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The ontogeny of pant hoot vocalisations and social awareness in wild chimpanzees

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Titre :

"The ontogeny of pant hoot vocalisations and social awareness in wild chimpanzees"

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1. Summary

While some scholars have regarded primate vocal communication as innate, inflexible, and insensitive to the context, recent advances suggest instead that vocal behaviours can be flexible, insofar as they are affected by individual and situational factors, notably the social context. However, whether the same is true for the acquisition of communicative capacities remains largely unknown, particularly in great apes.

In my thesis, I address this by examining the ontogeny of vocal behaviours in the pant hoots of immature chimpanzees (Pan troglodytes schweinfurthii) of the Budongo Forest, Uganda. Furthermore, I investigate audience effects on pant hoot sequences used during displays to determine the extent to which these vocal structures are flexibly modulated depending on the social environment. Pant hoots are a multi-phase vocal sequence typically used to maintain contact and coordinate movements between individuals and groups over long distances. The question of how this complex and flexible vocal signal develops is key for a better understanding of how chimpanzees navigate dynamic social interactions in fission-fusion societies from both an ontogenetic and a comparative perspective.

Results from my thesis show that chimpanzees produced rudimentary pant hoot sequences since birth, suggesting that vocal repertoires are largely innate. However, these sequences presented some structural and acoustic differences when compared to those of older individuals, suggesting they also undergo ontogenetic changes. In addition, the vocal usage and responses to pant hoots in immature chimpanzees was enhanced by greater vocal and social exposure to key group members, such as the mother and adult males, when compared to the development of less gregarious immature individuals. Finally, social context modulated the use of pant hoot phases during vocal displays, likely enhancing the communicative capacities of a species with limited vocal production learning and relatively small vocal repertoire.

Taken together, findings from my thesis suggest that the ontogeny of complex chimpanzee vocalisations is socially mediated and that chimpanzee vocal communication is flexibly adjusted depending on the social environment.

Keywords: Vocal development, chimpanzees, primates, audience effect, communication, call combinations, vocal behaviour, social learning.

2. Résumé

Alors que certains chercheurs ont considéré la communication vocale des primates comme innée, inflexible et insensible au contexte, des avancées récentes suggèrent plutôt que les comportements vocaux peuvent être flexibles, dans la mesure où ils sont affectés par des facteurs individuels et situationnels, notamment le contexte social. Cependant, s'il en est de même pour l'acquisition des capacités de communication reste largement inconnu, en particulier chez les grands singes.

Dans ma thèse, j'aborde cette question en examinant l'ontogénie des comportements vocaux dans les vocalisations de chimpanzés immatures (*Pan troglodytes schweinfurthii*) qui vivent dans la forêt de Budongo, en Ouganda. De plus, j'étudie les effets du public sur les séquences vocales nommées « pant-hoots » utilisées lors des exhibitions agonistiques afin de déterminer dans quelle mesure ces structures vocales sont modulées de manière flexible en fonction de l'environnement social. Les pant-hoots sont une séquence vocale multi-phase généralement utilisée pour maintenir le contact et coordonner les mouvements entre les individus et les groupes sur de longues distances. La question de savoir comment ce signal vocal complexe et flexible se développe est essentielle pour une meilleure compréhension de la façon dont les chimpanzés naviguent leurs interactions sociales dynamiques qui caractérisent les sociétés de fission-fusion d'un point de vue ontogénétique et comparatif.

Les résultats de ma thèse montrent que les chimpanzés produisent des séquences rudimentaires de pant-hoots depuis la naissance, ce qui suggère que les répertoires vocaux sont en grande partie innés. Cependant, ces séquences présentaient certaines différences structurelles et acoustiques par rapport à celles produites par des individus plus âgés, suggérant qu'elles subissent également des changements ontogénétiques. De plus, l'utilisation vocale et les réponses pant-hoots chez les chimpanzés immatures ont été renforcés par une plus grande exposition vocale et sociale aux membres clés du groupe, tels que la mère et les mâles adultes, par rapport au développement d'individus immatures moins grégaires. Enfin, le contexte social a modulé l'utilisation des phases de pant-hoots produites pendant les exhibitions agonistiques, potentiellement améliorant les capacités de communication d'une espèce avec un apprentissage de la production vocale limité et un répertoire vocal relativement réduit.

En conclusion, les résultats de ma thèse suggèrent que l'ontogenèse des vocalisations complexes des chimpanzés est socialement favorisée et que la communication vocale des chimpanzés est ajustée de manière flexible en fonction de l'environnement social.

Mots-clés : Développement vocal, chimpanzés, primates, effet d'audience, communication, combinaisons de vocalisations, comportement vocal, apprentissage social

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5. Declarations

5.1. Candidate's declaration

I, Adrian Soldati, do hereby certify that this thesis, submitted for the degree of PhD, which is approximately 42,000 words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for any degree. I confirm that any appendices included in my thesis contain only material permitted by the 'Assessment of Postgraduate Research Students' policy.

I was admitted as a research student at the University of St Andrews in September 2018.

I received funding from an organisation or institution and have acknowledged the funder(s) in the full text of my thesis.

Date 29/12/2022 Signature of candidate

5.2. Supervisor's declaration

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of PhD in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree. I confirm that any appendices included in the thesis contain only material permitted by the 'Assessment of Postgraduate Research Students' policy.

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Date 29/12/2022 Signature of candidate

Date 29/12/2022 Signature of supervisor

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7.1. Research Data/Digital Outputs access statement

Chapter 2: This chapter has been published in *International journal of primatology* as an open access article (doi:10.1007/s10764-022-00321-y). Supplementary material associated with this article is available at:
https://osf.io/v4k86/?view_only=309da3d6a7a54bca9e8c6dd9ae7bb4ed

Chapter 3: This chapter is in preparation for submission. Supplementary material associated with this article is available at:
https://osf.io/v4k86/?view_only=309da3d6a7a54bca9e8c6dd9ae7bb4ed

Chapter 4: This chapter has been published in *Animal Behaviour* as an open access article (doi:10.1016/j.anbehav.2022.05.010). Supplementary material associated with this article is available at:
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8. Dissemination of research

Chapter 2:

- Soldati, A., Muhumuza, G., Dezecache, G., Fedurek, P., Taylor, D., Call, J., Zuberbühler, K. (2022). The ontogeny of vocal sequences: insights from a newborn wild chimpanzee (*Pan troglodytes schweinfurthii*). Published in *International Journal of Primatology*. 10.1007/s10764-022-00321-y

Chapter 3:

- Soldati, A., Fedurek, P., Dezecache, G., Muhumuza, G., Call, J., Zuberbühler, K. (2021). The ontogeny of behavioural responses to pant hoot calls in wild chimpanzees. Oral presentation at PSGB Winter Conference (December 8th, 2021)
- Soldati, A., Fedurek, P., Dezecache, G., Muhumuza, G., Call, J., Zuberbühler, K. (2021). The ontogeny of behavioural responses to pant hoots in wild chimpanzees. Oral presentation at DPOB Meeting, University of Neuchâtel (December 9th, 2021).
- Soldati, A., Fedurek, P., Dezecache, G., Muhumuza, G., Call, J., Zuberbühler, K. (2022). The ontogeny of behavioural responses to pant hoots in wild chimpanzees. Oral presentation at EFP international conference, Arnhem, Netherlands (June 3rd, 2022).
- Soldati, A., Fedurek, P., Dezecache, G., Muhumuza, G., Hobaiter, C., Call, J., Zuberbühler, K. (2022). The ontogeny of behavioural responses to pant hoots in wild chimpanzees. Online Poster at Joint Conference on Language Evolution, Kanazawa, Japan (September 6th, 2022).

Chapter 4:

- Soldati, A., Fedurek, P., Dezecache, G., Call, J., Zuberbühler, K. (2022). Audience sensitivity in chimpanzee display pant hoots. Published in *Animal Behaviour*. 10.1016/j.anbehav.2022.05.010
- Soldati, A., Fedurek, P., Dezecache, G., Call, J., Zuberbühler, K. (2021). Vocal displays in wild chimpanzees. Invited presentation at Behaviour and Evolution Research Group (BERG), University of Stirling (March 10th, 2021).
- Soldati, A., Fedurek, P., Dezecache, G., Call, J., Zuberbühler, K. (2021). Sensitivity to audience in chimpanzee complex vocal displays. Oral presentation at ASAB virtual Summer meeting, University of Belfast (August 23rd, 2021).
- Soldati, A., Fedurek, P., Dezecache, G., Call, J., Zuberbühler, K. (2021). Audience sensitivity in chimpanzee display pant hoots. Oral presentation at PSGB Summer Conference (July 1st, 2022).

9. General abstract

While some scholars have regarded primate vocal communication as innate, inflexible, and insensitive to the context, recent advances suggest instead that vocal behaviours can be flexible, insofar as they are affected by individual and situational factors, notably the social context. However, whether the same is true for the acquisition of communicative capacities remains largely unknown, particularly in great apes. In my thesis, I address this by examining the ontogeny of vocal behaviours in the pant hoots of immature chimpanzees (*Pan troglodytes schweinfurthii*) of the Budongo Forest, Uganda. Furthermore, I investigate audience effects on pant hoot sequences used during displays to determine the extent to which these vocal structures are flexibly modulated depending on the social environment.

Pant hoots are a multi-phase vocal sequence typically used to maintain contact and coordinate movements between individuals and groups over long distances. The question of how this complex and flexible vocal signal develops is key for a better understanding of how chimpanzees navigate dynamic social interactions in fission-fusion societies from both an ontogenetic and a comparative perspective.

Results from my thesis show that chimpanzees produced rudimentary pant hoot sequences since birth, suggesting that vocal repertoires are largely innate. However, these sequences presented some structural and acoustic differences when compared to those of older individuals, suggesting they also undergo ontogenetic changes. In addition, the vocal usage and responses to pant hoots in immature chimpanzees was enhanced by greater vocal and social exposure to key group members, such as the mother and adult males, when compared to the development of less gregarious immature individuals. Finally, social context modulated the use of pant hoot phases during vocal displays, likely enhancing the communicative capacities of a species with limited vocal production learning and relatively small vocal repertoire. Taken together, findings from my thesis suggest that the ontogeny of complex chimpanzee vocalisations is socially mediated and that chimpanzee vocal communication is flexibly adjusted depending on the social environment.

10. General introduction

Communication involves one or more individuals (i.e., signallers) producing a behaviour that affects the present or future behaviour of one or more other individuals (i.e., receivers) (Bradbury & Vehrencamp, 2011; Maynard Smith & Harper, 1995). The act of signalling provides both benefits and costs to signallers and receivers depending on the context in which it occurs and on the information transmitted through the signal (Smith, 1997; Smith, 1965). While many animals produce signals using a wide range of modalities, including facial expressions and gestures, the focus of my work is on vocalisations. Signallers use vocalisations to inform conspecifics about their state or activity, e.g., when being the victim of an attack, about their individual characteristics, e.g., when displaying their social status, or about the external world, e.g., when finding an abundant source of food. Thus, receivers can use a signal to predict something about the social and ecological context as well as the signaller's future behaviours and by doing so reduce uncertainty about the signaller and the communicative interaction. A signal's information is typically encoded in acoustic variations of call structures and to infer its 'meaning' or function receivers use statistical regularities and patterns associated with the signal itself, the context of production, and the responses of other individuals (Beecher, 1989; Maynard Smith & Harper, 1995).

Many animal species produce a range of different call types, which represent their vocal repertoire when considered as a whole. Consistent patterns in the acoustic features (e.g., duration and fundamental frequency) and the context of production allow researchers to separate these sounds into different categories. Based on how far the signal travels through the environment and consequently which receivers and audiences can hear them, calls are typically separated into two broad categories as short-distance (or soft) and long-distance (or loud) vocalisations. Species living in large territories and widely spaced groups make frequent use of long-distance calls to maintain contact, coordinate movements between sub-groups, and assert control over their domain. Animals living in fluid fission-fusion societies, where the composition of groups varies regularly during the day, benefit particularly from using these long-distance signals, for instance bonobos (*Pan paniscus*: White et al., 2015), elephants (*Loxodonta africana*: Leighty et al., 2008), and lions (*Pantera leo*: McComb et al., 1994). Vocal communication appears to be a fundamental social tool that animals use to maintain contact and coordinate behaviours, particularly when receivers are out-of-sight due to large inter-individual spacing or in low-visibility habitats. In the following section I review relevant features of animal vocal behaviours, with a particular focus on vocal flexibility and social awareness and how they relate to the social lives of primates.

10.1. Social awareness during vocal communication

Vocal behaviours are particularly interesting to investigate from the perspective of signallers and receivers in species where social interactions and relationships are key to the survival and success of group members (Cheney & Seyfarth, 2018; Silk, 2007). Typically, increasing complexity in the social environment is associated with greater complexity in vocal communication, exemplified by the presence of larger repertoire sizes and the use of more complex vocal structures (Engesser & Townsend, 2019; McComb & Semple, 2005; Pougnault et al., 2022). Vocal and social interactions appear to be particularly complex in primate species (Bouchet, Blois-Heulin, et al., 2013; Dunbar & Shultz, 2007), where relatively large groups of individuals establish a rich network of social relationships. Here, signallers take into account the nature of relationships between signallers and receivers while coordinating group behaviours using a flexible communication system. Ultimately, vocal communication acts as a social tool to navigate complex interactions and dynamic situations.

10.1.1. Audience effects on vocal behaviours

Vocalisations, particularly long-distance calls, are often broadcasted to multiple potential listeners opening the possibility of eavesdropping, which entails both costs and benefits to signallers as well as receivers (Matos & Schlupp, 2005). These calls might be targeted at specific receivers to elicit specific responses when beneficial to the signaller, for instance when attracting a potential mate (McGregor & Peake, 2000). Alternatively, signallers might refrain from calling when it is costly or dangerous, for instance to conceal their identity and location to competitors (Fichtel & Manser, 2010). As a consequence, an interplay between benefits and costs imposed on both signallers and receivers by nearby individuals is likely responsible for the evolution of vocal behaviours. The proximate psychological processes that determine whether a call is produced or not as well as the acoustic modifications that signallers introduce based on the presence of others can inform us about the extent of control that animals have on their vocal output. Furthermore, they are important for identifying how more flexible and complex forms of communication evolved (Fichtel & Manser, 2010).

A large number of studies showed that animal callers are susceptible to social information, and in particular to the identity of nearby receivers (Evans, 1997; Marler et al., 1986), a phenomenon generally referred to as ‘audience effects’ (Zuberbühler, 2008). Here, the audience refers to all individuals considered as bystanders, which include receivers towards which calls are directed to, as well as individuals who hear broadcasted calls. This phenomenon is widespread in the animal kingdom, with many species capable of adjusting their vocal behaviour in the presence or absence of specific individuals, or based on the number of nearby individuals (e.g., *Gallus gallus*: Evans & Marler, 1994; *Betta splendens*: Matos et al., 2003; *Cynictis penicillata*: Le Roux et al., 2008). The presence of audience effects indicates that signallers can direct their vocalisations to specific receivers and audiences when beneficial, or instead withhold their vocalisations when costly, suggesting a strategic use of vocal behaviours. Furthermore, studying audience effects allows us to test whether vocalisations are produced in a goal-directed manner and examine the degree of control signallers have over vocal outputs (Evans, 1997; Schamberg et al., 2018).

Audience effects have typically been investigated by looking at whether or not or how many times a signaller calls in a defined period of time or during specific social context. In contrast, whether signallers modify the acoustic structure of their calls based on the audience has been rarely investigated (but see Slocombe & Zuberbuhler, 2007). Recent advances revealed that animals, including primates, demonstrate greater flexibility and complexity in their vocal behaviour than previously assumed (Freeberg et al., 2012; Gustison et al., 2012). However, whether primate callers produce variations of more complex vocal sequences depending on the composition of the audience is yet to be determined.

10.1.2. Audience effects in primates

A wide range of primate species possess the capacity to assess their audiences in terms of their identity and social relationships when calling while simultaneously being regarded as sophisticated receivers capable of extracting multiple information from vocalisations and change their behaviour accordingly (Ongstad, 2022; Seyfarth & Cheney, 2010). For instance, the presence of an audience affects the production of feeding calls in spider monkeys (*Ateles geoffroyi*: Chapman & Lefebvre, 1990), while the absence of an audience inhibits the production of alarm calls in vervet monkeys (*Cercopithecus aethiops*: Cheney & Seyfarth, 1985, 1990). Although effects resulting from the mere presence or absence of an audience may also be driven by an increase in arousal, for example due to the presence of oestrous females or more dominant males, the fact that dynamic and subtle variations in the audience compositions, their behaviours, and the social relationships between the signaller and the audience members affect vocal outputs suggests that callers possess some voluntary control over vocal outputs (e.g., Papworth et al., 2008; Schel, Machanda, et al., 2013; Wich & de Vries, 2006). This idea is corroborated by the fact that audience effects are one of the criteria used to assess first-order intentionality in animal communication (Townsend et al., 2017). However, whether these effects are the result of intentionally produced signals or are confounded by changes in arousal states is unclear (Ben Mocha & Burkart, 2021; Graham et al., 2020). Another challenge is represented by the fact that instances of vocal communication are typically the result of multiple co-occurring audience effects, reflecting the different levels of relationships that signallers share with both present and absent audience members. This is particularly true in complex fission-fusion societies composed by relatively large groups (Aureli et al., 2008), such as those of wild chimpanzees (*Pan troglodytes*).

10.1.3. Audience effects in chimpanzees

Observational studies and field experiments revealed that wild chimpanzee possess sophisticated vocal behaviours that are mediated by a multitude of social factors. Signallers take into account the audience composition and its layers of complexity by considering the identity of present, nearby or absent group members, their shared social and dominance relationship, and their ability to provide support during costly or dangerous situations. For instance, in the presence of a snake model, chimpanzees call more frequently when social partners approach them compared to when other individuals arrive in their proximity (Schel, Townsend, et al., 2013). In addition, chimpanzees monitor their nearby audiences and call more often in the presence of individuals who are unaware about the snake but stop calling after they are safe, indicating that alarm calls are likely used in a goal-directed fashion (Crockford et al., 2012; Schel, Townsend, et al., 2013). Female chimpanzees are more likely to produce greeting calls to adult males in the absence of the alpha male and more likely to produce copulation calls in the absence of high-ranking females, likely inhibiting their vocal output to prevent aggressions during competitive events (Fallon et al., 2016; Laporte & Zuberbühler, 2010;

Townsend et al., 2008). During feeding events, chimpanzees increase the production of food calls in the presence or close proximity of social partners, oestrous females, or when approached by higher ranking males (Fedurek & Slocombe, 2013; Kalan & Boesch, 2015; Schel, Machanda, et al., 2013; Slocombe et al., 2010). Short distance contact calls such as travel and resting hoos are more likely to be produced when allies are close by, likely to increase social cohesion between individuals who share stronger bonds (Bouchard & Zuberbühler, 2022a; Gruber & Zuberbühler, 2013). On the other hand, long distance contact calls are more likely to be produced in the absence of allies who are within ear-shot and when callers are in larger parties, likely to recruit more individuals (Crunchant et al., 2021; Mitani & Nishida, 1993). During agonistic interactions, callers address different audiences using barks and screams and seem to direct the first to the aggressor to make them desist while they direct the latter to potential allies for help (Fedurek et al., 2015). In addition, victims are more likely to modulate the acoustics of screams to encode information regarding the severity of the aggression and modify calls in the presence of individuals who are more dominant than the aggressors, potentially to solicit their support (Slocombe & Zuberbühler, 2005a; Slocombe & Zuberbuhler, 2007). Taken together, a large body of evidence indicates that adult chimpanzees use a wide range of call types selectively and flexibly across multiple behavioural contexts. Signallers are aware of subtle changes in the social context, in contrast with certain traditional views regarding vocal outputs as the mere product of arousal-based or reflexive processes (reviewed in: Slocombe et al., 2022; Townsend et al., 2020; Zuberbühler, 2017). Under Tinbergen's (1963) framework designed to explain animal behaviours, studies on audience effects help us better understand how proximate processes elicit the production of vocal behaviours. However, it is equally important to understand the ontogenetic processes that lead to the vocal behaviours we observe in mature individuals. Here, one outstanding question is whether the acquisition and development of vocal behaviours are equally flexible and socially mediated, or if they are instead innate and inflexible. Thus, a complementary level of analysis from Tinbergen's (1963) framework is to investigate the ontogeny of communicative competences.

10.2. Development of primate vocal behaviours

A series of distinct processes are responsible for the acquisition of communicative capacities in primates, including the ability to learn to produce, perceive, and interpret signals. The three main processes involved in vocal development are: 1) production learning - how signallers modify the acoustic features of their species' vocalisations or learn novel vocalisations by attending to or matching others' vocal outputs; 2) usage learning - how signallers use vocalisations that are part of the species repertoire in the appropriate contexts or order in a vocal sequence or use novel vocalisations learned through vocal production; and 3) comprehension learning - how receivers form associations between vocalisations and the external world, including the appropriate behavioural responses to the vocalisations of others (Janik & Slater, 2000; Seyfarth & Cheney, 1997; Vernes, Kriengwatana, et al., 2021).

Overall, comparative studies have largely focused on establishing the presence or absence of vocal production learning, particularly whether it is socially mediated, likely due to its appeal in the search for human language homologies (Snowdon, 2009). Primates communicate with relatively small vocal repertoires, which develops in species-specific fixed ways, and which can only undergo small acoustic modifications without the possibility to learn novel call types (Egnor & Hauser, 2004; Hammerschmidt & Fischer, 2008; Owren et al., 2011; Seyfarth & Cheney, 1997). In contrast, much fewer studies have focused on vocal usage and comprehension learning, despite their importance when evaluating the overall capacity for learning vocal behaviours in a determined species (Seyfarth & Cheney, 1997). Furthermore, recent advances challenged previous claims that vocal development in primates is inflexible, providing evidence that social factors may play an important role.

10.2.1. Socially-mediated vocal learning

Learning from others through social interactions has been documented in various contexts including tool use (chimpanzees: Hobaiter et al., 2014), foraging (whales, *Megaptera novaeangliae*: Allen et al., 2013), and communication (bats, *Rousettus aegyptiacus*: Prat et al., 2015). Social learning occurs whenever animals modify their behaviour after attending to social information by interacting or in the proximity of others and express the newly acquired behaviour consistently over time (Heyes, 1994; van Schaik, 2010). Social learning is favoured by frequent encounters between group members as well as by living in larger groups, particularly in those organised as fission-fusion societies since reduced within-group competition allows individuals to interact with more social learning models in a more tolerant social environment (van Boekholt et al., 2021; van Schaik et al., 2003). The ability to learn or modify vocalisations based on social experiences is rare among animals and seems to be limited to humans (Kuhl, 2004; Tomasello, 2008), birds (Baptista & Gaunt, 1997; Petkov & Jarvis, 2012), marine mammals (Garland & McGregor, 2020; Janik, 2014), elephants (Poole et al., 2005; Stoeger et al., 2021), and bats (Knörnschild et al., 2010; Prat et al., 2015), although data are still considered largely incomplete (Vernes, Kriengwatana, et al., 2021). Primates are notably absent, with evidence for their capacity to socially learn vocalisations regarded by some scholars as either lacking or unclear (Egnor & Hauser, 2004; Fischer, 2017; Owren et al., 2011; Tyack, 2020; but see Lameira, 2017). From an evolutionary perspective, the vocal abilities of more distantly related species can inform us about the selective pressures that favoured vocal learning across different communicative and social systems. However, studying species more closely related to our lineage is crucial for a better understanding of human language evolution (Fedurek & Slocombe, 2011; Fitch & Zuberbühler, 2013). In the following sections I review classic and recent primate studies for each of the three processes involved in the development of vocal behaviours of a species-repertoire calls, with particular attention to the role of social factors.

