses.

Received: 26 February 2020; Accepted: 18 August 2020
Published online: 22 September 2020

References
1. Darwin, C. R. The Expressions of the Emotions in Man and Animals (John Murray, London, 1872).
2. Taylor, P. W., Hasson, O. & Clark, D. L. Body postures and patterns as amplifiers of physical condition. Proc. R. Soc. B 267, 917–922. https://doi.org/10.1098/rspb.2000.1090 (2000).
3. Hasson, O. Amplifiers and the handicap principle in sexual selection: A different emphasis. Proc. R. Soc. B 235, 383–406. https://doi.org/10.1098/rspb.1989.0006 (1989).
4. Harper, D. G. C. Maynard Smith: Amplifying the reasons for signal reliability. J. Theor. Biol. 239, 203–209. https://doi.org/10.1016/j.jtbi.2005.08.034 (2006).
5. Hebets, E. A. & Papaj, D. R. Complex signal function: Developing a framework of testable hypotheses. Behav. Ecol. Sociobiol. 57, 197–214. https://doi.org/10.1007/s00265-004-0865-7 (2005).
6. Tomasello, M. & Call, J. Thirty years of great ape gestures. Anim. Cogn. 22, 461–469. https://doi.org/10.1007/s10071-018-1167-1 (2019).
7. Hare, B. & Yamamoto, S. (eds) Bonobos: Unique in Mind, Brain, and Behavior (Oxford University Press, Oxford, 2017).
8. Dixson, A. F. Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes and Humans 2nd edn. (Oxford University Press, Oxford, 2012).
9. Douglas, P. H., Hohmann, G., Murtagh, R., Thiessen-Bock, R. & Deschner, T. Mixed messages: Wild female bonobos show high variability in the timing of ovulation in relation to sexual swelling patterns. BMC Evol. Biol. 16, 140–157. https://doi.org/10.1186/s12862-016-0691-3 (2016).
10. Paoli, T., Palagi, E., Tacconi, G. & Tarli, S. B. Perineal swelling, intermenstrual cycle, and female sexual behavior in bonobos. (Pan paniscus). Am. J. Primatol. 68, 333–347. https://doi.org/10.1002/ajp.20228 (2006).
11. Rya, H. R., Hill, D. A. & Furuchi, T. Prolonged maximum sexual swelling in wild bonobos facilitates affiliative interactions between females. Behavioral 152, 285–331. https://doi.org/10.1163/1568539X-00003212 (2014).
12. Moscovic, L. R. et al. The cooperative sex: Sexual interactions among female bonobos are linked to increases in oxytocin, proximity and coalitions. Horm. Behav. 116, 104581. https://doi.org/10.1016/j.yhbeh.2019.104581 (2019).
13. Kuroda, S. Social behavior of the pygmy chimpanzees. Primates 21, 181–197 (1980).
14. Hunt K.D., et al. Standardized description of primate locomotor and postural modes. Primates 37:363-387; https://doi.org/10.1007/BF02381373 (1996).
The authors declare no competing interests.

Acknowledgements
This work was supported by LabEX ASLAN—Advanced Studies on LANguage complexity (ANR-10-LABX-0081) and IDELYON (ANR-16-IDEX-005 and ANR-11-IDEX-0007) of the University of Lyon. The 2012 and 2014 data collections were funded by the University of Parma (Italy). We thank the La Vallée des Singes staff, particularly Jean-Pascal Guéry (Zoo curator), Carole Michelet, Franck Alexieff, Lolita Bertrand, and Jeremy Mergault. Thanks to Sergio Castellano and Ivan Norscia for helpful comments on earlier versions of the manuscript. We also wish to thank Antonio Santucci and Marta Caselli for helping in data collection and coding, and Brigitte Pakendorf for English proofreading.

Author contributions
E.D. conceived the study, collected and coded the data. E.D., F.P., D.D., and F.L. jointly analysed the data, produced and discussed the results, and wrote the manuscript.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary information is available for this paper at https://doi.org/10.1038/s41598-020-72451-3.

Correspondence and requests for materials should be addressed to E.D.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher’s note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.