10.2.2. Ontogeny of vocal production

The ontogeny of primate vocal production has been traditionally regarded as highly constrained, with vocal repertoires composed of call types that are largely adult-like since birth (Hammerschmidt & Fischer, 2008; Seyfarth & Cheney, 2010). Classic studies conducted in captivity showed that auditory or rearing experiences have little effect on the development of vocal production, which is largely genetically fixed (Egnor & Hauser, 2004; Fischer & Hage, 2019). For instance, young squirrel monkeys (*Saimiri sciureus*) and rhesus macaques (*Macaca mulatta*) who have been socially or acoustically isolated, deafened, deprived of their parents, or cross-fostered, develop species-typical calls that are virtually identical to those of normally raised individuals (Hammerschmidt et al., 2000, 2001; Owren et al., 1993; Winter et al., 1973). Thus, authors concluded that immature primates do not require an adult model or other social stimuli to acquire their vocal repertoires. However, recent findings on marmoset monkeys (*Callithrix jacchus*) challenge the latter view. The visual and acoustic information that marmoset parents provide to their offspring enhances and accelerates the transition from immature to mature vocalisations (Gultekin & Hage, 2017, 2018; Takahashi et al., 2015, 2017). More specifically, more frequent turn-taking during vocal exchanges between offspring and parents enhances the vocal development of young marmosets (Takahashi et al., 2015). These early social interactions have a critical and long-term effect on marmosets' vocal ontogeny, even if individuals eventually acquire the capacity to produce adult call types regardless of the amount of parental feedback (Gultekin et al., 2021). Thus, while most evidence from primate studies is in line with the idea that the ontogeny of vocal production has a strong innate component, the vocal behaviour of at least one primate species undergo important changes as a result of an interplay between social feedback and physical growth. Whether marmosets represent a unique case of vocal learners among primates is yet to be determined (Margoliash & Tchernichovski, 2015).

10.2.3. Vocal production learning

Given the rare occurrence of vocal production learning during the ontogeny of primates, studies on the vocal learning abilities of adult individuals can potentially provide insights. Indeed, across several primate species, closely associated individuals produce vocalisations with greater acoustic similarities compared to non-preferred social partners, independently of genetic relatedness (e.g., Campbell's monkeys, *Cercopithecus campbelli*: Lemasson et al., 2011; chimpanzees: *Mitani & Gros-Louis, 1998*; marmosets, *Cebuella pygmaea*: Snowdon & Elowson, 1999). Similarly, the vocalisations of members of the same group tend to converge into acoustically similar 'dialects' (e.g., chimpanzees: Crockford et al., 2004; guinea baboons, *Papio papio*: Fischer et al., 2020; marmosets: de la Torre & Snowdon, 2009). These observations are corroborated by studies in captivity where individuals who transferred into new groups accommodated their vocalisations to match those of their new groupmates (e.g., chimpanzees: Watson et al., 2015a, but see Fischer et al., 2015; Watson et al., 2015b; marmosets: Snowdon & Elowson, 1999; Zürcher et al., 2019). However, in the case of chimpanzee dialects, replication studies indicated that community differences are likely explained by genetic or ecological factors that were unaccounted for (Desai et al., 2022; Mitani et al., 1999). Nevertheless, a growing number of studies suggest that auditory exposure drives acoustic convergence between close associates in both monkeys and great apes, and thus primate vocal production should not be assumed to be entirely constrained.

10.2.4. Ontogeny of vocal usage

Most scholars agree that the ontogeny of vocal usage is more flexible and to a larger extent affected by experience in primates when compared to vocal production (Fischer & Hammerschmidt, 2020; Seyfarth & Cheney, 1997; Snowdon, 2009). For instance, vervet infants are born with the capacity to broadly categorise other animals as predators or non-predators and use alarm calls in the presence of the former, albeit not always accurately (Seyfarth & Cheney, 1997). As they grow up, they refine their knowledge about each predator class (e.g., aerial or terrestrial) and its appropriate alarm call type by accumulating experience (Seyfarth & Cheney, 1980). Vervet infants may also benefit from positive reinforcement through the vocal behaviour of nearby group members given that vervet mothers tend to alarm call more often in the presence of their offspring, thus increasing the exposure to the correct association between predator and alarm call (Cheney & Seyfarth, 1990). Furthermore, following an infant's alarm call, adults tend to alarm call more often when the infant called after seeing a predator, potentially reinforcing the appropriate vocal usage learning (Seyfarth & Cheney, 1986). Indeed, vervet infants may benefit from auditory exposure to learn how to use other call types as well, as demonstrated by the fact that individuals exposed to intergroup vocal encounters at higher rates produce the appropriate call earlier than infants exposed at lower rates (Hauser, 1989). Corroborating evidence comes from the study of marmosets, where infants who receive more social feedback under the form of contingent parental responses learn to use adult calls in the appropriate context earlier than those who received less feedback (Gultekin & Hage, 2017; Takahashi et al., 2015), and of pigtail macaques (*Macaca nemestrina*), where infants learn to use scream calls during the appropriate contexts through experience (Gouzoules & Gouzoules, 1989). Although socially mediated usage learning appears in a few monkey species, it is less clear whether it also plays a role during great ape vocal ontogeny.

To my knowledge, there are no systematic studies on the ontogeny of vocal usage in wild bonobo, gorilla, and orangutan species. After early descriptive and qualitative investigations in wild chimpanzees (Goodall, 1986; Plooij, 1984), only a few systematic studies have been conducted in more recent years, focusing on soft and short-distance calls. For instance, the use of chimpanzee grunt calls transitions from a period of frequent production lacking target specificity during infancy to a period of less frequent production characterised by greater social specificity during adolescence, when they become adult-like pant grunts (Laporte & Zuberbühler, 2011). Infant grunts are used across a range of affective contexts and vary acoustically according to the context (Dezecache et al., 2021b), but do not appear to be learned through mother and offspring vocal or social interactions (Laporte & Zuberbühler, 2011). The appropriate usage of alarm calls is progressively learned by immature chimpanzees and may be facilitated by gaze alternations with their mothers, potentially indicating that chimpanzees become aware of their audiences early during vocal ontogeny (Dezecache et al., 2019). Overall, it remains unclear whether exposure to the social and vocal behaviours of others and their feedback affect great ape vocal ontogeny. Furthermore, chimpanzee studies largely focused on the acquisition of soft, short, and acoustically simple calls such as grunts and alarm hoos. However, adult chimpanzees frequently use more complex loud contact calls and vocal sequences composed of different call types (Girard-Buttoz, Zaccarella, et al., 2022; Marler &

Hobbett, 1975), though the ontogeny of these vocalisations is unknown. Addressing this gap in our knowledge is critical to understand how chimpanzees learn to associate the appropriate context or function to the same call produced in isolation and as part of a sequence. This information is particularly important from a comparative perspective, given the parallels between the combinatorial structures used by primates and human language (Engesser & Townsend, 2019; Zuberbühler & Lemasson, 2014).

10.2.5. Ontogeny of vocal comprehension and responses

It is highly adaptive for receivers to acquire information from others' vocalisations, use them as predictors or indicators of external events, and adjust their behavioural responses accordingly (Seyfarth et al., 2010). The association between a vocalisation and its response are expected to be flexible in primates given that the environment and social systems they live in can be highly dynamic. Indeed, vocal comprehension learning is regarded as the least inflexible of the three processes and as largely acquired through experience (Seyfarth & Cheney, 1997, 2010). Across several primate species, infants' responses to others' vocalizations differ markedly from adults' responses and take longer to develop than vocal production and usage (Seyfarth & Cheney, 1997). When initially exposed to alarm calls, vervet infants run towards their mother or produce inappropriate responses and must learn to recognize the different call types and their appropriate response through experience (Seyfarth & Cheney, 1986). Infant chacma baboons (*Papio cynocephalus ursinus*) necessitate experience to learn how to appropriately respond to the bark calls of their group members (Fischer et al., 2000), while infant barbary macaques (*Macaca sylvanus*) and Japanese macaques (*Macaca fuscata)* learn to recognise their mother's call signature through auditory exposure (Fischer, 2004; Masataka, 1985). Furthermore, primates are also able to recognize and respond to the alarm calls of other species, demonstrating that vocal comprehension is not entirely innate (Zuberbühler, 2000). Interestingly, just like with their own alarm calls, vervet infants need to be exposed to the alarm calls of starlings to learn to respond appropriately and the greater the auditory exposure the faster they learn to do so (Hauser, 1988). Rapid learning is essential when it comes to alarm calls due to the higher costs associated with mistakes. Indeed, both young vervet monkeys and sooty mangabeys (*Cercocebus atys*) learn rapidly and efficiently to identify and respond to novel predators by attending to the alarm calls and responses of their conspecifics (Deshpande et al., 2022; León et al., 2022). One hypothesis is that the development of responses to call types used in situations requiring additional social awareness would be slower when compared to those used during more 'evolutionarily urgent' contexts.

10.2.6. Summary of primate vocal ontogeny

Overall, primate vocal usage and comprehension learning are regarded as more flexible when compared to vocal production learning. The adult vocal repertoire of primates appears to be largely fixed since birth, while vocal usage and responses tend to develop later as a result of individual and social experiences. More specifically, auditory exposure and interactions with group members play an important role in the development of vocal behaviours in some species. While it is possible that immature individuals would develop adult-like vocal behaviours without social learning, evidence suggests that vocal ontogeny can be enhanced by social factors. However, our current understanding of primate vocal ontogeny is largely built on monkey studies and too little is known about great apes.

10.2.7. Revisiting great ape vocal ontogeny

With their high cognitive abilities and long periods of social development, great apes are good candidates for a socially-mediated acquisition of communicative capacities. Despite this, we know very little about their vocal ontogeny (Seyfarth & Cheney, 1997; Tomasello & Zuberbühler, 2002). Given that great apes share a more recent last common ancestor with humans, this 'gap' in our knowledge is particularly problematic in light of our current models of language evolution largely based on monkey studies (Egnor & Hauser, 2004). The comparative approach has been very productive to investigate how spoken language might have emerged gradually during our evolutionary history (Fedurek & Slocombe, 2011; Fischer & Hage, 2019; Fitch & Zuberbühler, 2013). However, despite increasing evidence for greater flexibility in adult great ape vocal behaviours (Slocombe et al., 2022; Townsend et al., 2020), it is now critical not to limit research efforts to comparisons of overall adult communicative features between species, but to investigate the learning processes that drive vocal communication from birth to adulthood (Griebel et al., 2016; Oller et al., 2016a). More specifically, Griebel and colleagues (2016) argue that researchers should adopt the 'evolutionary-developmental' approach, where comparisons between the vocal behaviours of different species are conducted at similar developmental stages, instead of comparing adult chimpanzees with human children for instance.

A series of additional issues limit our current understanding of primate vocal ontogeny. First, the majority of developmental studies focused on alarm calls, separation calls, and to a lesser extent greeting calls (Seyfarth & Cheney, 1997; Snowdon, 2009). The development of these acoustically simpler and more urgent vocal types is expected to be more conservative, rapid, and inflexible when compared to that of affiliative and more socially used calls (Snowdon et al., 1997). For instance, little is known about the ontogeny of long-distance contact calls, despite their central role in mediating social interactions and relationships in adult individuals (Mitani & Stuht, 1998). Second, the majority of studies have been conducted in captive or artificial settings, which can affect the expression of social behaviours (Leavens et al., 2010), including communicative ones (e.g., Fröhlich et al., 2021), likely due to an overall lack of important socioecological factors. Studying signals in an environment similar to the one in which they evolved is critical to understand the adaptive function of vocalisation and the potential role of social learning (Harrison & van de Waal, 2022; Schuppli & van Schaik, 2019). Furthermore, captive studies require extensive training or the use of methods that have been abandoned due to their questionable ethics such as deafening (e.g., Talmage-Riggs et al., 1972), social isolation (e.g., Winter et al., 1973), and hybridisation (e.g., Owren et al., 1992). Third, looking backward it is evident that improvements in methods of data collection and analyses can affect research outputs. For instance, Seyfarth and Cheney (1997) noted that the majority of studies conducted before 1987 concluded that primate vocal repertoires were entirely fixed, while the majority of studies conducted after 1987 concluded that acoustic changes can occur during primate vocal development. Detecting subtle changes in younger individuals is likely more challenging than in adults due to their softer vocal timbre, rarer vocal production, and greater difficulty in observing and following them, particularly in the wild. This might explain why most developmental studies claiming a lack of vocal learning capacities were carried out before studies on adults demonstrated some vocal learning capacities (Egnor & Hauser, 2004). Furthermore, differences between older and more recent studies are also to some extent driven by advances in the methods of acoustic data collection and analysis. To address all the aforementioned limitations, in my thesis I examine the vocal ontogeny of an acoustically complex, socially used, and long-distance contact call in wild chimpanzees. In the following sections I discuss aspects of the social organisation, developmental stages, and vocal behaviours that are relevant to the study of chimpanzee vocal ontogeny. I conclude Chapter one by reviewing our current knowledge of the pant hoot vocalisation, which represents the cornerstone of my thesis.

10.3. Chimpanzee social structure and vocalisations

Wild chimpanzees are a gregarious species that occupies and moves through relatively large territories in sub-groups referred to as 'parties' that often change composition and size during the same day. To navigate such a dynamic fission-fusion system, individuals rely on long-distance vocalisations and use them to maintain cohesion, coordinate, and recruit conspecifics between parties (Eckhardt et al., 2015; Fedurek et al., 2014; Mitani & Nishida, 1993). However, there are notable differences in the social behaviours of male and female chimpanzees. Males are the philopatric sex and constitute the core of the group, while females tend to emigrate to a neighbouring community upon reaching sexual maturity (Goodall, 1986; Pusey, 1980). Given that males remain in their natal community, they have more opportunities to socially interact with other males than females. This might explain why females are overall less gregarious (Gilby & Wrangham, 2008; but see Lehmann & Boesch, 2008) and prefer to spend time with their offspring (Thompson & Wrangham, 2006), while males invest time building strong and long lasting affiliative relationships with other males (Mitani, 2009a; Sandel et al., 2020). For males, competition and cooperation are the keys to increased mating success, reproductive success, and access to resources (Mitani, 2009b; Muller & Mitani, 2005). Therefore, to obtain high social positions in the community males regularly engage in aggression and agonistic displays, which can be accompanied by vocalisations (Muller & Mitani, 2005). The result is a linear dominance hierarchy that can be measured by looking at the use of pant grunt vocalisations, typically used for greeting and from subordinates towards more dominant individuals, as well as the outcome of agonistic interactions (Fedurek et al., 2021; Newton-Fisher, 2017).

10.3.1. Development

Chimpanzees are very helpless when they are born and undergo one of the longest periods of dependency from their mother (Goodall, 1986; Maestripieri & Call, 1996; Pusey, 1990). As a consequence, the early socialisation of young chimpanzees depends almost entirely on their mothers' social associations (Murray et al., 2014; Pusey, 1983). Then, during infancy, they progressively reduce physical contact with the mother and increase social interactions with other group members (Goodall, 1986; Plooij, 1984). Studies on human-reared chimpanzees showed that young infants become responsive to social stimuli very early on, produce behaviours such as mutual gaze and sensitivity to gaze direction of the mother, check the surrounding audience when producing vocal utterances, and follow the gaze of others (Tomonaga et al., 2004). Towards the end of infancy (approximately 4 years old), infants travel more often independently than carried by the mother, even if their association with others and movements between parties still depend on her and will continue to do so until they approach the end of the juvenile period (approximately 10 years old) (Goodall, 1986; Pusey, 1983). As they reach puberty, chimpanzees become almost entirely independent from the mother, although they maintain a strong bond with her (Reddy & Sandel, 2020). Sub-adult males increasingly associate with adult males and experience aggression and displays from older and more dominant males (Pusey, 1990). Immature males experience more social exposure and opportunities to learn from others due the fact that mothers with male offspring associate and interact more often with other group members, particularly with adult males, when compared to mothers with female offspring (Lonsdorf, Anderson, et al., 2014; Lonsdorf, Markham, et al., 2014; Murray et al., 2014). Thus, chimpanzee mothers play a critical role in the socialisation of their offspring (Murray et al., 2014; Pusey, 1983). As a consequence, differences in social exposure and interactions may shape how immature individuals develop social behaviours, including their communicative skills, and use them as independent adult members of the group.

10.3.2. Vocal repertoires

Wild chimpanzees communicate using a vocal repertoire that consists of a relatively small number of acoustically different call types that can grade within and between each other (Marler, 1976; Marler & Tenaza, 1977; Slocombe & Zuberbühler, 2010). Like in other primates, the chimpanzee vocal repertoire is constructed qualitatively from descriptions of characteristic audible features, visual classifications of spectrograms, and contextual information accompanying calls (Crockford, 2019; Goodall, 1986). However, more than 50 years after the first description of chimpanzee vocalisations, a systematic study of their vocal repertoire is still missing (Crockford, 2019). Despite this, there is a relatively large consensus about call types produced by adults (e.g., Slocombe & Zuberbühler, 2010), while very few studies made attempts to describe the vocalisations produced by immature individuals. As of today, no definitive vocal repertoire of immature chimpanzees has been described, only suggestive and descriptive classifications exist (e.g., Plooij, 1984). The call types produced by immature chimpanzees typically include grunts, barks, screams, squeaks, staccatos, and whimpers, with the notable exception of pant hoots (Marler & Tenaza, 1977; Plooij, 1984), although these early descriptions lack systematic and acoustic analyses. The development of vocalisations in wild chimpanzees remains a largely unexplored area of research, with a few notable exceptions (e.g., Dezecache et al., 2021b; Dunphy-Lelii & Mitani, 2019; Laporte & Zuberbühler, 2011; Taylor et al., 2021). Overall, findings suggest that the vocal ontogeny of alarm and greeting calls is partly flexible and partly rigid and highlight the potentially influential role of the mother. In order to clarify the role of innate and learned processes on the ontogenetic processes, it is important to identify the earliest utterances produced by newborn individuals, which represent the starting point of developmental trajectories (Fischer, 2002).

10.3.3. Newborn vocal behaviours

Live births are extremely rare events to observe in wild chimpanzees, with only a few direct observations published up to date (Fujisawa et al., 2016; Goodall & Athumani, 1980; Kiwede, 2000; Nishie & Nakamura, 2018; Zamma et al., 2012). Despite this, intensive research from chimpanzees' long-term field studies allowed the collection of valuable information on unique perinatal behaviours (Kappeler et al., 2012). However, very little is known about newborns first vocalizations. Goodall and Athumani (1980) reported that a newborn uttered the first sounds approximately five minutes after birth, which included cries, 'muffled sounds', and soft whimpers. Zamma et al. (2012) observed vocal sequences produced by the newborn which were described as "fa, ha-ha" and "hu, hu" sounds. However, both accounts are highly descriptive and lack sound recordings, which would allow exploring acoustic structures and call types. Overall, it is unclear which vocalisations appear prior to the effect of environmental and social auditory inputs during ontogeny and whether more structurally complex vocal sequences are produced since birth.

10.4. Pant hoots

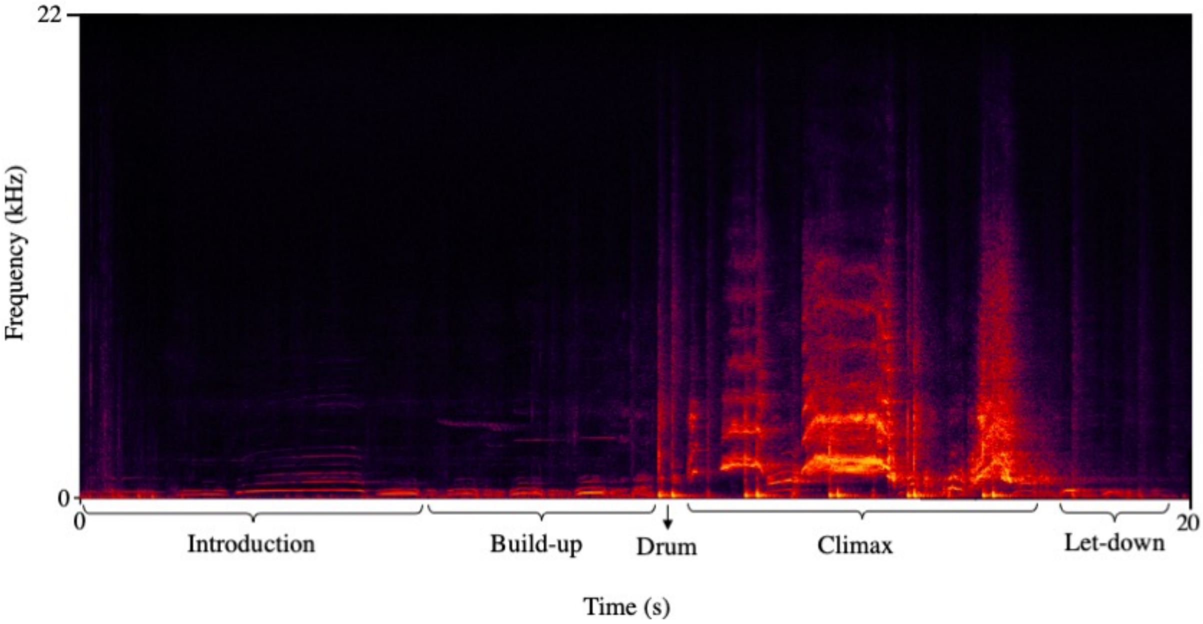

Figure 1 Spectrographic illustration of a pant hoot produced by an adult male chimpanzee (ZF). The vocalization includes all four phases and drumming beats.

10.4.1. Call definition and structure

One common chimpanzee call type, the pant hoot, is typically regarded as a long distance contact call and arguably one of the most complex and distinctive signals among great apes (Figure 1). Pant hoots are composed of four acoustically distinct phases, which are produced in an orderly sequence as introduction, build-up, climax, and let-down (Marler & Hobbett, 1975; Marler & Tenaza, 1977). Pant hoot phases, in turn, are composed of a varying number of voiced exhaled units, which are separated by short periods of either silence or panted inhaled units (Fedurek et al., 2017). The introduction is typically defined as a series of low-amplitude and low-frequency tonal units that acoustically resemble 'hoo' vocalizations but are longer in duration and alternate with inhaled tonal units. The build-up is a series of short low-amplitude and low-frequency units that are produced rapidly during both inhalations and exhalations. Build-up units can increase in intensity and frequency as the call approaches the climax phase. The climax phase is defined as one or more high-amplitude and high-frequency units that resemble screams. The climax phase has often characterised pant hoots and received the most attention overall likely due to its conspicuous long distance feature. Finally, the let-down is a series of low-amplitude and low-frequency units which acoustically resemble the build-up phase but tend to progressively decrease in intensity and frequency over time as they are further away from the climax phase.

The acoustic structure of pant hoots has been traditionally described as rather stereotypical and tied to callers' arousal states (Notman & Rendall, 2005). However, while the order of appearance of phases is largely consistent, some phases are regularly omitted resulting in different vocal sequences. For instance, the let-down is the most frequently omitted phase and it is produced so rarely by Western chimpanzees that it is typically excluded from studies (e.g., Crockford & Boesch, 2005; Kalan & Boesch, 2018). In Eastern chimpanzees, the let-down and build-up phases are more likely to be omitted during the feeding context than during travelling (Fedurek, Zuberbühler, et al., 2016; Notman & Rendall, 2005), although how pant hoots with different phase compositions affect the call's function or the responses of receivers has not been investigated. The flexibility of pant hoot sequences is likely one of the reasons why there is lack of consistency in the way authors define this call. For instance, some require the presence of at least two phases (Notman & Rendall, 2005), at least a climax (Arcadi, 1996; Fedurek et al., 2014; Mitani & Brandt, 1994), or at least an introduction and a climax (Mitani et al., 1999). Other authors consider pant hoot phases as equivalent to other chimpanzee call types or sub-types (Crockford & Boesch, 2005). For instance the climax would be equivalent to a 'panted scream', and the introduction and build-up would be equivalent to a 'panted hoo' (Girard-Buttoz, Bortolato, et al., 2022; Girard-Buttoz, Zaccarella, et al., 2022). As a result, comparing pant hoot studies from multiple field sites can be challenging. One solution to this issue is to rely less on the researchers' qualitative categorisations based on audible features and visual classifications of spectrograms and combine these with quantitative acoustic analyses whenever possible.

10.4.2. Call function

Pant hoots are socially used calls typically produced during travel or feeding events (Marler & Tenaza, 1977; Nishida et al., 1999). However, chimpanzees also use pant hoots during agonistic displays, intergroup encounters, patrolling, and resting events (Goodall, 1986; Nishida et al., 1999). This contextual flexibility is associated with different call functions, which include coordinating fission-fusion dynamics (Fedurek et al., 2014; Mitani & Nishida, 1993), signalling individual and group identity (Crockford & Boesch, 2005; Mitani et al., 1999), signalling social bonds (Fedurek, Machanda, et al., 2013; Mitani & Brandt, 1994), or signalling social status (Clark & Wrangham, 1994; Fedurek, Slocombe, et al., 2016). Finally, pant hoots can be produced either spontaneously, i.e., the signaller initiates a vocalisation that is not elicited by other calls, as part of vocal choruses, i.e., the signaller's call overlaps temporally with that of another individual, or as part of vocal exchanges, i.e., the signaller vocally responds to others' pant hoots without temporal overlap between calls (Fedurek, Machanda, et al., 2013; Goodall, 1986). Chorusing typically occurs when two or more individuals that are in spatial proximity adjust temporally and acoustically their calls to produce joint vocal bouts, and are regarded as signals of short- and long-term social bonds (Fedurek, Machanda, et al., 2013; Fedurek, Schel, et al., 2013; Mitani & Gros-Louis, 1998).

10.4.3. Sex differences

Female pant hoots are significantly understudied when compared to their male counterpart. In their seminal work, Marler and Hobbett (1975) noted that female pant hoots lacked the climax phase. As a consequence, these calls did not qualify as pant hoots but were instead considered "pant hoot-like loud calls" according to Arcadi (1996). However, other scholars noted that females produce the climax, albeit less often than males (Hosaka, 2015; Mitani & Nishida, 1993). Indeed, claims that females do not produce pant hoots or climax phases should be regarded as outdated (see also Holden, 2017). Instead, male and female pant hoot production differs with regard to the acoustic structure of the climax phase, with male calls possessing a higher fundamental frequency than females calls (Grawunder et al., 2018; but see Kalan, 2019). Furthermore, the use of pant hoots vary between the sexes. Females tend to call less frequently (Clark, 1993; Crunchant et al., 2021; Kalan, 2019; Notman & Rendall, 2005) and are more likely to join others' calls than to call spontaneously (Arcadi, 1996). On the other hand, males use pant hoots to mediate group decisions (Fedurek et al., 2014), attract allies (Mitani & Nishida, 1993), signal short- and long-term bonds (Fedurek, Machanda, et al., 2013; Mitani & Brandt, 1994), assert their dominance (Muller, 2002), and signal social status (Clark & Wrangham, 1994; Fedurek, Slocombe, et al., 2016). Adult females and sub-adult males are more likely to produce pant hoots in the presence of adult males or following adult males' pant hoots, suggesting that they take into account the identity and location of nearby individuals and callers (Arcadi, 1996; Clark, 1993; Clark & Wrangham, 1994). Taken together, current findings suggest that both males and females use pant hoots, albeit with some differences.

10.4.4. Call comprehension and responses

Despite early observations of frequent pant hoot exchanges between parties separated by the dense forest (Goodall, 1986; Marler & Tenaza, 1977), the behavioural responses of receivers to others' pant hoots have been rarely investigated and what we know is based on playback experiments. Chimpanzees are very accurate in locating the provenance of calls from hundreds of meters away and regardless of whether they are produced by a single caller or a group of callers (Wilson et al., 2001). In addition, chimpanzees discriminate between calls from their own community and those produced by strangers or their neighbours, and use this information to adjust their territorial behaviours (Herbinger et al., 2009). Upon hearing the pant hoot of a group member, chimpanzees tend to respond with pant hoots and males call more often than females (Herbinger et al., 2009). When hearing the pant hoots of strangers, chimpanzees orient their heads in the direction of the vocal stimulus and their vocal responses depend on the number of males in the party (Wilson et al., 2001), with the strongest behavioural responses produced by larger parties (Herbinger et al., 2009; Wilson et al., 2001). Upon the arrival of a male group member to a feeding tree, receivers look in the direction of the call and respond vocally, especially after the arrival of high ranking males and social partners (Schel, Machanda, et al., 2013). Thus, the two most common responses after hearing a pant hoot seem to be orientating the head towards the call and the production of a vocal response.

Chimpanzee receivers can potentially acquire a large amount of information from a pant hoot given that each phase is associated with different types of social information. For example, the identity of the caller strongly correlates with the introduction and the climax phases (Fedurek, Zuberbühler, et al., 2016), and receivers can recognise the identity of the caller (Kojima et al., 2003; Schel, Machanda, et al., 2013). The age of the caller is mainly encoded in the build-up and introduction phases (Fedurek, Zuberbühler, et al., 2016). The context of production is encoded in the let-down phase (Fedurek, Zuberbühler, et al., 2016; Notman & Rendall, 2005). The social status (or rank) of the caller is mainly encoded in the climax component (Fedurek, Zuberbühler, et al., 2016), in line with the idea that dominant males pant hoot more often (Fedurek et al., 2014; Mitani & Nishida, 1993) and produce more climax phases (Fedurek, Slocombe, et al., 2016; Riede et al., 2007). Because the acoustic structure of pant hoots show a certain degree of variability, different types of socially important information are encoded in the vocal signal and are potentially accessible to different audiences. However, how signallers modulate the structure of pant hoots as a function of the audience composition has not been tested yet and would provide further evidence of vocal flexibility and social awareness.

10.4.5. Call ontogeny

Although the pant hoot is one of the most studied primate vocalisations and the most frequently uttered call by chimpanzees (Marler & Tenaza, 1977), studies have almost exclusively focused on sub-adult and adult males. How and when these complex vocal sequences come to be and whether there are any sex differences during ontogeny remain outstanding questions. Early descriptive accounts vary greatly with regard to the onset of pant hoot production, with some reporting their absence until adolescence (Plooij, 1984), their appearance only after 2 years of age (Hiraiwa-Hasegawa, 1986), or the extremely rare occurrence in infants and juveniles (Marler & Tenaza, 1977; Taylor et al., 2021). Early observations suggested the presence of some sex differences during the development of pant hoots, with young males calling more often than young females (Pusey, 1990). In addition, while immature individuals seem to pant hoot more often by chorusing and rarely call spontaneously, their overall call rate is very low and only reaches adult-like levels when individuals become sexually mature (Marler & Tenaza, 1977; Pusey, 1990; Taylor et al., 2021). Due to its very rare occurrence in immature individuals, structure complexity, multiple social functions, and contextual flexibility, the pant hoot represents an ideal study case to examine the innate or flexible nature of vocal ontogeny in our closest living relatives.

10.5. Thesis outline

My thesis is part of a broader research effort to better understand the vocal communication of chimpanzees and how they use vocal signals to navigate their complex social world, by focusing on its ontogeny and audience effects. Together, the following three empirical chapters provide insights on two main aspects. First, how individual and social factors affect the ontogeny of pant hoots.

Next to nothing is known about the ontogeny of chimpanzee vocal sequences and whether they are produced since birth or acquired later on. In Chapter 2, I examine the utterances produced by a newborn to identify the starting point of vocal production. I describe the newborn's vocalisations with qualitative and quantitative methods of classifications, with a particular focus on more complex structures such as pant hoots.

The question of whether the vocal ontogeny of chimpanzees is inflexible or socially mediated is addressed in Chapter 3. Here, I investigate which individual and social factors mediate the development of pant hoot usage and responses. I predict that the vocal ontogeny follows a slow trajectory and is affected by exposure to vocal and social interactions, particularly with the mother and adult males.

The second aspect of vocal communication I investigate is how social awareness affects flexibility in the use of pant hoots and each pant hoot phase. Whether audience effects in chimpanzees are limited to vocal output and small acoustic changes or extend to the components of more complex vocal structures has not been investigated. In Chapter 4, I examine the use of pant hoots and their four phases during agonistic displays. I predict that chimpanzees flexibly adjust the inclusion and omission of calls and call components depending on the audience composition.

11. The ontogeny of vocal sequences: insights from a newborn wild chimpanzee (*Pan troglodytes schweinfurthii*)

11.1. Abstract

Observations of early vocal behaviours in non-human primates (hereafter primates) are important for direct comparisons between human and primate vocal development. However, direct observations of births and perinatal behaviour in wild primates are rare, and the initial stages of behavioural ontogeny usually remain undocumented. Here, we report direct observations of the birth of a wild chimpanzee (*Pan troglodytes schweinfurthii*) in Budongo Forest, Uganda, including the behaviour of the mother and other group members. We monitored the newborn's vocal behaviour for approximately 2 hours and recorded 70 calls. We categorised the vocalisations both qualitatively, using conventional call descriptions, and quantitatively, using cluster and discriminant acoustic analyses. We found evidence for acoustically distinct vocal units, produced both in isolation and in combination, including sequences akin to adult pant hoots, a vocal utterance regarded as the most complex vocal signal produced by this species. We concluded that chimpanzees possess the capacity to produce vocal sequences composed of different call types from birth, albeit in rudimentary forms. Our observations are in line with the idea that primate vocal repertoires are largely present from birth, with fine acoustic structures undergoing ontogenetic processes. Our study provides rare and valuable empirical data on perinatal behaviours in wild primates.

11.2. Introduction

Primates communicate using a limited vocal repertoire, which largely develops in species-specific ways (Seyfarth & Cheney, 1997). The acoustic structure of calls uttered by infants typically resemble the corresponding adult call types, suggesting that vocal structures develop under strong genetic control (Hammerschmidt and Fischer 2008; Janik and Slater 2000; Owren et al. 2011), with some room for socially acquired call variants (Ruch et al., 2018; Snowdon, 2009). The acquisition of novel call types is virtually absent in wild primates (Fischer and Hammerschmidt 2020; Tyack 2020; but see Lameira 2017). Overall, primate development of species-typical calls results from a combination of genetic, social, and environmental influences, though the relative role of each is still debated (Fedurek & Slocombe, 2011). Data on very early utterances shortly after birth are critical to assess the departure point in vocal ontogeny, prior to social and environmental influences. However, most primate births occur at night (Dunn, 2012) and are difficult to observe due to the unpredictability of parturition and maternal avoidance of other group members (Nishie & Nakamura, 2018; Otali & Gilchrist, 2006; Ramsay & Teichroeb, 2019), probably as a response to infanticide risk (Palombit, 2012). As a result, primate perinatal behaviours remain poorly understood (Trevathan, 2015), despite their theoretical relevance for developmental research (Nagy, 2011).

Vocal development has usually been analysed at three different levels: (1) production learning - how individuals modify specific acoustic features of calls after exposure to others' calls; (2) usage learning - how individuals give existing calls in new contexts or combine them as part of new vocal sequences; and (3) comprehension learning - how individuals respond appropriately to the vocalisations of others (Janik and Slater 2000; Seyfarth and Cheney 1997; Vernes et al. 2021). In primates, production learning is regarded as mostly fixed, while usage and comprehension learning are considered more flexible (Seyfarth & Cheney, 1997; Snowdon, 2009). However, this model is largely based on studies of alarm calls, which are expected to be less flexible than calls with more social functions, which should instead be the focus when making comparisons with human vocal development (Elowson et al. 1992; Snowdon et al. 1997).

The majority of data on primate vocal development stem from studies of monkey vocalisations (Seyfarth & Cheney, 1997; Tomasello & Zuberbühler, 2002). However, monkeys are arguably less directly relevant to studies of language evolution than great apes, who share a more recent last common ancestor with humans (Langergraber et al., 2012) (Fischer & Hage, 2019; Fitch & Zuberbühler, 2013). Great apes often produce sequences of calls (e.g., chimpanzees, *Pan troglodytes verus*: Girard-Buttoz et al. 2022), including combinatorial structures (e.g., bonobos, *Pan paniscus*: Schamberg et al. 2016; gorillas, *Gorilla gorilla beringei* and *Gorilla gorilla gorilla*: Hedwig et al. 2014) with some evidence for socially-learned call variations (e.g., orangutan, *Pongo pygmaeus wurmbii* and *Pongo pygmaeus abelii*: Lameira et al. 2022). While both humans and great apes use a limited set of sounds comparable in size (e.g., McComb and Semple 2005; Moran et al. 2012), the ability to combine these sounds hierarchically to form vocal sequences varies greatly between humans and other apes, and sets apart human language from the communication of other animals (Hauser et al., 2002; Townsend et al., 2018). Although vocal learning abilities in great apes are clearly more constrained than in humans, investigating the degree to which great apes vocal sequences are socially learned or hard-wired, and thus present from birth, can inform us about the evolution of more complex vocal structures.

There are only a handful of direct observations of perinatal behaviour in our one of our two closest living relatives, the chimpanzees (Fujisawa et al., 2016; Goodall & Athumani, 1980; Kiwede, 2000; Nishie & Nakamura, 2018; Zamma et al., 2012). As a consequence, very little is known about newborn chimpanzee vocal behaviour, although subsequent stages of vocal development are somewhat better documented (e.g., Dezecache et al. 2019; Laporte and Zuberbühler 2011; Plooij 1984; Taylor et al. 2021). Early qualitative descriptions indicate that the first vocalisations of wild chimpanzees are comparable to the corresponding adult call types, such as grunts, whimpers, cries, and screams (Plooij, 1984). Human-reared chimpanzees initially exhibit vocal output that have some similarities to that produced by human infants in the first months of life (Kojima, 2008), although these are often elicited by human caretakers or researchers (Bard, 1995; Kojima, 2008). Human infants are special, however, in producing highly variable and functionally flexible vocal sequences, referred to as babbling a form of vocal exploration considered a milestone during language acquisition (Oller 2000; Oller et al. 2021). Typically, babbling starts soon after birth, consists of a subset of the acoustic features characterising the adult repertoire, and does not require a social context or to be communicative

(Oller 2000; ter Haar et al. 2021). In addition to simple vocal practice, one likely function of this peculiar behaviour is to enhance social interactions and bonding with caregivers (Locke 2006; Oller and Griebel 2008). However, evidence for babbling-like vocal behaviour is absent in chimpanzees (Oller et al. 2019; ter Haar et al. 2021).

The vocal repertoire of wild chimpanzees consists of a relatively small number of acoustically distinct call types that can grade into each other (Crockford, 2019; Goodall, 1986; Marler & Tenaza, 1977). Different call types often appear in sequences (Crockford & Boesch, 2005; Girard-Buttoz, Zaccarella, et al., 2022; Leroux & Townsend, 2020), such as pant hoots and food grunts (Leroux et al., 2021) or screams and barks (Fedurek et al., 2015). Whether such call combinations function to convey different information is still unclear and a topic of ongoing research (Engesser & Townsend, 2019; Zuberbühler & Lemasson, 2014). Furthermore, no study to date has investigated how and when the capacity to produce vocal sequences appears during chimpanzee ontogeny.

One vocalization commonly produced by chimpanzees, the pant hoot, comprises smaller vocal components (i.e., phases) produced in an orderly sequence of introduction, build-up, climax, and let-down (Marler & Hobbett, 1975; Marler & Tenaza, 1977). Pant hoot phases, in turn, consist of a varying number of voiced exhalations, which are the smallest units of this vocal sequence and are separated by short periods of silence or panted inhalations (Fedurek et al., 2017). Pant hoots are flexibly produced across many contexts suggesting various functions, including coordinating fission-fusion dynamics (Fedurek et al., 2014), signalling individual and group identity (Mitani et al. 1996; Crockford et al. 2004), signalling social bonds (Fedurek, Machanda, et al., 2013; Mitani & Brandt, 1994), or signalling social status (Clark & Wrangham, 1994; Fedurek, Slocombe, et al., 2016). Some phases can be omitted (Fedurek, Zuberbühler, et al., 2016; Notman & Rendall, 2005) or produced in isolation (Soldati, Fedurek, et al., 2022). In addition, phases are sometimes regarded as equivalent to distinct call types or sub-types within the vocal repertoire (e.g., climax as panted scream: Crockford 2019; Girard-Buttoz et al. 2022). Although pant hoots are amongst the most common and most studied vocalisation in wild chimpanzees (Marler & Tenaza, 1977), data are mainly from sub-adult and adult males (e.g., Crockford et al. 2004; Fedurek et al. 2014; Mitani and Brandt 1994) and pant hoots are only rarely uttered by immature individuals from around two years of age (Hiraiwa-Hasegawa, 1986), with the rate of production increasing with age (Marler & Tenaza, 1977; Pusey, 1990). Importantly, to our knowledge, newborns have never been reported uttering pant hoots and no study has systematically investigated the development of this vocal sequence.

In this study, we report on the vocal behaviour of a new-born wild chimpanzee in the Sonso community of Budongo Forest, Uganda. We used two methods of call classification: (1) qualitative spectrographic and auditory categorisation of calls supplemented by auditory categorisation by human experts; and (2) quantitative soft clustering analysis to determine distinct acoustic clusters and discriminant function analyses to investigate pant hoot production across age categories.

11.3. Methods

11.3.1. Study site and population

We studied the Sonso chimpanzee community in Budongo Forest, western Uganda. Chimpanzees from the Sonso community have been studied and followed daily by field assistants since 1990 (Reynolds, 2005). At the time of the study, the community was composed of 71 individuals, including 9 adult males and 31 adult females (Appendix Table A1). The main individuals involved in the study were members of the Kutu family (Table 1).

Table 1 Key chimpanzee individuals of the Kutu family involved in the birth of KU7 at Sonso, Budongo forest, Uganda, in November 2019. Kinship status refers to the relation between KU and her offspring

Name	ID	Age & sex class	Age (years)	Kinship status (birth order)
Kutu	KU	Adult female	40	Mother
N/A	KU7	Newborn male	0	Son (7th)
Kefa	KF	Juvenile male	5	Son (6th)
Kathy	KH	Sub-adult female	11	Daughter (4th)
Kato	KT	Adult male	26	Son (1st)

11.3.2. Ethical note

Data collection was entirely observational, adhering to the ASAB guidelines for the treatment of animals during behavioural studies (2018). The study was approved by the Uganda Wildlife Authority (UWA/COD/96/5) and the Uganda National Council for Science and Technology (NS 637). The research ethics committees of the University of Neuchâtel (38/2019-B) and University of St Andrews (No 171) also approved this project. We evaluated the scope for bias in our study subjects using the STRANGE framework (Webster & Rutz, 2020) (see Supplementary Material).

11.3.3. Data collection

On the 20th of November 2019 at 10:12 am, the first and second authors observed the birth of KU7. Three additional researchers attended part of the afterbirth period and assisted with data collection and identification of callers. We collected audio recordings of all vocalisations produced by KU7 and collected the vocalisations produced by other individuals in the party opportunistically with a directional microphone Sennheiser MKH416 (Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany) with a Marantz PMD661 MkII (Marantz, Kanagawa, Japan) solid-state recorder (sample rate 44.1 kHz, resolution 32 bits, ‘wav’ format). We defined party composition as all individuals present within a radius of approximately 35 m of the focal individual (Newton-Fisher, 1999). We set the recorder's gain on level 9 to maximise the signal/noise ratio due to the softness of calls and the distance from the subject (approx. 15 m). We maintained this distance due to the delicate nature of the event and to reduce any effects of our presence on the chimpanzees' behaviour. We dictated observations to the microphone or noted them using CyberTracker (ver. 3.496) on a Samsung Xcover 4 portable device (Samsung Group, Seoul, South Korea). We recorded videos using a Panasonic VHC-770 HD (resolution: 1920*1080/50p). We recorded all relevant events and changes in the behaviour of all individuals in the party and recorded the composition of the party continuously.

Table 2 Terms used to describe the vocalisations produced by a newborn chimpanzee in the Sonso community, Budongo forest, Uganda, in November 2019.

	Definition	Reference
Call type	Vocalisation belonging to the species' repertoire.	See Table 3
Call unit	Distinct emitted vocal sound separated by a silent gap before and after.	Kershenbaum et al. 2016
Single call	One call unit of any type separated from other calls by more than two seconds of silence.	Kershenbaum et al. 2016
Call sequence	Series of two or more call units belonging to either the same or different call type and separated by maximum two seconds of silence.	Hedwig et al. 2014
Call combination	Call sequence consisting of two or more units of different types.	Crockford and Boesch 2005

11.3.4. Qualitative acoustic analysis

We inspected audio recordings to extract vocalisations using spectrograms generated with Praat software (ver. 6.0.42) and Sennheiser HD650 headphones. We transformed calls with the Fourier function using a Hanning window function and 1024 time steps. Four authors independently categorised call types (Table 2) types based on auditory features and inspection of spectrograms using published chimpanzee vocal repertoires composed of 9 call types (Table 3). If one of the four authors disagreed with the categorisation, we used group majority to determine the call type. There were no instances where more than one author disagreed with the categorisation.

To provide a more comprehensive and diverse assessment of the call types, we asked seven independent experts in chimpanzee vocal communication (Appendix Table A2), blind to any information about the recordings, to categorise the calls recorded from KU7, estimate the age of the caller, and comment on the vocal structures. We provided an unlabelled audio file in which we collated all the calls produced by KU7 in chronological order, with sequences separated by 1 s of silence (Online Resource 1).

Table 3 Call types produced by chimpanzees based on Marler and Tenaza (1977), Slocombe and Zuberbühler (2010), and Taylor et al. (2021). The definition of pant hoot is based on Marler and Hobbett (1975) and Notman and Rendall (2005). Example spectrograms for each call type produced by chimpanzees in the Sonso community, Budongo Forest, Uganda, are presented in Slocombe and Zuberbühler (2010)

Call type	Definition
Bark	Short, loud, and noisy call with abrupt onset. Generally low-frequency.
Grunt	Short and soft call that can be either tonal or noisy. Generally low-frequency and produced with variable rhythm.
Hoo	Short and tonal call with highest frequency and amplitude at the start then decreasing over the duration of the call. The call can be either soft (e.g., rest hoo) or loud (e.g., alarm hoo).
Laughter	Short, soft, and noisy sounds produced while inhaling and exhaling. Generally low-frequency and produced with irregular rhythm.
Pant	Short, soft, and low-frequency unvoiced sounds.
Scream	Loud and high-frequency call that can be either noisy or harmonic. Acoustic energy is usually present during exhalation.
Squeak	Short, high-frequency, and clear tonal call.
Whimper	Soft, low-frequency and tonal call similar to “hoo” calls. Units can increase in frequency within a sequence.
Pant hoot	Vocal sequence composed of up to four acoustically distinctive phases produced in this order and composed by:
Introduction	Low-frequency and tonal calls that acoustically resemble “hoo” calls but are longer in duration and alternated with inhaled tonal elements.
Build-up	Short and low-frequency calls produced both during inhalations and exhalations in rapid rhythm. Intensity and frequency typically increase over the phase.
Climax	High-amplitude and high-frequency calls that resemble “scream” calls.
Let-down	Short and low-frequency acoustic calls which acoustically resemble the build-up phase but with decreasing intensity and frequency.

11.3.5. Quantitative acoustic analysis

We manually extracted six acoustic features from each call unit using Praat software (ver. 6.0.42): duration of each exhaled unit, fundamental frequencies (F0) at the start, middle, and end of the unit, maximum and minimum F0, and range of the F0. We selected these features based on the acoustic data extractable from the recordings and on measurements typically considered when determining call types in chimpanzees (e.g., Marler and Tenaza 1977; Mitani et al. 1999; Mitani and Brandt 1994; Slocombe and Zuberbühler 2010). We only considered exhaled vocal units to make our acoustic analyses comparable with previous studies of pant hoots (e.g., Clark & Wrangham, 1993; Desai et al., 2022; Fedurek et al., 2017; Fedurek, Schel, et al., 2013; Mitani et al., 1992, 1999; Riede et al., 2007; but see Crockford et al., 2004), but also noted the number of inhaled (panted) units produced between exhaled units when these were visible on the spectrogram. Because of the quiet nature of the newborn vocalisations, the presence of environmental background noise, and the distance between the newborn and the microphone, we could not use automated procedures to extract acoustic features.

11.3.6. Clustering analysis

The general approach to studying how experience mediates vocal development is to catalogue the different call types across developmental stages, using acoustic measurements and classification algorithms (Bradbury & Vehrencamp, 2011; Kershenbaum et al., 2016). A common problem is that vocal repertoires are often graded, making objective classifications particularly challenging (Fischer et al., 2017). However, human vocal behaviour is also highly graded, but receivers still perceive transitions in categorical ways, suggesting that human perceptual judgements can be used to disambiguate gradual transitions (Deecke and Janik 2006; Janik 1999). For animal vocal repertoires, data-driven categorisation approaches are preferable, mainly because the degree to which human perceptual bias reflects that of other species remains unclear, and because they allow systematic comparisons across communities (Fischer et al. 2017; Crockford 2019). Soft clustering methods based on fuzzy-set theory (Zadeh, 2008) are very suitable to describe graded vocal repertoires of primates (e.g., chacma baboons, *Papio ursinus*: Wadewitz et al. 2015), an approach that is also promising for chimpanzees (e.g., immature chimpanzees: Taylor et al. 2021).

We used fuzzy c-means clustering to identify the best fitting model for the number of clusters representing different call types in the newborn vocalisations. Fuzzy c-means algorithm measures the degree to which sounds belong to categories based on their acoustic proprieties without restricting them to a single category, capturing more details than hard clustering methods, including the graded transition between call types. We analysed the stability and reliability of model solutions to evaluate the extent to which the optimal description of the calls depended on a small number of acoustic parameters and how robust optimal descriptions were to overlap between clusters. We z-transformed the acoustic features prior to analysis to prevent the influence of measurements with different scales (i.e., Hz and s) on cluster solutions. Since fuzzy c-means clustering is based on the individual acoustic features of each call instead of the total number of calls available (Wadewitz et al., 2015), the small number of newborn vocalisations we recorded was not a limiting factor because a minimum number of data points for each call type is not required.

We adjusted two parameters to identify the best cluster solution to describe the newborn calls: the maximum number of clusters extracted (K), and the 'fuzziness parameter' (μ) which limits the degree of overlap between clusters (i.e., lower values allow less overlap between clusters). We ran fuzzy models using the "fanny" implementation in the "cluster" package (ver. 2.1.2, Maechler et al., 2021) varying K values from a minimum of two (required to quantify gradation) and a maximum of seven, which matched the number of call types we assessed qualitatively and was in line with Taylor et al. (2021). We varied μ values starting at 1.1 with increments of 0.5 following Taylor et al. (2021) and stopped at 3.0 when all membership coefficients were too close to 1/K, which corresponds to the limit of the algorithm to assign cluster membership to calls (Zadeh, 2008). All models considered converged within 500 iterations. We evaluated the fit and confidence of each solution based on the mean silhouette value of all data points combined, which represents how separable the acoustic clusters are. Silhouette values range from -1 to 1, with positive values representing data points that are closer to their primary cluster and indicate some degree of confidence regarding their cluster membership, while negative values represent datapoints that overlap between clusters and are potentially misclassified (Wadewitz et al., 2015). We assessed the reliability of the model by looking at the range of μ values obtained for any given K value, which provided an indicator of 'gradedness'. Solutions for which low and high μ values can be extracted are regarded as more robust to overlap between clusters (Fischer et al., 2017). Using the "clValid" package (ver. 0.7, Brock et al. 2008) we assessed the stability of the clusters by calculating four measurements that compare the result of the clustering algorithm by systematically removing one variable at a time and measuring how much the clusters are based on a small number of acoustic parameters, which represented how 'generalisable' the cluster separations are. The four measurements we used are: the mean proportion of non-overlap between data points (APN); the mean distance between data points in the same cluster (AD); the mean distance between the cluster's centre and the data points in the same cluster (ADM); and the mean variance of data points in the same cluster (FOM) (Brock et al. 2008). Given that our aim was to categorise calls into clusters, we gave priority to mean silhouette values to identify the best model. We extracted a hard-clustering solution for the best-fitting model and assigned all the calls to their primary cluster membership. We then examined the distribution of qualitatively categorised call types in each cluster.

11.3.7. Comparison with pant hoots

We conducted additional acoustic analyses to compare vocal sequences produced by the newborn which contained calls resembling pant hoot phases with pant hoots from infant, juvenile, sub-adult, and adult males of the Sonso community. We selected pant hoots produced during resting or feeding events because pant hoots vary depending on the behavioural context of production (Fedurek, Zuberbühler, et al., 2016; Notman & Rendall, 2005), and the newborn vocalised while resting or potentially before/after nursing. Although pant hoot sequences can be composed of repeated vocal units from a single phase (Soldati, Fedurek, et al., 2022), we selected calls composed of two or more phases to be consistent with previous studies (e.g., Fedurek et al. 2014; Mitani et al. 1999; Notman and Rendall 2005). To control for potential differences between the sexes in the acoustic structure of pant hoots (e.g., Holden 2017), we only selected male pant hoots. We selected recordings based on their overall quality (lack of background noise or overlap with other callers) and good signal-to-noise ratio. Although these recordings were of higher quality than recordings of the newborn, we extracted the acoustic measurements manually in the same way to avoid introducing a potential bias. We sampled the first and the middle vocal units of the introduction and climax phases for four units from each pant hoot. This allowed us to take into consideration the acoustic gradation that can occur within phases. Where there were an even number of units, we chose the first of the two middle units (as in Desai et al., 2022). In total, we extracted features from 189 vocal units (42 pant hoots) produced by 3 infants, 4 juveniles, 4 sub-adults, and 4 adults, with a minimum of two pant hoots per individual (Appendix Table A8).

To determine whether the acoustic structure of Phase 1 and 2 calls produced by the newborn differed from the introduction and climax phases produced by infant, juvenile, sub-adult, and adult individuals from the Sonso community, we used permuted discriminant function analyses (pDFA; Mundry and Sommer 2007), following previous studies (e.g., Leroux et al. 2021; Soldati et al. 2022). To analyse the introduction phase, we used 19 vocal units from 11 calls produced by 4 adults, 21 units from 11 calls produced by 4 sub-adults, 6 units from 4 calls produced by 3 juveniles, and 19 units from 10 calls produced by 4 infants. Together with the Phase 1 calls (N = 26), we obtained a total of 91 calls. To analyse the climax phase, we used 17 units from 11 calls produced by 4 adults, 20 units from 11 calls produced by 4 sub-adults, 18 units from 9 calls produced by 4 juveniles, and 10 units from 10 calls produced by 3 infants. Together with the Phase 2 calls (N = 18), we obtained a total of 93 calls. Before analysis, we assessed multicollinearity to avoid including correlated acoustic parameters. We removed at a time the parameter with the highest variance inflation factor (VIF) using the 'performance' R package (version 0.8.0, Lüdecke et al., 2021) until we obtained a set of variables with low correlation. In the final set of four variables (Duration, Start F0, End F0, Range F0), the highest VIF for introduction calls was 2.85 and the highest VIF for climax calls was 1.63. We assessed the distribution of the data and when variables were not normally distributed and this could be improved, we applied a log or squared-root transformation. We then used nested pDFA with 1000 permutations to test whether the acoustic structure of newborn's Phase 1 & 2 calls differed significantly from the corresponding phases produced by the other age categories (Mundry & Sommer, 2007). In comparison with a conventional DFA, a pDFA allows the inclusion of repeated data points per individual and controls for unbalanced data sets at the same time. We included the 'ID' of the caller as a control factor. We conducted all statistical analyses in R (version 4.1.2, R Core Team, 2020).

11.4. Results

A detailed report of the birth is available in the Supplementary Material. Video and audio recordings are available as Online Resources (1, 3 - 5).

11.4.1. Qualitative call classification

We recorded 70 call units from the newborn during 2 hours and 15 minutes of observation (0.5 per minute). These calls were divided into 12 separate vocal occurrences (also referred as 'utterances'; call rate 0.1 per minute), of which three were single calls and nine were call sequences (see Online Resource 2 for the acoustic spectrograms). Vocal sequences contained a mean of 7.4 vocal units (range 2 - 17). We identified barks (N = 2), grunts (N = 8), hoos (N = 6), squeaks (N = 2), whimpers (N = 8), and units that we labelled as part of a pant hoot (N = 44). We distinguished two variants which we refer to as "pant hoot phase 1" (N = 26), hereafter Phase 1 for brevity, and "pant hoot phase 2" (N = 18), hereafter Phase 2 (Figure 2). The four vocal sequences that included Phase 1 or Phase 2 were composed of a mean of 11 vocal units (range 5 – 15) when excluding other call types. Of all the newborn's Phase 1 and 2 units, 36% (N = 15) included panted units between exhaled units (Figure 2).

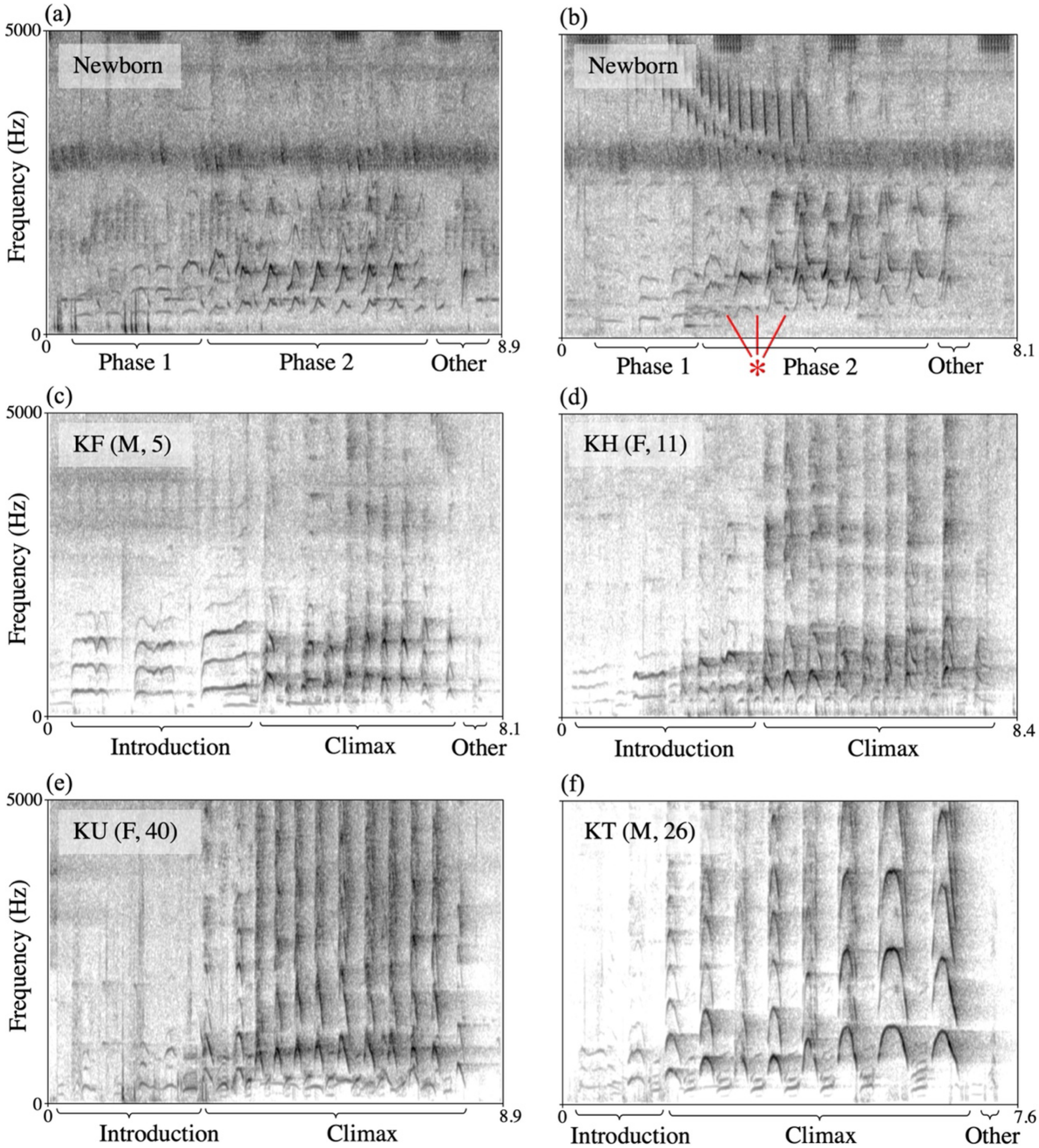

Figure 2 Spectrographic representations of pant hoot calls produced by a newborn chimpanzee in the Sonso community, Budongo Forest, Uganda on 20 November 2019 with pant hoots produced by members of the mother's family for comparison (sex and age (yr) are shown). For each call the different phases or types are indicated underneath (other = other call type). The red asterisk indicates three examples of panted units. Duration (s) on the x-axis. Note the presence of bird songs and cicada sounds above frequencies of approx. 2500 Hz in spectrograms a) and b).

Five of seven independent experts agreed with our decision to classify KU7's Phase 1 and Phase 2 calls as resembling adult pant hoots (Appendix Table A4). One expert classified the calls as either pant hoots or whimpers and one expert classified the calls as whimpers. The experts did not reliably classify the other call types (barks, grunts, hoos, squeaks, and whimpers) citing challenging conditions (soft signal volume and background noises), but two experts reported the presence of quiet hoos and grunts among these other call types. Three experts classified the caller as a young individual, one as a juvenile, one as an infant, one as immature, and one as either a juvenile or a young adult.

Table 4 Mean ± SD of extracted parameters for call types produced by a newborn chimpanzee in the Sonso community, Budongo Forest, Uganda on 20 November 2019. Table A3 (Appendix) contains extracted data from each call unit separately

Type	N	Duration (s)	Start F0 (Hz)	Middle F0 (Hz)	End F0 (Hz)	Max F0 (Hz)	Min F0 (Hz)	Range F0 (Hz)
Bark	2	0.09±0.03	545.9±11	537.0±30	518.4±49	550.1±15	518.4±49	31.7±33
Grunt	8	0.06±0.02	256.1±135	255.4±122	251.7±12	264.8±131	248.5±118	16.3±16
Hoo	6	0.30±0.14	338.2±29	349.7±16	353.1±30	358.6±25	333.9±27	24.7±22
Phase 1	26	0.32±0.06	356.6±59	408.2±83	396.5±84	421.3±86	354.8±60	66.5±40
Phase 2	18	0.29±0.05	386.7±55	624.0±184	504.0±11	646.6±192	386.4±55	260.2±146
Squeak	2	0.15±0.08	408.0±133	849.6±180	936.1±11	1025.6±17	408.0±133	617.7±115
Whimper	8	0.10±0.05	253.7±38	272.3±48	260.7±53	272.3±47	246.7±45	25.6±19

11.4.2. Quantitative analyses

We extracted six acoustic features from 70 call units and used them to model the best clustering of acoustically similar units using fuzzy analyses (Table 4). Overall, we obtained 20 unique models varying between two to seven clusters (K) and fuzziness parameters (μ) of 1.1, 1.5, 2.0, and 2.5 (

Figure 3). Two-, three-, four-, and five-cluster solutions could be calculated up to $\mu = 2.0$, while six- and seven-cluster solutions could be calculated up to $\mu = 2.5$. The model that best fit our data was calculated with three clusters (K = 3) and with a fuzziness parameter of 1.1 (

Figure 3), scoring the highest mean silhouette value of 0.450, which indicates confidence in the overall solution. Although this model was not the most stable, only 6% of call units (N = 4) changed membership when we recalculated the model with one less variable (Appendix Table A5 and Figure A1). In the most stable model (K = 2, $\mu = 1.1$) 2% of call units (N = 1.3) changed membership, but this model had a mean silhouette value of 0.374 which is considerably lower than the best fitting model. Six- and seven-cluster solutions could be calculated for a larger range of fuzziness values, suggesting they might be more reliable. However, these solutions were less consistent in mean silhouette value (range: 0.177 for six clusters, 0.174 for seven) than three-cluster solutions (range: 0.095) (Appendix Table A6).

Furthermore, six and seven-cluster solutions had lower mean silhouette values (0.399 and 0.343 respectively) than the best fitting model with a three-cluster solution.

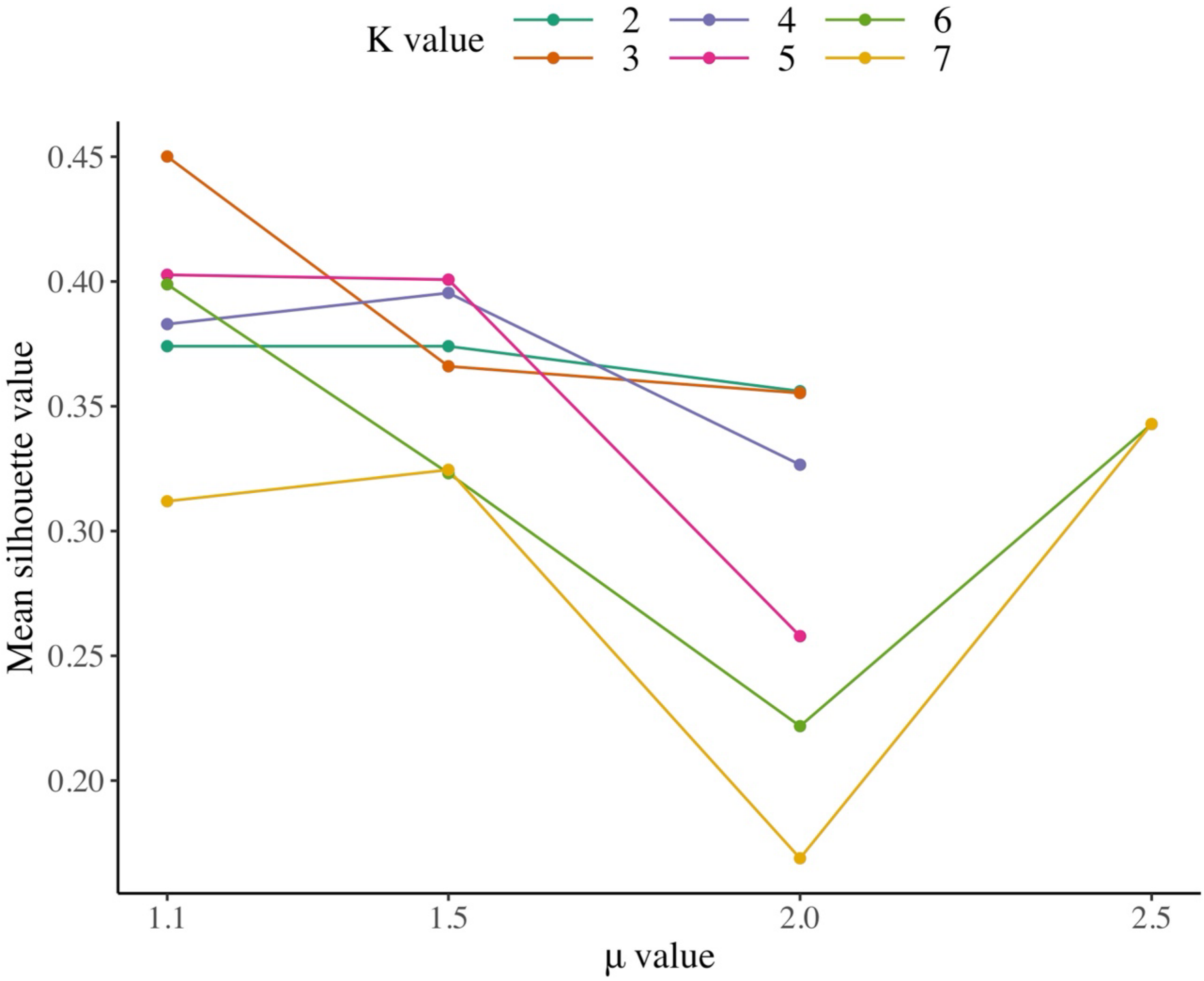

Figure 3 Mean silhouette values obtained by varying the number of clusters (K = 2 to 7) and fuzziness values (μ = 1.1 to 2.5) using fuzzy c-means clustering. Mean silhouette values measure the confidence of the overall cluster solution of calls produced by a newborn chimpanzee in the Sonso community, Budongo forest, Uganda on 20 November 2019; the higher the silhouette values, the more distinct the acoustic clusters are and the better the model fits the data.

11.4.3. Cluster composition

We calculated the percentage of each call type (determined qualitatively) that belonged to each of the three clusters in the best fitting model identified by the quantitative analysis (Appendix Figure A2). The first cluster was composed of grunts and whimpers (Table 5). The second cluster consisted of barks, squeaks, Phase 2 calls, Phase 1 calls, and grunts (Table 5). The third cluster consisted of hoos, Phase 1 calls, and Phase 2 calls (Table 5).

Table 5 Percentage and number (in brackets) of calls per call type in each cluster produced by a newborn chimpanzee in the Sonso community, Budongo Forest, Uganda on 20 November 2019. See Table A7 in the Appendix for within-cluster call type percentages

	Grunt	Bark	Hoo	Phase 1	Phase 2	Squeak	Whimper	Total
Cluster 1	88 (7)	-	-	-	-	-	100 (8)	15
Cluster 2	12 (1)	100 (2)	-	8 (2)	33 (6)	100 (2)	-	13
Cluster 3	-	-	100 (6)	92 (24)	67 (12)	-	-	42
Total	8	2	6	26	18	2	8	70

11.4.4. Call combinations

KU7 produced single calls in three instances (grunts only) and nine different call sequences (range: 2 - 17 units). Of the nine sequences, four were combinations of units from different call types (Figure 4). Overall, calls from two or three different clusters were produced in a single combinatorial structure and two to four different calls were combined in a structure.

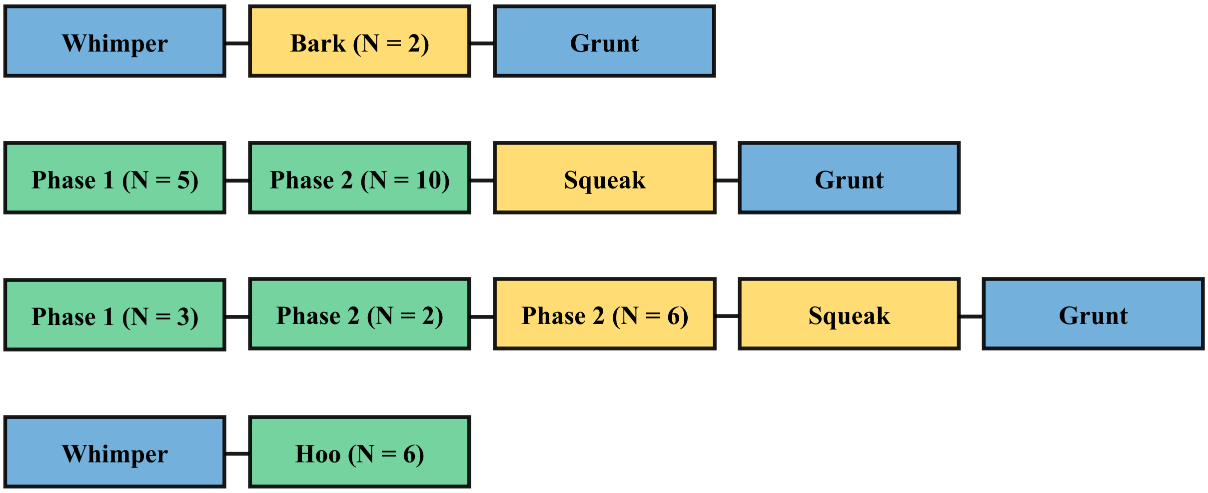

Figure 4 Four vocal sequences composed of different call types produced by a newborn chimpanzee in the Sonso community, Budongo Forest, Uganda on 20 November 2019. Each series of connected ‘blocks’ represents one of the four vocal sequences. Each ‘block’ indicates the call type and the number of repeated call units of the same call type. Colours represent clusters (Cluster 1 = blue; Cluster 2 = yellow; Cluster 3 = green).

11.4.5. Comparison with pant hoots

Pant hoots were composed of a mean of 15 vocal units in infants (range 1 – 18), 12.6 units in juveniles (range 1 – 12), 10.2 units in sub-adults (range 1 – 15), and 8.1 units in adults (range 1 – 15). A panted unit followed 43% of vocal units produced by infants (N = 21), 59% of units in juveniles (N = 20), 73% of units in sub-adults (N = 37), and 94% of units in adults (N = 44). Vocal usage rate varied with phase and age category (Appendix Table A9). While introduction, build-up, and climax phases were observed across all age categories, the let-down phase was not observed in infants and juveniles (Appendix Table A9). Furthermore, the let-down phase was rarely produced by sub-adults and adults, and the build-up phase was rarely produced by adults (Appendix Table A9).

The discriminant function could not operate when including the introduction (produced by infant, juvenile, sub-adult, and adult males) and the Phase 1 calls produced by the newborn. This was likely because the within-group variance of the variables was lower than the level accepted by the function, which might indicate that variables are collinear or constant (Venables & Ripley, 2002). Because the variables we considered were not collinear and since pant hoots have mainly been studied in sub-adult and adult males, we repeated the analysis including only individuals from these age categories. The results are not compatible with the idea that calls are acoustically different in newborn vs. sub-adult and adult males (expected correctly cross-classified: 42%, $P = 0.257$). For the climax and Phase 2 calls, the results are also not compatible with the idea that calls are acoustically different in newborn vs. infant, juvenile, sub-adult, and adult males (expected correctly cross-classified: 26%, $P = 0.164$). We repeated the analysis including only the newborn, sub-adult, and adult individuals and found similar non-significant results (expected correctly cross-classified: 40%, $P = 0.266$).

11.5. Discussion

We qualitatively discriminated seven call types from the 70 units produced by a newborn chimpanzee immediately after birth, in line with what was previously reported for older chimpanzee infants (Plooij, 1984). The majority of units were given as part of sequences. Interestingly, the newborn also produced vocal structures resembling pant hoots. Quantitative analyses revealed three acoustically distinct clusters of calls, with calls from different clusters combined into the same sequence. All call types were also produced in isolation, with the exception of Phase 2 (pant hoot) calls and squeaks, which were only produced in combination with other calls. From these data we concluded that chimpanzees have the capacity to combine some call types into larger structures from birth.

We can suggest four hypotheses explaining what could trigger the newborn's vocal production. First, the newborn produced a series of long vocal sequences to attract the mother's attention, for example due to discomfort or desire to be nursed. However, we did not notice any of the more typical calls for such contexts (i.e., cries and whimpers; Dezecache et al. 2021) and the newborn was always in bodily contact with the mother during our observations, making this explanation unlikely.

Second, the newborn's vocal behaviour may represent a rudimentary form of babbling (Oller 2000), which serves as vocal practice and to elicit care-giving (ter Haar et al., 2021). However, the newborn produced vocal sequences composed of repeated vocal units that were rhythmically produced and only contained a subset of adult calls. Furthermore, the sequences lacked variable acoustic structures, did not elicit vocal or social responses from the mother, were produced at lower call rates than human and marmoset infants (Elowson et al., 1998a; Oller et al., 2021; Snowdon & Elowson, 2001) and at comparable rates with chimpanzee and bonobo infants (Kojima, 2008; Oller et al., 2019; Taylor, 2020), making the babbling hypothesis an unlikely explanation. In marmosets, one of the few primates where babbling has been reported, parents engage in vocal feedback and exchanges (Takahashi et al., 2015), while chimpanzee mothers rarely direct vocalisations to their offspring (Schick et al., 2022). While language-trained or human-raised chimpanzees have been reported to produce vocalisations similar to babbling when interacting with researchers (Hayes and Hayes 1951, p. 106-108), the behaviour is different from human infant babbling in terms of variety, quantity, and duration (Kellogg, 1968; Kojima, 2008). In contrast, the newborn vocalisations presented some similarities with protophone-like sounds produced by young bonobo infants (Oller et al. 2019). These sounds are regarded as akin to the exploratory protophones produced by human infants since birth during low- to moderate arousal contexts, without requiring social stimulation, and prior to babbling (Oller 2000; Oller et al. 2016). However, the newborn chimpanzee produced sounds at much lower rates than humans, without clear signs of playfulness, and without interacting vocally with the mother, all of which also characterise vocal behaviours in infant bonobos (Oller et al. 2019). One possibility is that the period of vocal exploration in great apes is very reduced and limited to the earliest developmental phase, although further observations are necessary to test this possibility.

Third, the newborn vocal behaviour may have been an artefact resulting from limited vocal control. Interestingly, Phase 1 calls were always followed by Phase 2 calls in sequences, but never the other way around, and terminated with squeaks followed by grunts. This call order is akin to that of pant hoots, in which introduction units are followed by climax units, and akin to how pant hoots tend to be followed by food grunts in call combinations (Leroux et al., 2021). These observations do not support the artefact hypothesis, although there may have been anatomical constraints on vocal production. For instance, in adult pant hoots, the climax is never produced in isolation but is always preceded by an introduction or build-up phase (Soldati, Fedurek, et al., 2022), perhaps because producing high-pitch and high-amplitude calls requires more time and effort (Riede et al., 2007).

Finally, intra-uterine auditory exposure to conspecifics' calls may have affected the newborn's vocal development. While we cannot address this hypothesis with our data, it has been documented in marmosets (Narayanan et al., 2022), humans (Gervain, 2018; Varga et al., 2019), and songbirds (Colombelli-Négrel et al., 2021), all of which are regarded as vocal learners (Vernes, Kriengwatana, et al., 2021). Further studies are needed to clarify the effects of pre- and post-natal auditory exposure on the development of great ape vocalisations.

The most puzzling aspect of the newborn's vocal behaviour was the presence of vocal structures that acoustically and visually resembled chimpanzee pant hoots, with clear resemblance to adult as well as infant and juvenile pant hoots. Most experts rated these structures as pant hoot attempts. Although some experts rated them as whimpers, cluster analyses revealed that they did not belong to the whimper cluster. Phase 1 calls closely resemble the introduction phase and Phase 2 calls closely resemble the climax phase, which was supported by the results of the discriminant analyses. All the hoo calls produced by the newborn belonged to the Phase 1 cluster, in line with the idea that the introduction can be seen as a variant of hoos (Crockford, 2019). The production of panted units, a characteristic feature of pant hoots, followed an incremental pattern from the newborn through all age categories, suggesting that it develops during ontogeny. In addition, we agree with the experts, who pointed out that the overall 'rhythmicity' of the newborn sequences is characteristic of pant hoots. Thus, the newborn produced vocal structures resembling pant hoots, suggesting that such complex structures are part of the innate vocal repertoire of chimpanzees. However, the newborn utterances differed from adult pant hoots in terms of absence of phases that correspond to the build-up and let-down. Alternating phases with a relatively low rate of unit production, such as the introduction and climax, with phases exhibiting a fast-paced and panted unit production, such as the build-up and let-down, is a key feature of pant hoots.

The differences between the arguably rudimentary form of the newborn pant hoot and adult pant hoots suggest that this call type undergoes some ontogenetic processes. Immature individuals might learn to produce certain phases in specific contexts or as part of structurally varying sequences (usage learning; Janik and Slater 2000; Marshall et al. 1999), as well as pant hoots that resemble the pant hoots of group members or social partners (production learning; Ruch et al. 2018). The latter hypothesis is supported by the presence of community dialects (Crockford et al., 2004; Mitani et al., 1992) and by the stronger call similarity between social partners (Mitani & Brandt, 1994; Mitani & Gros-Louis, 1998), although genetic or ecological factors might also explain community differences (Desai et al., 2022; Mitani et al., 1999). While some developmental changes result from the maturational process (Nishimura et al., 2003), systematic study of the acquisition of vocal capacities, especially at the early ontogenetic stages, is a key missing element in the current debate on vocal learning in primates, particularly in great apes (e.g., Watson et al. 2015a, 2015b; Fischer et al. 2015). Our observations fit with the idea that primate vocal repertoires are largely fixed and present from birth (Fischer & Hammerschmidt, 2020), although they also indicate that fine acoustic structures undergo ontogenetic processes.

The limitations of our study include the short observation period and the small dataset, which reduce our ability to generalise from our study. Having complete access to the context of production typically facilitates call classification, although it can also be misleading with graded and flexible calls (Fischer & Price, 2017; Schamberg et al., 2018). For instance, pant hoots are produced across most contexts and in response to conspecific calls (Goodall, 1986), while food grunts are related to both feeding and agonistic events (Ischer et al., 2020; Marler & Tenaza, 1977). The categorisation of calls based on acoustic features is less subject to biases when the context of production is particularly unclear or flexible, as in pant hoots and immature calls. When applying fuzzy clustering on small datasets, calls can appear more discrete since they are less likely to represent the entire repertoire. In addition, extracting a small number of features can lead to higher spread of values but does not necessarily indicate better separation (Wadewitz et al., 2015). Because we did not observe the production of typical newborn utterances like cries or screams (Kojima, 2008) it is possible that their absence affected our quantitative analyses. Specifically, the best solution was the most distinct but was also more influenced by a smaller subset of features. However, in a recent study the repertoire of infant chimpanzees was best described by a two-cluster model, with evidence of a potential third cluster (Taylor et al., 2021), which provides further validity to the model describing the newborn vocalisations. We do not claim that there are only three call types in the repertoire of newborn chimpanzees. To determine its true size, it will be necessary to investigate how receivers react to each vocalisation (Seyfarth & Cheney, 2017), including to graded variants (e.g., Fischer, 1998; Fischer et al., 2001).

The observation of a birth in a wild chimpanzee community provided a rare opportunity to investigate the vocal behaviour of a newborn chimpanzee, the starting point of a long developmental trajectory. The newborn demonstrated the capacity to combine different call types into larger vocal sequences. Some of these combinatorial structures were composed of unique calls that shared several characteristics with pant hoots and were identified by expert human listeners as such. Consequently, our study suggests that acoustically complex structures, akin to adult pant hoots, are part of the chimpanzee vocal repertoire from birth, and that these sequences are subject to ontogenetic processes that shape their acoustic structure. While extensive work has been conducted on adult male calls, and combinatorial capacities have recently gained attention, further work is necessary to elucidate the production, usage, and comprehension of complex vocal sequences in primates from an ontogenetic perspective. Although we remain careful in interpreting observations from a single individual, we believe it provides a valuable contribution to the study of chimpanzee vocal development that will hopefully encourage further research on the ontogeny of great ape vocalisations.

12. Social and individual factors mediate chimpanzee vocal ontogeny

12.1. Abstract

The vocal ontogeny of non-human primates has received relatively little empirical attention, despite its relevance for understanding the evolution of language acquisition. In particular, the role of social learning from mothers and other group members in our closest living relatives, the great apes, remains largely unknown. Here, we examined the development of pant hoots, a complex multi-phase call for close-range and long-distance communication, in 13 immature wild chimpanzees (*Pan troglodytes schweinfurthii*) of the Sonso community of the Budongo Forest, Uganda. More specifically, we investigated how maternal gregariousness, age and sex impacted on responses to other group members' calls. We found that the older sons of gregarious mothers were more likely to orient and respond vocally to callers compared to other immature individuals. This effect was strongest in the presence of males and when their mothers also responded vocally, demonstrating how great ape vocal development is enhanced by social and vocal exposure. A flexible and socially mediated ontogeny of primate vocal behaviour is consistent with a gradual view of language evolution.

12.2. Introduction

Language is arguably the key feature that distinguishes humans from other animal species, a fact that continues to foster scientific debate and major research efforts (Berwick et al., 2013; Fitch, 2017; Hauser et al., 2014; Jarvis, 2019). Language does not leave direct fossil traces, but comparative research on other species' communicative systems can provide insights about possible precursor stages and evolutionary patterns (Fitch & Zuberbühler, 2013; Hauser et al., 2002). Given their biological proximity, non-human primate vocal communication, especially that of great apes, is of particular interest and is critical to assess how spoken language might have emerged gradually during our evolutionary history (Fedurek & Slocombe, 2011; Fischer & Hage, 2019).

Although the comparative approach has turned out to be very productive, so far it is typically based on research conducted on adult individuals that are already fully-competent communicators (Eaton et al., 2018). However, considerably less researched but equally important for understanding of the evolution of spoken language is the evolution of vocal ontogeny, i.e., the learning processes that drive vocal communication from birth to adulthood and the cognitive apparatus responsible for it (Bard & Leavens, 2014; Locke, 2009; Oller et al., 2016b). In humans, social interactions and social feedback are essential for language learning (Kuhl, 2004; Schick et al., 2022; Tomasello, 2008). Socially mediated vocal development has also been documented in animals, though the evidence is mostly from birds, with relatively few studies on mammals (Janik & Knörnschild, 2021; Kuhl, 2003; Lattenkamp & Vernes, 2018). In songbirds, the typical pattern is that male offspring learn their songs during social interactions with their fathers (Baptista & Gaunt, 1997; Brainard & Doupe, 2002), while comparable evidence is rare and more restricted for primates (Petkov & Jarvis, 2012). A notable exception is research conducted on marmosets demonstrating that infants learn when and how to call through vocal feedback and auditory exposure from their caregivers (common marmosets, *Callithrix jacchus*: Takahashi, 2019; Takahashi et al., 2017; pygmy marmosets, *Cebuella pigmae*: Elowson et al., 1998; Snowdon et al., 1997). In contrast, there is no comparable evidence from great apes, despite increasing evidence for complex and flexible adult vocal behaviour (Slocombe et al., 2022; Snowdon, 2009; Townsend et al., 2020).

A useful way to conceptualise vocal development is to distinguish between three processes: 1) production learning - how to modify the vocal output by attending to others' vocal behaviour; 2) usage learning - how to use vocalisations that are part of the repertoire in specific contexts; and 3) comprehension learning - how to form associations between vocalisations and mental representations of the world (Janik and Slater 2000; Seyfarth and Cheney 1997; Vernes et al. 2021). Current theory states that primate vocal development is rather inflexible in these three domains, especially in terms of production learning (Egnor & Hauser, 2004; Owren et al., 2011; Snowdon, 1990). However, production learning has received the most attention among the three processes, partly driven by interest in the evolutionary origins of human speech (Seyfarth & Cheney, 1997; Snowdon, 2009). This view has led some scholars to conclude that not much can be learned about language acquisition from primate vocal communication (Bolhuis et al., 2014; Hauser et al., 2014). In this view, socially learned vocal communication has likely emerged through convergent evolution in a limited number of biologically distant species (e.g., bats, cetaceans, elephants, and songbirds: Fischer & Hammerschmidt, 2020; Janik & Knörnschild, 2021; Nowicki & Searcy, 2014).

Here, we revisit the notion of inflexible great ape vocal development for the following reasons. First, primate studies have largely focused on alarm calls, a signal class that is expected to be less flexible than calls with more social functions, due to its narrow and evolutionary urgent function (Elowson et al., 1992; Snowdon et al., 1997). Second, the majority of data stem from studies of monkey vocalisations, which are arguably less directly relevant for studies of language evolution than great apes who share a more recent last common ancestor with humans (Fischer & Hage, 2019; Fitch & Zuberbühler, 2013), despite a small increase in studies about great ape vocal development in the recent years (e.g., Dezecache et al., 2019; Lameira et al., 2022; Laporte & Zuberbühler, 2011). Third, several key studies on primate vocal development have been conducted in captivity or in artificial settings, where individuals might not express the same social behaviours, including communication (e.g., Fröhlich et al., 2021), when compared to a natural setting given the absence or alteration of relevant socioecological factors (Harrison & van de Waal, 2022; Schuppli & van Schaik, 2019). Fourth, many developmental studies have been carried out under abnormal social contexts, such as social isolation (squirrel monkeys, *Saimiri sciureus*: Lieblich et al., 1980; Winter et al., 1973), deafening (squirrel monkeys: Talmage-Riggs et al., 1972), cross-fostering (rhesus and japanese macaques, *Macaca mulatta* and *M. muscata*: Owren et al., 1992), or translocation (common marmosets: Zürcher et al., 2019). While these studies offered an opportunity to control some potentially influential external factors, they may have introduced limitations on the opportunity to detect social learning (Boesch, 2007, 2020; Seyfarth & Cheney, 2017), and are otherwise not ethically permissible on great apes or wild animals.

How do primates learn to communicate? A first prerequisite concerns the ability to socially learn vocal production and usage by attending to others' vocal behaviour, which has been demonstrated in some mammals (Janik & Slater, 2000; Vernes, Janik, et al., 2021), including in monkeys (marmosets: Takahashi et al., 2015, 2017; vervets, *Cercopitheciis aethiops*: Hauser, 1988, 1989), although there is no clear evidence in great apes (e.g., adult chimpanzees: Watson et al., 2015a, 2015b; Fischer et al., 2015). A notable exception is a recent study on wild orangutans (Pongo pygmaeus wurmbii and P. abelii), showing that the degree of an individual's gregariousness affects vocal output and structure (Lameira et al., 2022). Another relevant finding with regard to vocal production is that the calls of adult chimpanzees are acoustically more similar between close social partners (Mitani & Brandt, 1994; Mitani & Gros-Louis, 1998) and may differ between communities as vocal 'dialects' (Crockford et al., 2004; Mitani et al., 1992). These findings suggest an ability to socially learn some vocal structures, though the between group differences described are relatively small and may be also driven by genetic or ecological factors (Desai et al., 2022; Mitani et al., 1999). For comprehension learning, a prerequisite in both human infants (Colombo & Bundy, 1981; Vouloumanos & Werker, 2004) and songbirds (Doupe & Kuhl, 1999; Marler, 1990) is a preference for attending to conspecific vocalisations, but it is not known whether primates also have such an attentional bias (Fischer, 2008; Seyfarth & Cheney, 1997). The occurrence and type of responses to others' calls can be used as a measure of whether or not individuals acquired specific information from a call (Seyfarth et al., 2010; Seyfarth & Cheney, 2003). There is good evidence that adult primates can extract relevant social information from attending to calls, such as changes in the hierarchy (Bergman et al., 2003; Cheney et al., 1995) or the arrival of a social partner (Schel, Machanda, et al., 2013; Schel, Townsend, et al., 2013), which is arguably learned from experience of interacting with others. Critically, however, the previous findings on vocal production, usage, and comprehension come predominantly from studies on adult great apes, with not much being known about infants and juveniles in this respect. Furthermore, a wide range of chimpanzees' social-cognitive skills are affected by social experience (Boesch, 2020; van IJzendoorn et al., 2009) during the long dependency period from the mother (Goodall, 1986; Maestripieri & Call, 1996; Pusey, 1990), suggesting that there is rich potential for social factors to also play a role in the ontogeny of vocal behaviour.

High fission-fusion societies such as those of chimpanzees are characterised by a dynamic social system in which mature individuals navigate a complex network of kin and non-kin social relationships often mediated by the use of vocal signals. Females are typically less gregarious than males, although with some variation across populations (Gilby & Wrangham, 2008; Lehmann & Boesch, 2008; Williams et al., 2002), and often emigrate at sexual maturity, while males are philopatric and build strong and long lasting bonds with other males (Gilby & Wrangham, 2008; Mitani, 2009a; Sandel et al., 2020). Given a long period of dependency from the mother that continues after weaning (at approximately 4-5 years old; Pusey, 1983), the early socialisation of immature individuals depends almost entirely on their mothers' social associations (Murray et al., 2014; Pusey, 1983). When compared to human infants, however, infant apes have been suggested to produce spontaneous vocalisations less frequently, which represents a challenge in the study of vocal ontogeny (Marler & Tenaza, 1977; Oller et al., 2019; Seyfarth & Cheney, 1997). Apart from early qualitative chimpanzee studies (e.g., Goodall, 1986; Plooij, 1984; Pusey, 1990), only a limited amount of systematic research on vocal development in immature individuals is available and only for two call types: alarm and greeting. For instance, the development of vocal usage in greeting calls occurs in distinct developmental phases during which the frequency of use and the specificity of the recipients varies as individuals mature (Laporte & Zuberbühler, 2011). Furthermore, the development of greeting calls is influenced by the mother's behaviour and social interactions with male infants being more vocal compared to female infants (Dunphy-Lelii & Mitani, 2019; Laporte & Zuberbühler, 2011). For alarm calls, maternal vocal behaviour and gaze alternation with the offspring may impact the development of vocal usage (Dezecache et al., 2019).

In this study, we focus on one call type in the chimpanzee vocal repertoire, the pant hoot, which stands out for its flexibility and complexity. Little to nothing is known about its ontogeny, despite a long research tradition (Marler & Hobbett, 1975; but see Soldati, Muhumuza, et al., 2022). Pant hoots are the most frequently uttered call type by both sexes (Marler & Tenaza, 1977), and are composed of four acoustically distinct phases typically produced in an ordered sequence of introduction, build-up, climax, and let-down, with each phase often containing multiple vocal elements (Marler & Hobbett, 1975; Marler & Tenaza, 1977). Pant hoots are produced spontaneously or as part of vocal choruses or vocal exchanges over both short- and long-distances (Fedurek, Machanda, et al., 2013; Goodall, 1986). They are used to maintain social cohesion, helping to coordinate and recruit conspecifics while navigating a dynamic fission-fusion system (Eckhardt et al., 2015; Fedurek et al., 2014; Mitani & Nishida, 1993) across a wide range of behavioural and social contexts (Goodall, 1986; Mitani & Nishida, 1993; Soldati, Fedurek, et al., 2022). Adult females pant hoot less frequently than adult males (Clark, 1993; Crunchant et al., 2021; Kalan, 2019; Notman & Rendall, 2005) and are more likely to join others' calls than to call spontaneously (Arcadi, 1996), while immature individuals of both sexes are very rarely observed pant hooting (Marler & Tenaza, 1977; Pusey, 1990; Taylor et al., 2021).

The aim of our study was to focus on the ontogeny of vocal usage and comprehension of pant hoots in wild chimpanzees. We first compared the spontaneous call rate and response patterns of mature and immature individuals to establish their developmental trajectories. We predicted increased vocal usage and greater responsiveness to the pant hoots of others with increasing age. Second, we predicted that the offspring of more gregarious mothers, exposed to more social interactions, would show greater responsiveness to others' calls. Third, given the importance of pant hoot chorusing between close social partners (Fedurek, Machanda, et al., 2013), we predicted that offspring would vocally respond more often when their mother vocally responded too. Finally, since pant hoots are most frequently used by adult males for spatial coordination and during social interactions, we predicted that immature males would show greater responsiveness than immature females.

12.3. Methods

12.3.1. Study site

The study was conducted with the chimpanzees of the Sonso community (*Pan troglodytes schweinfurthii*) of the Budongo Forest in western Uganda. The community is well habituated to human observers with ongoing research since the early 1990s (Reynolds, 2005). At the beginning of the study (September 2018) the community was composed of 74 individuals (11 adult males, 25 adult females, 15 sub-adults, 8 juveniles, and 15 infants). At the end of the study (March 2020) the community was composed of 68 individuals (9 adult males, 26 adult females, 15 sub-adults, 9 juveniles, and 8 infants) (Appendix Table A10).

12.3.2. Ethical note

The project adhered to the ASAB guidelines for the treatment of animals during behavioural studies. It was approved by the Uganda Wildlife Authority (UWA/COD/96/5), the Uganda National Council for Science and Technology (NS 637) and the research ethics committees of both the Universities of Neuchâtel and St Andrews (38/2019-B; No 171). Data collection was terminated on 17 March 2020, due to the Covid-19 pandemic (UWA ref: EDO/73/01), to avoid putting the health of the animals at risk (Matsuzawa, 2020; Patrono et al., 2018).

12.3.3. Study subjects

We used age categories following Reynolds (2005) of infants (0–4 years), juveniles (5–9 years), sub-adults (males: 10–15 years, females: 10–14 years), and adults (males: >16 years, females: >15 years). Study subjects were selected to obtain balanced samples of each age category in the community (Appendix Table A10): 2 of 4 available female infants, 4 of 7 male infants, 3 of 4 female juveniles, 4 of 4 male juveniles, all of which are collectively referred to as immature individuals hereafter (Appendix Table A11). We did not consider sub-adult individuals as immature as they already associate with other group members independently from their mother (Pusey, 1990) and so we classified them as mature individuals (Appendix Table A12).

12.3.4. Definition of pant hoot vocalisations

Pant hoots are long-distance vocal sequences composed of up to four acoustically distinct phases, typically produced during traveling and feeding events (Marler & Hobbett, 1975; Marler & Tenaza, 1977; Notman & Rendall, 2005) (Figure 5). Each phase contains one or more acoustically similar voiced elements produced in the following order: (1) introduction: series of low-amplitude, low-frequency tonal elements that acoustically resemble "hoo" vocalisations but are noticeably longer in duration and alternated with inhaled tonal elements; (2) build-up: series of short low-amplitude and low-frequency elements produced both during inhalations and exhalations in rapid rhythm which can increase in intensity and frequency as the call proceeds; (3) climax: one or more scream-like high-amplitude and high-frequency elements; (4) let-down: series of low-amplitude and low-frequency acoustic elements which acoustically resemble the build-up phase but tend to progressively decrease in intensity and frequency over time. Because pant hoot phases can be omitted or produced in isolation (Fedurek, Zuberbühler, et al., 2016; Notman & Rendall, 2005; Soldati, Fedurek, et al., 2022), we considered a pant hoot when a caller produced at least one of the four phases (see also Soldati, Fedurek, et al., 2022).

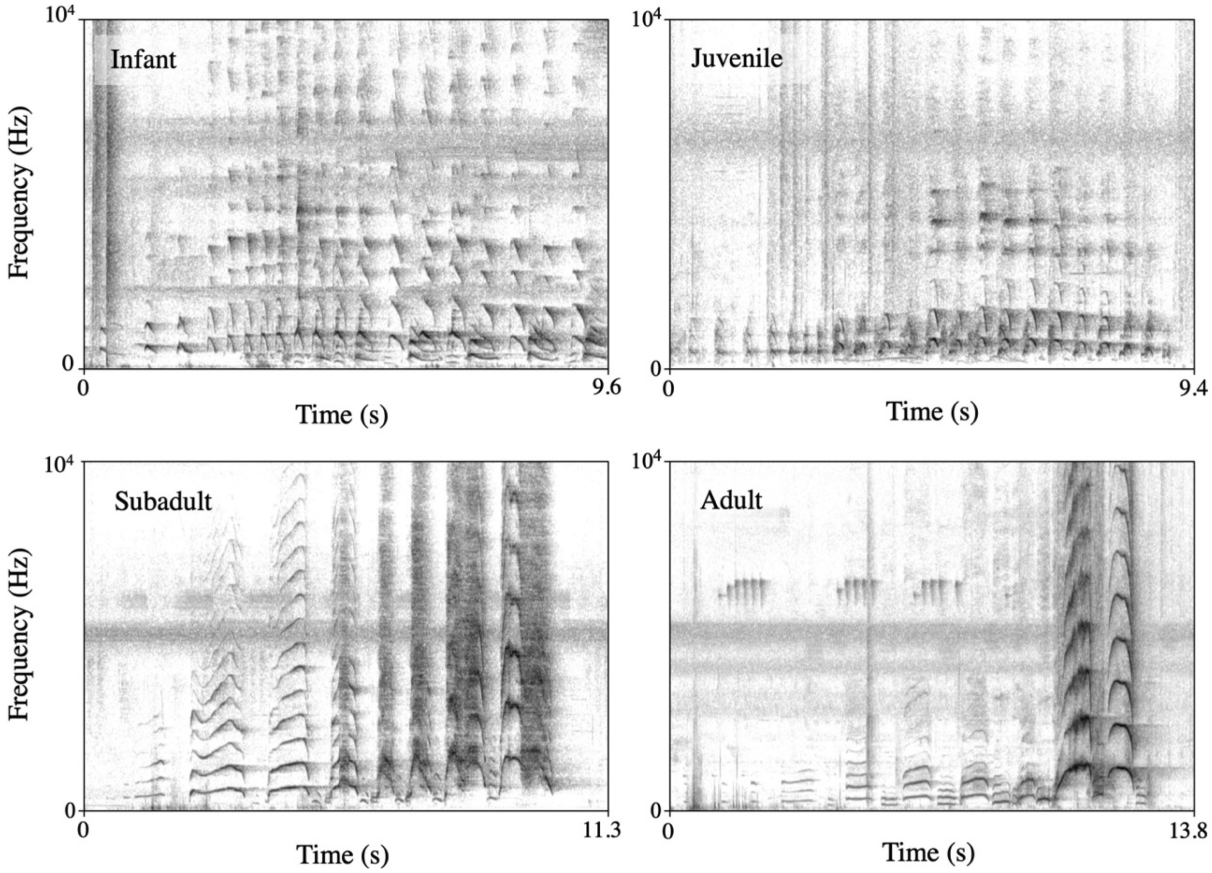

Figure 5 Spectrographic representations of pant hoots produced by an infant, a juvenile, a subadult, and an adult chimpanzee from the Sonso community.

12.3.5. Data collection

Data were collected between September and December 2018, February and July 2019, and November 2019 and March 2020, for a total of 15 months. We used focal animal sampling as the main method of data collection (Altmann, 1974), following a different individual each day from 0700 to 1630 hours, approximately 5.5 days a week. We avoided following the same individual on consecutive days while balancing sampling time across individuals. Each focal animal was followed for at least three separate days. We calculated the duration of focal follows by taking into consideration periods of time when the face of the focal animal was visible to ensure we were able to reliably observe any behavioural changes. Consequently, focal durations reported here are more conservative than typical focal follow durations. With regard to the immature individuals, we collected a total of 170.7 hours of observations with a mean of 13.1 hours per individual (SD = 4.4, range 6.5 – 21.2; Appendix Table A11). With regards to mature individuals, we collected a total of 451.9 hours of observations with a mean of 18.1

hours per individual (SD = 8.7, range 8.7 – 34.6; Appendix Table A12). We recorded whenever the focal individual produced a 'spontaneous' pant hoot, i.e. when no other calls were produced by other individuals within 15 s before the call. We recorded the activity of the focal individual (rest, feed, social, other; see below), and party composition, continuously on a portable device (Samsung Xplorer 4) using a custom-built CyberTracker database (version 3.496). In addition, when the pant hoot of another individual was produced, we recorded the behavioural changes of the focal after being exposed to the call (head movement and vocal response; see below). We also opportunistically collected audio recordings of pant hoots using a Sennheiser MKH416 directional microphone (Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany) with a Marantz PMD661 MkII (Marantz, Kanagawa, Japan) solid-state recorder (sample rate 44.1 kHz, resolution 32 bits, 'wav' format).

12.3.6. Behavioural responses

We considered as responses visible behaviours and vocalisations produced by the focal in response to hearing a pant hoot vocalisation from a group member. Considering that the range of hearing of chimpanzees is comparable to that of humans (Kojima, 1990), all calls audible to human observers were likely also audible for the focal individuals. In response to a pant hoot a focal individual can: 1) produce a vocalisation, typically a pant hoot, that follows without temporal overlap when the call originated from a distant party (Mitani & Nishida, 1993); 2) produce a pant hoot that overlaps temporally with the pant hoot of another individual (i.e., chorusing), which typically occurs between individuals in the same party (Fedurek, Schel, et al., 2013); 3) produce one or more non-vocal behaviours (e.g., head movement towards the vocal stimuli: Wilson et al., 2001); or 4) produce no behavioural response (i.e., no visible change in behaviour). We noted all the visible behavioural responses of the focal individual within five seconds of the pant hoot from another individual. When the pant hoot heard by the focal was a call that was subsequently joined in chorus by one or more individuals (hereafter 'group' call), we noted the behavioural responses that followed the first heard call. We chose to do so given that several individuals can chorus in a pant hoot, so it would be extremely challenging to reliably assess the behavioural changes associated with each caller that joined the chorus, and that we were interested in the changes between two states - before and after hearing a pant hoot - and not in the changes occurring between pant hoots.

We recorded 'head movement' as a response if the focal individual moved the head in the direction of a pant hoot for ≥ 1 s within five seconds of the pant hoot being heard, and the movement was at least a 45 degrees change from the position of the head before the call. We did not record the response as 'head movement' if the head of the focal individual was already oriented within a 45 degrees angle from the source of the pant hoot before hearing it. Thus, this variable is a conservative measure of responsiveness. We recorded 'vocal response' as a response if within five seconds of hearing a pant hoot the focal individual produced a vocalisation. The response could have been a solo call (only the focal animal responded vocally), or a chorus between one or more individuals responding vocally to the pant hoot. We recorded the type of vocalisation produced following those described by Slocombe & Zuberbühler (2010). Observations of wild chimpanzees in dense secondary forest are often challenging, for instance when focal individuals are in large trees. Whenever it was not possible to assess the head orientation with certainty, we did not consider this measure. However, because in some instances it was still possible to assess whether the focal produced a vocal response, the number of pant hoots recorded with behavioural responses is greater for vocal responses than head movements (see Statistical analyses below).

We noted whether the call heard by the focal individual was produced by a single individual or more individuals (solo vs. chorus), whether the mother of the focal produced a vocal response, and whether the call was uttered from within the party of the focal individual or outside of the focal individual's party. Party was defined as all mature individuals present in the visual range, which corresponds to a radius of approximately 35 meters with the focal individual as radius centre (Newton-Fisher, 1999). We excluded calls estimated to be produced by neighbouring chimpanzee communities (on the basis of distance, location, and the chimpanzees' reaction). To assess how the different physical activities could affect a focal individual we continuously recorded the behavioural activity of the focal using four categories: 1) resting, which included self-directed grooming; 2) feeding; 3) social, which included grooming (focal gave, received, or reciprocated grooming) and play (interacting with another individual); 4) other activity, which included traveling (movement on the ground), aggression (focal was the victim or perpetuator of an aggression or was involved as audience member), and solo play (without interacting with others).

12.3.7. Gregariousness

We assessed the gregariousness level (hereafter 'gregariousness') by measuring how frequently an individual was recorded in a party while not being the focal animal (Thompson & Wrangham, 2006). We calculated the index from party composition (identity of all mature individuals present in the focal party) scans recorded by field assistants every 15 min during focal follows during the period December 2017 – June 2020. The maternal gregariousness of immature individuals had a mean of 11.5 (SD = 4.9, range 5.6 – 20.7; Appendix Table A11) and the gregariousness of mature individuals had a mean of 17.7 (SD = 6.2, range 5.8– 29.2; Appendix Table A12).

12.3.8. Statistical analyses

12.3.8.1. General procedure for linear models

Before running the models, to improve the accuracy of the parameter estimates (McElreath, 2016), we z-transformed the distribution of quantitative variables into a distribution with mean of 0 and standard deviation of 1 (Schielzeth, 2010). To assess the significance of the test predictors, we compared each model with a 'null' model comprising only the intercept, control variables, and random effects using a likelihood-ratio test (LRT) (Faraway, 2006). We assessed variance inflation of variables using the 'performance' package (version 0.5.1, Lüdecke et al., 2021). Variance inflation factor (VIF) represents a sensitive measure of collinearity (Field, 2005) and was considered acceptable when < 4.0 (Quinn & Keough, 2002). We reported coefficient estimates, standard errors, confidence intervals (95%), significance tests with their respective p-values, and p-values from Wald's test for the categorical variable 'Activity'. We calculated p-values using LRT comparing each model with the respective null model using the ‘drop1’ function of the package ‘stats’ (version 4.0.2, R Core Team, 2020) or the ‘lrtest’ function of the package ‘lmtest’ (version 0.9-40, Zeileis & Hothorn, 2002). Test results and p-values of the intercept are omitted because of limited interpretation. In the linear models, we checked that residuals were normally distributed and homogenous by inspecting a scatterplot and quantile-quantile plot of the residuals as a function of the fitted values.

12.3.8.2. Comparison with mature chimpanzees’ spontaneous call rate

To examine differences in the ‘spontaneous’ production of pant hoots (as opposed to in response to another pant hoot) of mature and immature chimpanzees, we compared the call rates of mature individuals (Appendix Table A12) with the call rates of immature individuals (Appendix Table A11). We calculated call rates for each individual dividing the number of spontaneously produced pant hoots by the number of focal hours. Given the small sample size of pant hoots produced by immature individuals, we performed a Shapiro-Wilk test to check whether the distribution of the data departed significantly from normality. While the data from mature chimpanzees did not significantly depart from normal distribution ($W = 0.935$, p-value $= 0.115$), the data from immature individuals did ($W = 0.653$, p-value < 0.001). Consequently, we used the non-parametric Wilcoxon test for the analyses.

12.3.8.3. Comparison with mature chimpanzees’ responses

To examine differences in the behavioural responses of mature and immature chimpanzees, we created two generalised linear mixed model (GLMM) with a binomial error structure using the R package ‘lme4’ (version 3.6.3, Bates et al., 2015). In the first model, as the dependent variable we included whether or not (0/1) the focal individual moved their head towards the pant hoot they were exposed to ($N = 1269$ pant hoots, 726 of which had a head movement). In the second model, as the dependent variable we included whether or not (0/1) the focal individual vocally responded to the pant hoot they were exposed to ($N = 2177$ pant hoots, 325 of which had a vocal response). We included the age category of the focal (mature or immature) as the main predictor. We included as control variables the sex of the focal (reference level: male), maternal gregariousness, whether the pant hoot heard by the focal individual originated from the same party as the focal or from outside the focal’s party, whether the call was a solo or group call, the behavioural activity of the focal when the call was heard (reference level: resting), and the number of females and number of males in the party. Since we had repeated observations from the same individuals, we included the identity of the focal as a random effect to control for replicated observations (Pinheiro & Bates, 2000; Waller et al., 2013). There was no collinearity between the examined independent variables (maximum VIF value: 1.55 and 1.59 respectively). The dependent variables were not over-dispersed (dispersion ratio: 0.97 and 0.92 respectively).

12.3.8.4. Behavioural responses of immature individuals

To investigate which factors impact the behavioural responses of immature individuals to others’ pant hoots, we created two generalised linear mixed model (GLMM) with a binomial error structure. In the ‘head movement model’ we considered as the dependent variable whether or not (0/1) the focal individual moved their head towards the pant hoot they were exposed to (N = 402 pant hoots, 198 of which had a head movement). We excluded all instances in which the head movement was not visible or clear and in which the head of the focal was already oriented in the direction of the call. Second, we created a 'vocal response' model where the dependent variable was whether or not (0/1) the focal individual produced a vocalisation in response to the pant hoot (N = 554 pant hoots, 51 of which had a vocal response). In both models, we included as independent variables the age of the focal (years), the sex of the focal (reference level: male), maternal gregariousness, and whether the mother and the focal individual joined each other's vocal response ('mother chorus' hereafter). We included as control variables whether the pant hoot heard by the focal individual originated from the same party as the focal or from outside the focal's party, whether the call was a solo or group call, the behavioural activity of the focal when the call was heard (reference level: resting), and the number of females and number of males in the party. We initially included the following interactions between variables to control for confounding factors. We included a three-way interaction between age, sex, and maternal gregariousness given that 1) mothers with male offspring are more gregarious (Murray et al., 2014), 2) the association of offspring with adult group members changes during ontogeny (Pusey, 1983), and 3) behavioural differences between the sexes can appear at different ontogenetic stages (Pusey, 1990). Because more gregarious mothers tend to spend more time in larger parties, we included an interaction between the number of males and the gregariousness level as well as an interaction between the number of females and the gregariousness level. We then removed non-significant interactions (estimates with $P > 0.05$) one at a time from the model. We included the identity of the focal as a random effect. There was no collinearity between the examined independent variables (maximum VIF value: 1.95 and 1.71 respectively) and the dependent variables were not over-dispersed (dispersion ratio: 1.04 and 0.66 respectively).

12.3.8.5. Maternal gregariousness and vocal exposure

In addition, we tested whether maternal gregariousness was related to the offspring's rate of exposure to others' pant hoots. We created a linear model (see below) in which we used the number of pant hoots heard by the immature individuals per hour of focal following as the dependent variable and the age, sex, and maternal gregariousness of the focal as independent variables (for details see Appendix 'Offspring's exposure to pant hoots'). We predicted that the offspring of more gregarious mothers would be exposed to more pant hoots than the offspring of less gregarious mothers.

All analyses were carried out using R (version 4.1.2, R Core Team, 2020). Figures were created using the R packages 'ggplot2' (version 3.3.0, Wickham et al., 2018) and 'interactions' (version 1.1.3, Long, 2019).

12.4. Results

12.4.1. Descriptive results

We recorded a total of 554 behavioural responses to others' pant hoots produced by 13 immature chimpanzees (Appendix Table A11). The most frequently recorded response was a head movement towards a pant hoot (49.4%, N = 198 from 13 individuals). All immatures produced a head movement at least once, including the youngest individual (16 months-old). The second most frequently recorded response was a vocal response (9.3%, N = 51 from 13 individuals). All immatures responded with a vocalisation on at least one occasion, including the youngest individual. The youngest individual uttering a pant hoot as a vocal response was 19 months old. Of all the vocal responses recorded, 70.6 % were pant hoots (N = 36 from 12 individuals). After hearing a pant hoot from others, mothers and immatures joined each other's vocal response as part of a chorus in 26.7% instances (N = 12 from nine individuals), including the pant hoot response of the youngest individual.

12.4.2. Offspring exposure to pant hoots

The difference between the full and null models was significant (LRT: $\chi^2_2 = 10.059$, $p = 0.007$, $R^2_m = 0.59$, $R^2_c = 0.38$). We found an interaction effect between the sex of the offspring and maternal gregariousness: the male offspring of more gregarious mothers were more likely to be exposed to pant hoots (Table A13; Figure A4).

12.4.3. Mature and immature spontaneous call rates

Immature individuals rarely produced pant hoots that were not in response to others' pant hoots and we only observed immature males spontaneously call (N = 9 from four individuals). A Wilcoxon Signed-Ranks test indicated that spontaneous pant hoot production rate of mature individuals (mean = 0.48 ± 0.36 per hour) was approximately 10 times greater than that of immature individuals (mean = 0.05 ± 0.08 per hour) ($W = 30.5$, $p < 0.001$).

12.4.4. Comparison with mature responses

When considering the frequency of head movement in response to others' pant hoots, the difference between the full and null models was significant (LRT: $\chi^2_1 = 7.592$, $p = 0.006$). Mature individuals were more likely to move their head towards a pant hoot than immature individuals (Appendix Table A14). When looking at the frequency of vocal responses to others' pant hoots, the difference between the full and null models was significant (LRT: $\chi^2_1 = 8.978$, $p = 0.003$). Mature individuals were more likely to vocally respond after hearing a pant hoot than immature individuals (Appendix Table A15).

12.4.5. Factors affecting head movement

The difference between the full and null models was significant (LRT: $\chi^2_4 = 11.131$, $p = 0.025$). We found that there was a positive relationship between the age of immatures and the likelihood of the focal moving their head towards a pant hoots (Table 6, Figure 6a). Immature offspring of more gregarious mothers were more likely to move their head towards to caller than immature offspring of less gregarious mothers (Table 6, Figure 6b). Males were more likely to do this than females (Table 6, Figure 6c). In addition, individuals were less likely to move their head during social behavioural activities (LRT: $\chi^2_4 = 20.926$, $p < 0.001$) and after hearing a group call (Table 6).

Table 6 Relationship between whether or not the focal individual moved their head towards the pant hoot produced by another individual and the investigated independent variables.

Term	estimate	SE	lower CI	upper CI	X2	z-value	P
Intercept	-1.097	0.386	-1.816	-0.233			
Age	0.226	0.053	0.104	0.322	9.486		**<0.001**
Gregariousness	0.411	0.150	0.075	0.690	5.758		**0.006**
Sex	0.613	0.251	0.080	1.117	5.373		**0.015**
Mother chorus	0.299	0.601	-1.134	1.499	0.250		0.619
Call from within party	0.284	0.321	-0.382	0.948	0.784		0.376
Solo call	-0.479	0.222	-0.917	-0.003	4.713		**0.031**
Number of females	0.047	0.121	-0.205	0.292	0.152		0.697
Number of males	0.078	0.131	-0.209	0.343	0.361		0.548
Activity (feeding)	-0.101	0.286	-0.677	0.489		-0.354	0.723
Activity (other)	-0.785	0.420	-1.586	0.154		-1.868	0.062
Activity (social)	-1.205	0.333	-1.826	-0.461		-3.623	**<0.001**

CI: confidence interval. Control variables are in italic. Significant results are depicted in bold.

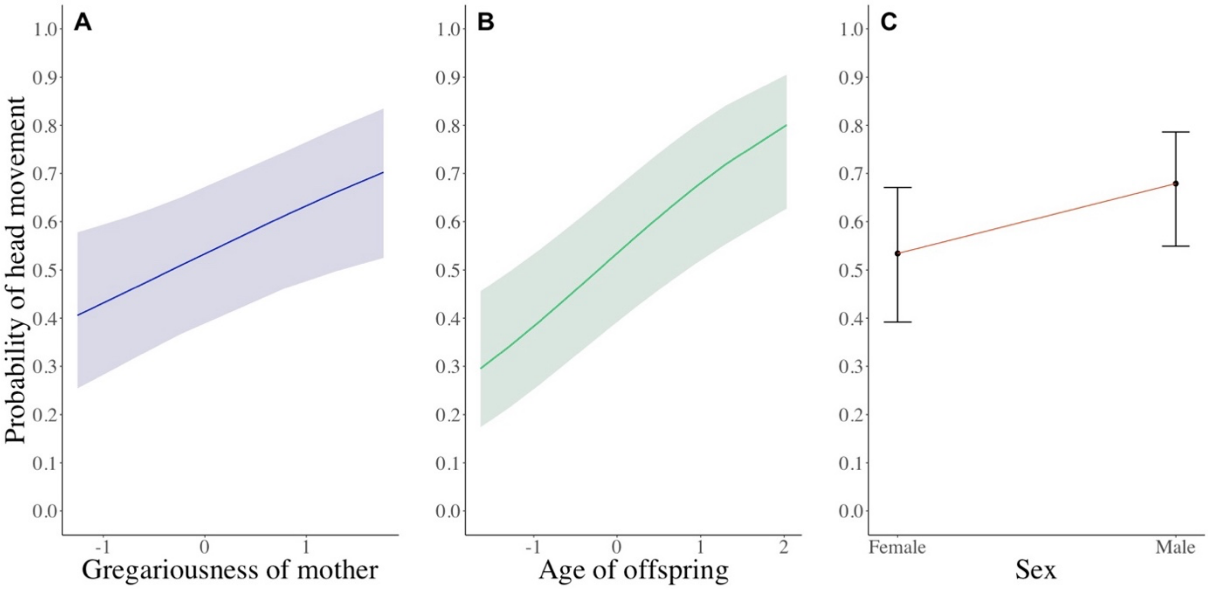

Figure 6 Likelihood of moving the head towards the source of the pant hoot depending on A) maternal gregariousness B) offspring's age, and C) offspring's sex. The fitted model lines are presented with confidence bands for the fitted values based on standard errors (95%). Gregariousness and age values were z-standardized.

12.4.6. Factors affecting vocal response

The difference between the full and null models was significant (LRT: $\chi^2_7 = 31.508$, $p < 0.001$). Immatures were more likely to vocally respond to pant hoots when their mother vocally responded with others as part of a chorus (Table 7). However, likely due to the small number of datapoints, the confidence intervals for the following significant results contained the zero and the pattern of results should be interpreted with caution. We found an interaction effect between the age and sex of immatures: older male individuals were more likely to vocally respond (Table 7, Figure 7a). We found an interaction effect between the age of immatures and maternal gregariousness: male immatures of more gregarious mothers were more likely to vocally respond, while the opposite was true for female immatures (Table 7, Figure 7b). In addition, immatures of more gregarious mothers were more likely to respond vocally as the number of males in the party increased (Table 7, Figure 7c).

Table 5 Relationship between whether or not the focal individual produced a vocal response to the pant hoot produced by another individual and the investigated independent variables.

Term	estimate	SE	lower CI	upper CI	X2	z-value	P
Intercept	-2.269	0.967	-4.032	0.416			
Age	-0.061	0.517	-1.453	1.160			
Gregariousness	-0.386	0.410	-1.195	0.714			
Sex	-1.024	0.860	-3.128	0.840			
Mother chorus	2.630	0.659	0.787	3.792	17.123		**<0.001**
Call from within party	0.436	0.548	-0.694	1.723	0.621		0.431
Solo call	-0.218	0.375	-0.976	0.622	0.341		0.559
Number of females	-0.480	0.256	-0.933	0.181	3.696		0.055
Number of males	0.353	0.243	-0.208	1.048			
Activity (feeding)	0.634	0.481	-0.642	1.553		1.318	0.187
Activity (other)	0.614	0.592	-0.797	1.899		1.037	0.300
Activity (social)	-0.200	0.624	-1.619	1.306		-0.320	0.749
Age*Sex	2.286	1.050	-0.322	4.458	4.411		**0.036**
Age*Gregariousness	1.759	0.791	-0.535	3.237	4.655		**0.031**
Gregariousness* ***Number of males***	0.501	0.235	-0.228	1.066	4.554		**0.033**

CI: confidence interval. Interactions are represented by an asterisk between variables. Control variables are in italic. Significant results are depicted in bold.

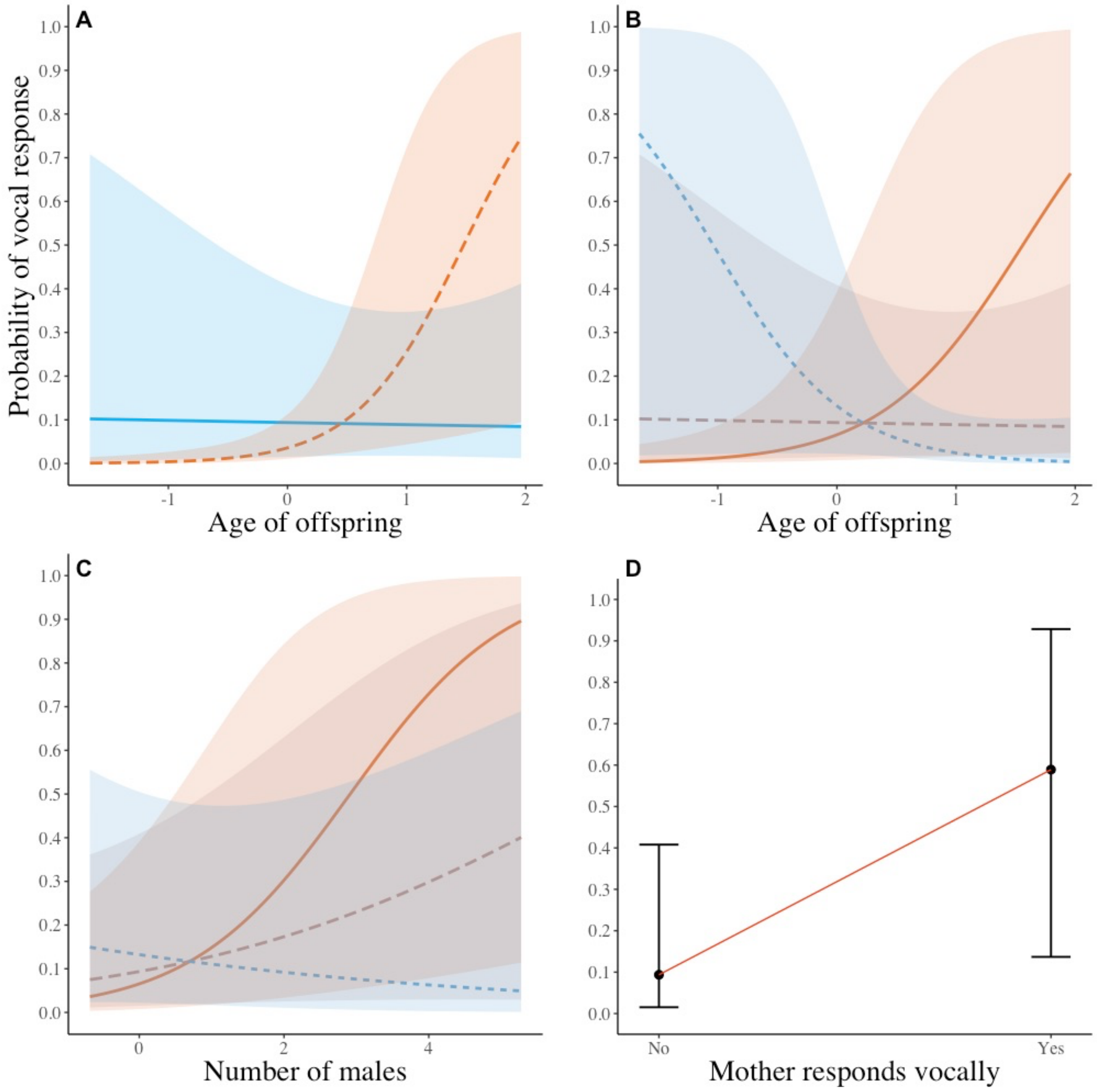

Figure 6 Likelihood of vocally responding to a pant hoot depending on A) the interaction between age and sex of the offspring (red dashed line: male; blue solid line: female), B) the interaction between the age of the offspring and the maternal gregariousness (red solid line: +1 Standard Deviation (SD), blue dashed line: -1 SD, grey dashed line: mean), and C) the interaction between the number of males in the party and the maternal gregariousness (red solid line: +1 SD, blue dashed line: -1 SD, grey dashed line: mean). The fitted model lines (continuous and dashed) are presented with confidence bands for the fitted values based on standard errors (95%). Age values were z-standardized.

12.5. Discussion

We investigated the role of individual and social factors, including the role of the mother's vocal behaviour and gregariousness, on the ontogeny of chimpanzee vocal usage and behavioural responses to the calls of others. Immature chimpanzees very rarely produced spontaneous vocalisations, doing so considerably less often than mature individuals. However, immature individuals produced vocal responses (as opposed to spontaneous calls) and moved the head towards their conspecifics' calls more frequently, albeit less often than mature individuals. We observed immature individuals produce both behavioural responses, including vocal responses as part of a chorus with their mother, as early as 1.3 years old. Overall, we found that older and male immatures and the offspring of more gregarious mothers were more likely to move their head towards the calls of others. Older and male immatures and the offspring of more gregarious mothers, particularly in the presence of larger male audiences, were also more likely to respond vocally. In addition, immatures were more likely to respond vocally when their mother also responded vocally to the same call. Finally, the exposure to others' vocalisations was greater in the male offspring of more gregarious mothers. Taken together, these results suggest that responsiveness of immature chimpanzees undergoes developmental changes, is affected by social factors, and varies according to their sex.

We found that there was a positive effect of the age of individuals on the two key behavioural responses investigated. Immature chimpanzees were capable of producing both behavioural responses at the youngest age recorded (circa 1 year old), although only reached adult levels of responsiveness as late juveniles. In addition, spontaneous vocal usage was very rare in both infants and juveniles, only becoming frequent in mature individuals. One possibility is that the increase in spontaneous calling rate coincides with individuals engaging independently from their mother in social contexts that are mediated by pant hoots (e.g., coordination between distant parties during travelling). Interestingly, chimpanzees appear capable of producing rudimentary pant hoots immediately after birth (Soldati, Muhumuza, et al., 2022), suggesting that infants may be capable of pant hoot responses to the calls of others at a younger age. However, because we did not follow infants in their first year, further studies on the earliest developmental stages are necessary to determine when in ontogeny the capacity to respond to other chimpanzees' pant hoots is manifested. Our observations suggest that the trajectory of vocal usage and comprehension is progressive and slow, consistent with the idea that the acquisition of social calls is less hard-wired than that of alarm calls (Snowdon et al., 1997; Wegdell et al., 2019) and that the acquisition of communicative skills is extended in great apes (Bründl et al., 2021). It is possible that the development of acoustically more complex calls used in short- and long-distance communication necessitates a longer acquisition period as compared to acoustically less complex and less flexible social calls (e.g., Laporte & Zuberbühler, 2011). Extended vocal practice might be necessary to develop vocal sequences composed by phases that vary greatly in acoustic range (Notman & Rendall, 2005; Riede et al., 2007), similarly to how songbirds learn complex and detailed song sequences more slowly (Baptista & Gaunt, 1997; Kroodsma, 1982) and mice develop more complex socially used vocal structures only gradually (Grimsley et al., 2011). While the development of traits associated with physical maturation likely contributes to the ontogeny of vocal behaviours (Nishimura et al., 2003), our observations indicate that great ape vocal ontogeny is more flexible than previously assumed.

Our study supports the idea that immature chimpanzees develop their pant hoot vocal behaviour by interacting with their conspecifics, in particular with their mother and with adult males. By spending more time in groups, gregarious mothers increase the exposure of their offspring to social events including vocal interactions. This likely increases opportunities to learn associations between vocal signals and appropriate usage and responses, positively affecting the speed of vocal development. Mature individuals and particularly males produce pant hoots most often and can act as ‘models’ for younger individuals. Although the need for experience of others’ vocalisations is not widespread among animals, the importance of auditory feedback has been clearly demonstrated in the way in which several songbird species acquire their songs through exposure to the communicative interactions of unrelated adults and their fathers (Baptista & Gaunt, 1997). Other animal examples include the way in how dolphins model their whistle signatures based on those of community members (Fripp et al., 2005), in how seals acquire the vocal types of older and more successful dominant males (Sanvito et al., 2007; Sjare et al., 2003), in how penguins accommodate their calls to those of colony members and social partners (Baciadonna et al., 2022), and in how bats learn territorial songs from adult males in their community (Knörnschild et al., 2010). Although evidence in primates is more limited, social factors can affect their vocal development. For instance, vervet infants exposed more frequently to adult vocalizations during intergroup encounters and predators learn to produce appropriate calls earlier (Hauser, 1988, 1989) and marmoset infants exposed to contingent parental feedback develop adult calls earlier (Takahashi et al., 2015). The importance of exposure to conspecifics vocal communication is further exemplified by the increased frequency of unusual social behaviours, including abnormal vocal outputs, expressed by primates reared in isolation (Seyfarth & Cheney, 1997; Snowdon et al., 1997). In addition, early social interactions and inputs from conspecifics also play an important role in the acquisition of gestural communication in chimpanzees (Fröhlich et al., 2017; Fröhlich & Hobaiter, 2018), which, like their vocal repertoire, is based on a largely innate and species-typical repertoire of signals that are used flexibly (Byrne et al., 2017; Hobaiter & Byrne, 2011). Overall, greater auditory and social inputs provide younger individuals with a head start with their communicative skills. Whether this advantage has a role in adulthood and, if so, which adaptive functions it provides, remain open questions.

Immature chimpanzees were more likely to vocally respond to others’ calls when their mother also vocally responded. By joining each other’s call, offspring and mother pairs might signal their bond strength, given that chorusing functions as a bonding signal (Fedurek, Machanda, et al., 2013; Mitani & Gros-Louis, 1998). In addition, chorusing might act as positive reinforcement facilitating the learning process, similarly to how social reinforcement and vocal feedback from parents increases call rate and appropriate usage in infant marmosets (Takahashi et al., 2017). While we were not able to investigate the temporal order of callers during chorused calls (i.e., whether the mother or immature called first) due to the low number of chorused responses, we did not observe neither mothers nor offspring directing their vocalisations at each other. This is in contrast with humans where adults may use immature-directed communication, i.e., vocalisations accompanied by head orientation toward the immature receiver and characterised by changes in the acoustic structure, to facilitate language acquisition in many cultures (Golinkoff et al., 2015; Schieffelin & Ochs, 1986), while similar evidence in great apes is so far lacking (Schick et al., 2022). On the other hand, our observations suggest that the sheer exposure to non-directed and group broadcasted vocalisations from conspecifics might play an important role in great ape vocal development. One possibility that requires further investigation is whether chorusing represents an intermediate stage between directed and broadcasted vocalisations and enhances the development of vocal behaviours.

Our observations are in line with the idea that mothers and other mature individuals in the group do not actively or directly 'teach' immature chimpanzees their vocal behaviour (*sensu* Caro & Hauser, 1992). Instead, our findings are more consistent with the 'master-apprenticeship' hypothesis which posits that young chimpanzees acquire behaviours through repeated exposure and observation of a tolerant model in close proximity (Matsuzawa et al., 2001). Greater social learning opportunities may enhance the acquisition of vocal communication, similarly to how they positively affect the acquisition of gestural communication (Fröhlich et al., 2017), tool use (Hobaiter et al., 2014; Humle & Matsuzawa, 2002), and social behaviours (Maestripieri, 2009, 2018). Looking at maternally deprived chimpanzees (i.e., orphans), whose development of some cognitive abilities is negatively affected (Boesch, 2020), would provide an avenue to further elucidate the role of mothers as opposed to other mature individuals as models. One possibility is that immature chimpanzees who experience greater learning opportunities and respond more often to the calls of others would develop adult-like vocal structures and usage at an earlier age.

A refined and flexible development of social skills is beneficial in species living in large and complex social groups, especially those characterised by a fission-fusion system in which group members may be dispersed over substantial distances (Aureli et al., 2008). In addition to social and individual factors, we observed that the responses of immatures varied depending on the audience composition, the type of call, and their behavioural context, providing further evidence that primate vocal responses are flexible and sophisticated (Seyfarth & Cheney, 2010). As other group members were typically out of sight when calling, we were not able to explore the effects on immature chimpanzees' responses of the caller's identity, or their affiliative or dominance relationship. Future studies are necessary to investigate how these fine social factors may impact the responses of immature chimpanzees and whether these responses undergo developmental changes as individuals approach independency from the mother. Given that pant hoots are structurally complex calls, with different social information encoded within the different phases (Fedurek, Zuberbühler, et al., 2016; Soldati, Fedurek, et al., 2022), immature individuals may start to produce specific phases and phase combinations depending on the social and behavioural context (i.e., usage learning: Janik & Slater, 2000; Marshall et al., 1999). When, during ontogeny, individuals acquire the capacity to extract information from calls and which kind of information is prioritised should be further investigated, particularly on calls that carry social information and individual signatures such as pant hoots (Fedurek, Zuberbühler, et al., 2016; Kojima et al., 2003; Mitani et al., 1996).

The predominant role of pant hoots in the social lives of adult males is reflected in the greater responsiveness and spontaneous usage we observed in immature males. In a similar way, male infants produce pant grunts, a short-range call important in establishing and reinforcing social hierarchy, more frequently and earlier as compared to female infants (Dunphy-Lelii & Mitani, 2019). The importance of social calls in the development and maintenance of the relationships and interactions between male chimpanzees likely explains the presence of sex differences during ontogeny. As compared to immature females, males experience more social exposure and opportunities to learn from others due their mothers typically associating and interacting more with group members and particularly with adult males (Lonsdorf, Anderson, et al., 2014; Lonsdorf, Markham, et al., 2014; Murray et al., 2014).

As a result, immature males may develop their responses to the calls of others and vocal usage earlier due to greater exposure to the vocal behaviour of group members. Our findings are consistent with the idea that the development of social skills, including vocal behaviour, occurs ontogenetically earlier in male chimpanzees (Lonsdorf et al., 2004; Lonsdorf, Markham, et al., 2014), and that these differences between sexes are in-part explained by the different adaptive sex-dependent pressures in adulthood. It is important to note that sex differences were of degree and not of kind and might be differently expressed in populations where females are more gregarious (e.g., Taï chimpanzees: Lehmann & Boesch, 2008, 2009), or restricted to specific developmental phases or have a combined effect with other factors, as seen in human speech development (Barbu et al., 2015; Etchell et al., 2018).

In conclusion, our study shows that the ontogeny of chimpanzee vocal usage and to some extent that of vocal comprehension are mediated by social and individual factors. Immature chimpanzees develop their vocal behaviour by attending to and interacting with their conspecifics and their calls. Social learning enhances the development of vocal communicative skills, even in species with limited vocal production learning and vocal repertoires. Given that adult great ape vocal usage and vocal production have recently been demonstrated to be more flexible than previously assumed (Slocombe et al., 2022; Townsend et al., 2020), future studies should investigate whether the ontogeny of vocal production is also flexible and socially mediated, in particular the possibility that subtle acoustic features might be socially learned. Our findings are consistent with the view that the emergence of human language was a continuous and gradual evolutionary process built upon precursors that can be found in the vocal communication of other primate species.

13. Audience sensitivity in chimpanzee display pant hoots

13.1. Abstract

Audience effects are key in studies of animal social cognition and are typically investigated during directed social interactions. Male chimpanzees, *Pan troglodytes*, regularly perform aggressive displays in the presence of others, often targeting a specific group member, and combine this agonistic behaviour with acoustic signals. Here, we were interested in whether the production and structure of pant hoots, a long-distance signal, were influenced by audience composition (i.e. presence and absence of specific individuals). We investigated pant hoots produced during displays by adult and subadult males of Budongo Forest, Uganda. We found that males overall called more often when their preferred social partners and females were absent from the party, as well as when more dominant males were present. We then separately analysed the four phases of pant hoots, introduction, build-up, climax, and let-down, and found that audience composition and social context could often explain the presence or absence of each phase. In addition, displays were often accompanied by drumming, especially by older males and when male audiences were small. Our study adds to the growing body of literature on audience effects and other social factors and shows their impact on the structure of a sophisticated vocal sequence, which enhances the communicative capacity in a species with limited vocal control.

13.2. Introduction

In animal communication, vocal behaviour is often moderated by the identity of nearby listeners (Evans, 1997; Fichtel & Manser, 2010; Marler et al., 1986), generally referred to as 'audience effects' (Zuberbühler, 2008), with evidence from a wide range of taxa, including birds (chickens, *Gallus gallus*: Evans & Marler, 1994; zebra finches, *Taeniopygia guttata*: Vignal et al., 2004), fish (Siamese fighting fish, *Betta splendens*: Matos et al., 2003; three-spined sticklebacks, *Gasterosteus aculeatus*: Dzieweczynski & Rowland, 2004), and mammals (lions, *Panthera leo*: Grinnell & McComb, 2001; vervet monkeys, *Cercopithecus aethiops*: Hector et al., 1989; yellow mongooses, *Cynictis penicillata*: Le Roux et al., 2008). Audience effects are typically studied during close-range social interactions and their corresponding vocal signals. However, some animal calls, usually referred to as long-distance or loud calls, reach both distant and nearby recipients (Matos & Schlupp, 2005). Consequently, to minimize eventual eavesdropping costs and maximize social benefits, long-distance callers should be sensitive to the audience composition and adjust call production accordingly (Johnstone, 2001; McGregor & Peake, 2000). Arguably, this type of audience sensitivity might indicate goal-directed and flexible call production (Fichtel & Manser, 2010; Fischer & Price, 2017; Schamberg et al., 2018).

There is a consensus that social complexity acts as an evolutionary driver for communicative complexity (Freeberg et al., 2012; McComb & Semple, 2005; Schamberg et al., 2018). Audience effects, that is, when a signaller takes the composition of its audience into account, is considered one such manifestation of complexity (Evans, 1997; Zuberbühler, 2008). In chimpanzees, *Pan troglodytes*, audience effects have been reported in a number of contexts (e.g. predator encounters: Crockford et al., 2012; greeting: Laporte & Zuberbühler, 2010; feeding: Schel, Machanda, et al., 2013; mating: Townsend et al., 2008), in terms of both production rates (e.g. aggression: Fedurek et al., 2015) and call structure (agonistic interaction: Slocombe & Zuberbuhler, 2007). However, it remains unknown whether these effects extend to more complex acoustic structures (*sensu* Johnstone, 1996), such as calls composed of acoustically distinct components.

In this study, we continued this line of investigation by studying whether audience effects were also present in pant hoot vocalizations. Structurally, pant hoots are arguably one of the most complex signals produced by great apes, consisting of four acoustically distinct phases produced in an orderly manner: introduction, build-up, climax, and let-down (Marler & Hobbett, 1975; Marler & Tenaza, 1977). The climax is a high-amplitude signal that travels over longer distances than the other phases, which are lower amplitude (Mitani & Gros-Louis, 1998). Individual phases contain different types of information and can be omitted in context-specific ways (Goodall, 1986; Zuberbühler, 2019). In particular, identity is strongly encoded in the introduction and climax (Fedurek, Zuberbühler, et al., 2016; Mitani et al., 1996) and is recognizable to listeners (Kojima et al., 2003; Schel, Machanda, et al., 2013). Age is mainly encoded in the introduction and build-up, social rank in the climax, and context mainly in the let-down phase (Fedurek, Zuberbühler, et al., 2016). Given that social status is not a fixed property in chimpanzee societies and physical condition varies with age (Muller & Mitani, 2005; Thompson et al., 2020), advertising these attributes can be beneficial for both callers and receivers (baboons, *Papio cynocephalus ursinus*: Fischer et al., 2002, 2004; chimpanzees: Fedurek, Slocombe, et al., 2016; Riede et al., 2007). At the proximate level pant hoot production could be largely explained as expressions of basic arousal states (Notman & Rendall, 2005), nevertheless, receivers can obtain multiple sets of information about the caller's attributes simultaneously (Fedurek, Zuberbühler, et al., 2016). Although it is unclear which information is used, or prioritized, when multiple sets of information are transmitted, each call element independently encodes different socially important information, consistent with the idea that pant hoots serve multiple social functions (Fedurek, Zuberbühler, et al., 2016).

Pant hoots are generally produced in three distinct behavioural contexts: travel, feeding, and displays (Marler & Tenaza, 1977; Nishida et al., 1999). During displays, pant hoots are combined with exaggerated locomotion, piloerection, and throwing or shaking objects, for example during visually impressive agonistic interactions by males seeking to assert their social status while challenging the status of others (Goodall, 1986; Muller, 2002). In addition, males often accompany displays with drumming, an acoustic signal produced by pounding hands and feet against the buttress roots of trees (Arcadi et al., 1998; Arcadi & Wallauer, 2013). While during travelling drumming is used to communicate over long distances and is often combined with pant hoots (Babiszewska et al., 2015), during displays, males may use drumming to intimidate competitors and acquire social status (Goodall, 1986). Although intimidating, display behaviours rarely lead to physical attacks, injuries or death (Fawcett & Muhumuza, 2000; Muller & Mitani, 2005). Display pant hoots can be given jointly with others which appears to play a role in social bonding (Gilby et al., 2013; Mitani & Gros-Louis, 1998; Muller & Mitani, 2005). Indeed, males can adjust the build-up phase of display pant hoots in a coordinated way with audience members which then results in chorusing (Fedurek, Schel, et al., 2013). This coordinated calling is also seen in the climax phase and signals social bonding (Fedurek, Machanda, et al., 2013). Not all displays contain pant hoots, with nonvocal displays mostly directed at specific individuals in contrast to nondirected vocal displays (Goodall, 1986), which may be directed towards distant individuals (Bygott, 1979; Muller, 2002). Given that pant hoots are produced across several social contexts, different functional hypotheses have been proposed (signalling social status: Clark & Wrangham, 1994; signalling social bonds: Fedurek, Machanda, et al., 2013; Mitani & Brandt, 1994; signalling subgroup formation: Fedurek et al., 2014). During long-distance communication, pant hoots are mainly used to maintain spatial contact between conspecifics and to recruit associates (Mitani & Nishida, 1993) or group members (Kalan & Boesch, 2015). Overall, high-ranking males tend to pant hoot more often than low-ranking individuals, in line with the idea that pant hoots are involved in male–male competition (Clark, 1993; Fedurek, Slocombe, et al., 2016; Riede et al., 2007). Importantly, when callers use pant hoots depends on the composition of the nearby audience to, for example, signal dominance and bonded relationships towards party members (e.g. Bouchard & Zuberbühler, 2022b; Fedurek et al., 2014; Fedurek, Machanda, et al., 2013; Mitani & Nishida, 1993). Furthermore, several social functions of pant hoots are linked to fine details of their acoustic structure (e.g. Fedurek, Zuberbühler, et al., 2016; Notman & Rendall, 2005).

The aim of this study was to examine the factors mediating male pant hoot production during displays. First, we tested whether pant hoot production is affected by the identity of nearby individuals (immediate audience composition) and varies according to the type of display (i.e. directed versus nondirected, see

Table 6). Because signalling social status during a display may provoke aggression from other individuals, we predicted that dominant males would be more likely to pant hoot when displaying than lower-ranking individuals. Similarly, considering that displays increase the risk of aggression from males in the audience, displaying callers might seek to solicit social partners for support. Therefore, we predicted that males would pant hoot more often when preferred social partners are absent in the caller's party. We also predicted that males would be more likely to pant hoot when their displays are not targeted at another individual since these nondirected displays could serve to communicate to distant individuals. The second aim of our study was to test whether phase production is influenced by audience composition, the type of display (directed versus nondirected), and whether another individual choruses with the displaying male. Since omitting the high-amplitude phase of the call may limit eavesdropping by distant competitors, we predicted that males would be more likely to produce the low-amplitude introduction, and less likely to produce the loud climax, during displays directed at nearby individuals as opposed to nondirected displays. In addition, since the climax is related to signalling social status, we predicted that higher-ranking males would produce the climax phase more often than lower-ranking individuals. Given that joint pant hoots and chorusing are important signals in male–male competition, we expected the build-up and climax phases to be more likely to be chorused. Finally, we examined whether drumming is also influenced by the social context. We hypothesized that, due to its loud and visually impressive features which might function to intimidate others, drumming would be more often produced by more dominant individuals.

13.3. Methods

13.3.1. Study Site

The study was conducted with the Sonso community (*P. t. schweinfurthii*) of the Budongo Forest in Western Uganda. The community is well habituated to human observers with research ongoing since the early 1990s (Reynolds, 2005). At the beginning of the study (September 2018) the community consisted of 74 individuals (11 adult males, 25 adult females, 15 subadults, eight juveniles, and 15 infants). At the end of the study (March 2020), the community consisted of 68 individuals (nine adult males, 26 adult females, 15 subadults, nine juveniles, and eight infants; Appendix Table A16).

13.3.2. Study Subjects

Study subjects were 12 male individuals: four subadults (10–15 years old), three young adults (16–20 years old), and five adults (>20 years old; Appendix Table A17). We initially sampled all subadult and adult males, but three males died during the study period. We did not include juveniles and infants since they were unable to produce complete pant hoots and did not engage in displays, other than during play (Pusey, 1990).

13.3.3. Data Collection

Data were collected between September and December 2018, February and July 2019, and November 2019 and March 2020, for a total of 15 months. We used focal animal sampling as the main method of data collection, following a different individual each day from 0700 to 1630 hours, approximately 5.5 days a week, together with a field assistant. We avoided following the same individual on consecutive days while at the same time balancing the sampling time across individuals. Audio recordings of display events and pant hoots were collected using a Sennheiser MKH416 directional microphone (Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany) with a Marantz PMD661 MkII (Marantz, Kanagawa, Japan) solid-state recorder (sample rate 44.1 kHz, resolution 32 bits, ‘wav’ format). We collected a total of 302 h of focal data, with a mean of 25.2 h (range 13.7–34.6) per subject (Appendix Table A18). Because of the rarity of display events, we also collected display data opportunistically from other individuals in the same party. Information regarding behavioural context, identity of displaying male and target, type of display, communicative signals, other participants, outcome, and continuous party composition were either dictated into the microphone or noted using CyberTracker (version 3.496) on a Samsung Xcover 4 portable device (Samsung Group, Seoul, South Korea). The identification of the displaying individual, target and type of display (Table 8) were determined in agreement between A.S. and the field assistant. Whenever a display was performed by more than one individual (i.e. joint display), we collected data only from the individual that initiated the behaviour. We focused on pant hoot vocalizations (Table 8) associated with displays from the perspective of the signaller only.

Table 6 Descriptions and definitions of behaviours and vocalizations produced by chimpanzees during displays investigated in this study

Term	Definition	Source
Display	Intimidatory behaviour characterized by piloerection, exaggerated locomotion, branch shaking, object throwing, stomping, vocalizing, or drumming	Hosaka, 2015; Nishida et al., 1999
Directed display	Aggression including charges (pursuit distance < 7 m) and chases (pursuit distance > 7 m) towards one specific victim. The body and behaviour of the focal are oriented towards one victim throughout the display. Directed displays are considered ‘mid-severity’	Fedurek et al., 2015; Muller, 2002
Nondirected display	Display without a specific target. Nondirected displays are considered ‘low severity’	Goodall, 1986
Vocal display	Display accompanied by a pant hoot	Nishida et al., 1999
Pant hoot	Complex vocal signal composed of up to four acoustically distinctive phases produced in the sequence introduction, build-up, climax, and let-down	Marler & Hobbett, 1975; Marler & Tenaza, 1977; Mitani et al., 1992; Notman & Rendall, 2005
Introduction	Series of low-amplitude, low-frequency tonal elements that acoustically resemble ‘hoo’ vocalizations but are noticeably longer in duration and alternate with inhaled tonal elements	
Build-up	Series of short low-amplitude and low-frequency elements produced during both inhalations and exhalations in rapid rhythm which can increase in intensity and frequency as the call proceeds	
Climax	One or more scream-like high-amplitude and high-frequency elements	
Let-down	Series of low-amplitude and low-frequency acoustic elements which acoustically resemble the build-up phase but tend to progressively decrease in intensity and frequency over time	

13.3.4. Ethical Note

The project adhered to the ASAB guidelines for the treatment of animals during behavioural studies. The study was approved by the Uganda Wildlife Authority (UWA/COD/96/5), the Uganda National Council for Science and Technology (NS 637), and the research ethic committees of both the Universities of Neuchâtel and St Andrews (38/2019-B; N. 171). Data collection was terminated on 17 March 2020, due to the Covid-19 pandemic, to avoid putting the health of the study animals at risk (Matsuzawa, 2020; Patrono et al., 2018), a decision subsequently reinforced by The Ugandan Wildlife Authority (25 March 2020; UWA ref: EDO/73/01).

13.3.5. Data Analyses

13.3.5.1. Dominance distance

The dominance hierarchy was assessed by calculating Elo-ratings for each individual using the R package 'EloRating' (version 0.46.11, Neumann & Kulik, 2020) in R Studio (version 3.6.3, R Core Team, 2020). Scores were calculated from pant grunts produced by or towards the focal animal as recorded by field assistants during focal follows thorough the whole study period (Neumann et al., 2011). Pant grunts are vocal signals produced by subordinate chimpanzees towards dominant ones and are widely considered a reliable indicator of dominance relations (Fedurek et al., 2021; Newton-Fisher, 2017). To take the possibility of changes in group dynamics and their effects on rank (e.g. loss of individuals or natural changes in social dynamics) into account, we calculated the Elo-ratings for each individual for three separate periods of approximately 6 months each (Appendix Table A19). We then calculated dominance distance as the difference in Elo-rating between the agent (i.e. the individual conducting the display) and the patient (i.e. the party member with the highest Elo-rating; negative distance: agent lower ranking than patient; positive distance: agent higher ranking than patient).

13.3.5.2. Preferred social partners

Preferred social partners (PSP) were identified using a modified social index from Gilby and Wrangham (2008), further developed by Schel, Townsend et al. (2013; see Appendix for details on the procedure and Appendix Table A20). We used long-term data on focal follows collected by field assistants as a basis of the social index: 15 min scan samples with the following information: party composition (identity of all individuals present in the focal party), the focal individual's nearest neighbour (identity of the closest individual to the focal), and the focal individual's grooming interactions (partner identity and duration). Party composition was defined as all individuals present within a radius of approximately 35 m with the focal individual as the radius centre (Newton-Fisher, 1999). For each individual, dyadic affiliative relationships were established using a composite social index based on three different dyadic association measures: a simple ratio index, a nearest-neighbour association index, and a grooming index. The composite index, as with dominance distance, was calculated separately for the three 6-month periods.

13.3.5.3. Acoustic data

Recordings of display pant hoots were visually inspected using spectrograms generated by Adobe Audition software (version 12.0.1) at a sampling rate of 22 kHz and acoustically assessed using Sennheiser HD650 headphones (Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany). This procedure was only used for visualization and did not modify the original recordings used in the acoustic analyses (see below). A.S. classified pant hoot calls and pant hoot phases following previous definitions (Table 8). We only used recordings where the caller's identity could be established and, in the case of choruses, where overlapping elements from a second caller (chorus) allowed us to determine the individual call structure. Chorusing from another individual in the audience always occurred after the initial call from the subject performing the vocal display. Whenever more than one pant hoot was produced during the same display event, we only coded the first occurrence. In addition, we carried out an interobserver reliability test for classification of each phase. P.F. independently classified the presence or absence of the four pant hoot phases in 20% of randomly selected calls from the original set (N = 33). P.F.'s classification showed very high levels of agreement with A.S.'s classification (Cohen's k = 0.91; 95% agreement).

As mentioned (Table 8, Figure 8), pant hoots are usually defined as long-distance calls comprising up to four distinct phases (Marler & Hobbett, 1975), although there is no consensus as to whether the term 'pant hoot' should also be used when one or more phases are missing. For example, some authors require the presence of at least two phases (Notman & Rendall, 2005), at least a climax (Arcadi, 1996; Fedurek et al., 2014; Mitani & Brandt, 1994), at least an introduction and a climax (Mitani et al., 1999), or at least an introduction and a build-up (Crockford & Boesch, 2005). In this study, we used the broadest possible definition, by including any utterance with up to three phases missing, regardless of which phase(s) was/were missing. Example recordings of display pant hoots are available as Supplementary Material (Audio S1–S5) and as figures (Appendix Figure A5–Figure A9).

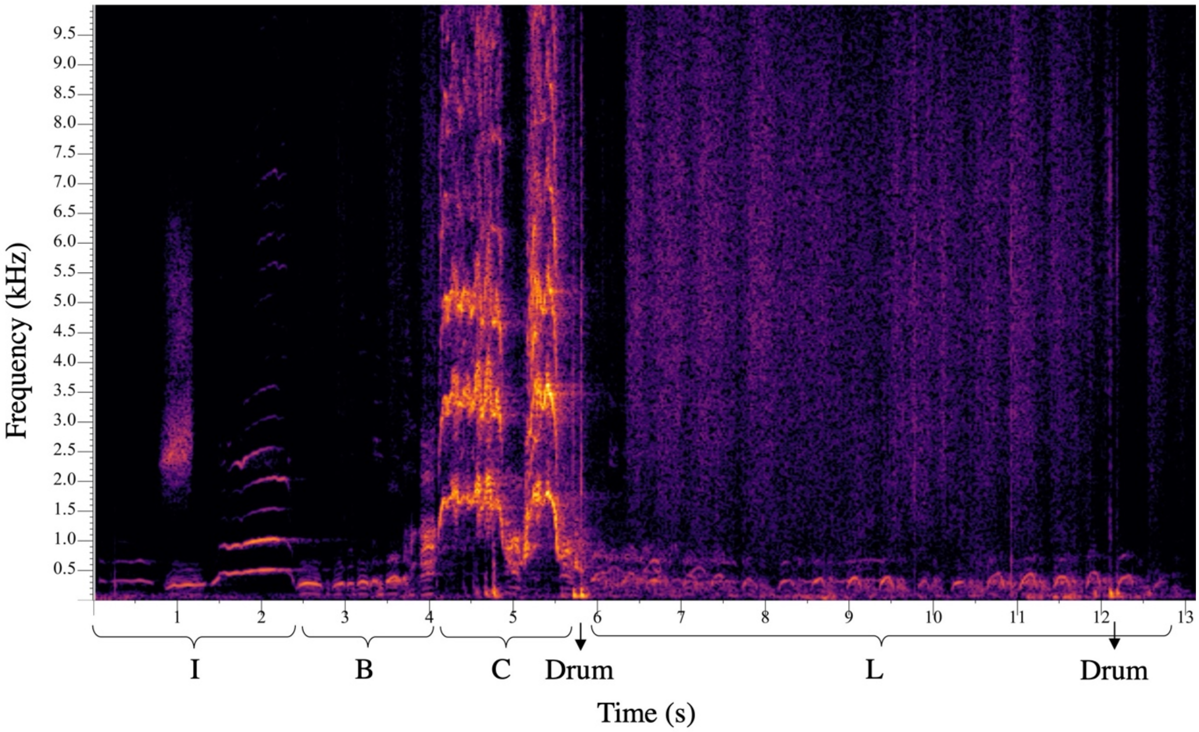

Figure 7 Spectrographic illustration of a pant hoot produced by a subadult male chimpanzee (JS). The vocalization includes all four phases (I = Introduction, B = Build-up, C = Climax, L = Let-down) and is combined with a series of drumming beats (Drum). The figure was created using Raven Pro (version 1.6.1, https://ravensoundsoftware.com/).

13.3.6. Statistical Analysis

To determine whether the acoustic structure of single phases differed from the same phases produced as part of a multiphase pant hoot, we performed crossed permuted discriminant function analyses (pDFA; Mundry & Sommer, 2007). We selected nine calls composed of a single introduction phase, 17 multiphase pant hoots including an introduction, 11 calls composed of a single build-up phase, and 22 multiphase pant hoots including a build-up that were suitable for acoustic parameter extraction from five adult individuals combined (Appendix Table A21). To ensure an acceptable signal-to-noise ratio for the analyses, we selected the first available tonal element that did not contain background noise and that did not overlap with other calls. From each element, we extracted a series of spectral and temporal acoustic parameters (Appendix Table A22) using a custom-built script in Praat (version 6.0.42, see Briefer et al., 2019; Leroux et al., 2021; Watson et al., 2018). We compared the extracted F0 contour to the F0 from the spectrogram to guarantee accurate pitch tracking. For each phase type, we assessed multicollinearity to avoid including correlated acoustic parameters. We removed seriatim the parameter with the highest variance inflation factor (VIF) until we obtained a set of five acoustic parameters, the same as the number of individuals tested. In the final set, the highest VIF for introduction calls was 1.20 and the highest VIF for build-up calls was 1.11. We assessed the normal distribution of the data and when variables were not normally distributed and could be improved, we applied a log transformation. To test whether the acoustic structure of each single phase differed significantly from the same phase produced as part of a multiphase pant hoot we used pDFA with 1000 permutations (Mundry & Sommer, 2007). In comparison with a conventional DFA, a pDFA allows the inclusion of repeated data points per individual (nonindependence) and controls for unbalanced data sets at the same time. We included the 'ID' of the caller as a control factor. Statistical analyses were conducted in R studio (version 1.2.5033, R Core Team, 2020).

To investigate whether certain components of displays were affected by the audience composition and display features, we created six generalized linear mixed models (GLMM) with a binomial error structure using the R package 'lme4' (version 3.6.3, Bates et al., 2015).

First, in the 'pant hoot model' we considered whether a pant hoot vocalization was present (0/1) during a display as the dependent variable. As independent variables, we included the number of males in the party, the number of females in the party, the number of PSPs in the party, the age of the displaying individual (years), whether the display was directed (0/1), and the dominance distance ($N = 392$ displays, 132 of which were vocal).

Second, we created a model for each of the four pant hoot phases. As the dependent variable we put the presence (0/1) of the introduction phase ($N = 122$ displays, 79 of which had an introduction), build-up phase ($N = 122$ displays, of which 110 had a build-up), climax phase ($N = 125$ displays, of which 26 had a climax), and let-down phase ($N = 122$ displays, of which 25 had a let-down). We kept the same independent variables as in the 'pant hoot model' but added whether it was chorused with a pant hoot by another adult individual or not (0/1). Finally, in the 'drumming model' the dependent variable was whether drumming occurred or not (0/1) and the independent variables were the same as in the 'pant hoot model' ($N = 394$ displays, of which 140 included drumming).

Since we had repeated observations from the same individuals, the identity of the displaying individual was included as a random effect to control for replicated observations (Pinheiro & Bates, 2000; Waller et al., 2013). Before running the models and to improve the accuracy of the parameter estimates (McElreath, 2016) we z-transformed the distribution of quantitative variables into a distribution with mean of 0 and standard deviation of 1 (Schielzeth, 2010). To assess the significance of the test predictors, we compared each model with a 'null' model comprising only the intercept, control variables and random effects, using a likelihood ratio test (LRT; Faraway, 2006). We controlled for the false discovery rate by adjusting the P values of each LRT using the Benjamini and Hochberg method and we report the corrected P values (P^*). To explore whether the directedness of display interplayed with other predictors and test previous hypotheses, we included interactions between the independent variables and the directedness of a display (0: nondirected; 1: directed).

Subsequently, nonsignificant interactions (estimates with $P > 0.05$) were removed seriatim from the model. To avoid high correlations among predictor variables causing unreliable estimates of the regression coefficients, when the expected correlation of the regression coefficients was greater than 0.5, we ran two models one with each variable removed and kept the variable that was associated with the lowest Akaike information criterion value of the model (i.e. best fit for the model; Akaike, 1974). Variance inflation of variables in each linear model without random effects and interactions was assessed using the function vif of the R package 'car' (version 3.0.3, Fox & Weisberg, 2011), which represented a sensitive measure of collinearity (Field, 2005) and was considered acceptable when < 4.0 (Quinn & Keough, 2002).

There was no collinearity between the examined independent variables (maximum VIF values in each model: pant hoot = 2.51; introduction = 1.57; build-up = 1.49; climax = 1.53; let-down = 1.54; drumming = 1.55). The response variable was not overdispersed (dispersion parameter in each model: pant hoot = 0.971; introduction = 0.932; build-up = 1.189; climax = 1.088; let-down = 0.987; drumming = 1.027). The *P* values of the fixed effects were calculated with likelihood ratio tests comparing the full model with the respective reduced models using the 'drop1' function of the R package 'stats' (version 4.0.2, R Core Team, 2020).

We report coefficient estimates, standard errors, confidence intervals (95%), and significance tests for each investigated variable after dropping the levels of random effects one at a time, and *P* values for all effects from models that contained explanatory power. Test results and *P* values of intercept and single interaction terms were omitted because of limited interpretation. All analyses were carried out using R Studio (version 1.2.5033, R Core Team, 2020). Figures were created using the R packages 'ggplot2' (version 3.3.0, Wickham et al., 2018) and 'interactions' (version 1.1.3, Long, 2019).

13.4. Results

13.4.1. Acoustic Analysis

Males produced eight of 15 possible pant hoot variants (Figure 9, Appendix Table A23 and Table A24). In particular, the climax phase was never produced without either an introduction and/or a build-up phase. Similarly, the let-down phase was never produced on its own but always followed the climax phase. Callers revealed most variability in whether they produced introduction and build-up phases, both of which were also produced on their own: 6.7% of vocalizations were composed of a series of repeated introduction elements (*N* = 11; Appendix Figure A9), while 30.5% of vocalizations were composed of a series of repeated build-up elements (*N* = 50; Appendix Figure A8). We tested whether the vocal elements of the introduction and build-up phases, produced alone or in combination, were acoustically different and found no such evidence (introduction elements: expected correctly cross-classified: 52.76%, *P* = 0.662; build-up elements: expected correctly cross-classified: 51.28%, *P* = 0.575), suggesting that they should be considered as pant hoot variants.

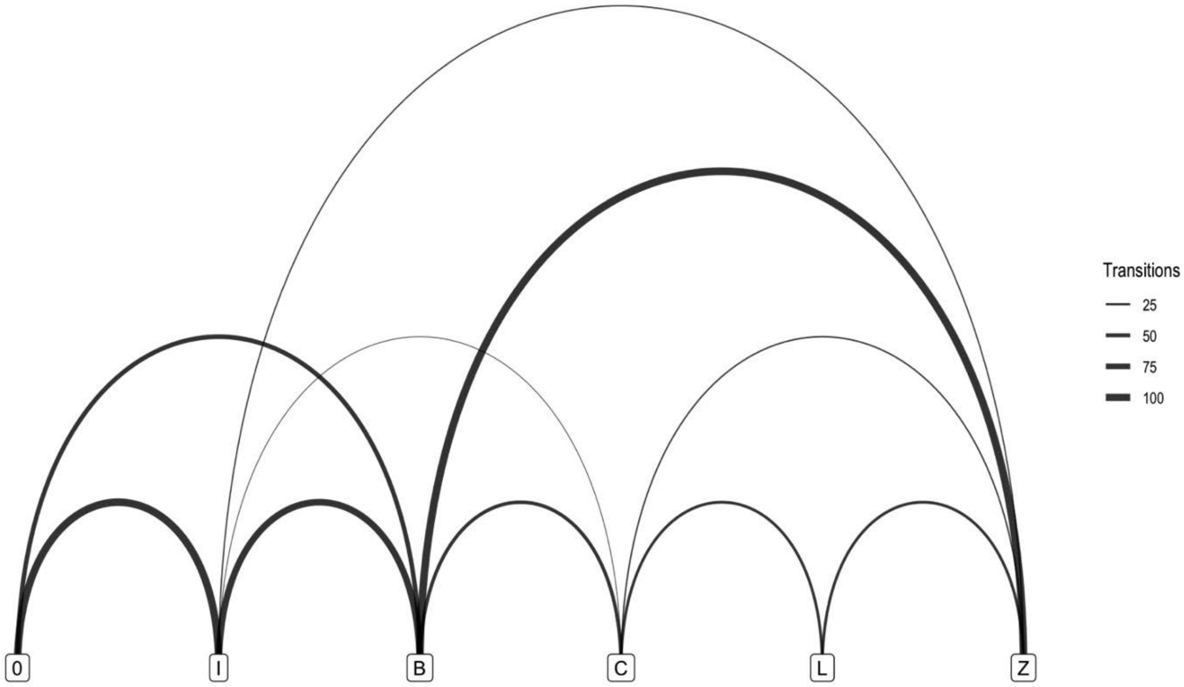

Figure 8 Arc diagram visualization of the order of succession of pant hoot phases in a vocal sequence. Arc lines show the transition probabilities of the inclusion of each phase (I: Introduction, B: Build-up, C: Climax, L: Let-down) and the number of transitions is represented by their thickness. Arcs starting from '0' indicate which phase occurred as the first component in the structure. Arcs ending in 'Z' indicate which phase was produced as the last component in the structure. For example, arcs from point '0' to point 'I', from 'I' to 'B', and from 'B' to 'Z', represent a pant hoot structure composed of introduction and build-up (I–B). See Appendix for details.

13.4.2. Descriptive Results

We analysed data on 454 vocal and nonvocal display events produced by 12 males (Appendix Table A17). Of these, 51% were directed at another individual (N = 220), while the remaining 49% were not directed (N = 209). Females were the target of 58% of all directed displays (N = 124) and on average there were slightly fewer females than males in the party during directed displays (party composition: mean number of males: 4.27, range 0–12; mean number of females: 4.01, range 0–18). Only 2% of displays were associated with physical aggression (N = 9). Only 6% of displays were performed by more than one individual simultaneously ('joint display' or 'coalitionary aggression', N = 24), half of which were vocal (N = 12).

Of all pant hoots produced (i.e. both during displays and in other contexts) by the study subjects during focal following (N = 542), 6.5% were produced as part of a display. Regarding the pant hoots produced in display contexts, males accompanied 38.1% of their displays with a pant hoot vocalization (N = 173). Of the display pant hoots, 62.2% were targeted at another individual (N = 97), of which 52.2% were directed towards males (N = 47) and 47.8% towards females (N = 43). The phases present in the structure of display pant hoots varied: 63.4% contained an introduction (*N* = 104), 91.5% a build-up (*N* = 150), 28.7% a climax (*N* = 47), and 20.7% a let-down (*N* = 34).

Overall, 62.8% of pant hoots (*N* = 103) were two-, three- or four-phase structures, whereas the remaining 37.2% (*N* = 61) had a single phase (either introduction or build-up). Of single-phase pant hoots, 57.3% were targeted at another individual (*N* = 34), while 42.7% were not targeted at others (*N* = 27). During directed display pant hoots, 30.8% of calls contained a climax (*N* = 28), while during nondirected display pant hoots 23.2% of calls included a climax (*N* = 13). Of display pant hoots, 24.1% were chorused with another individual (*N* = 39). Males accompanied 33.8% (*N* = 154) of the vocal and nonvocal displays with drumming. Specifically, drumming was produced during 21.2% of vocal displays (*N* = 58) and during 35.0% of nonvocal displays (*N* = 97). Vocalizations and drumming were produced in combination during 7.5% of displays (*N* = 30).

13.4.3. The Pant Hoot Model

In a first analysis, we investigated what factors best explained whether males produced pant hoots during displays, irrespective of their sequential structure. We tested whether audience composition and type of display (directed or nondirected) affected call production. Overall, the difference between the full and null models was significant (LRT: $\chi^2_7 = 33.47$, $P^* < 0.001$). More specifically, males were more likely to call as the number of other males in the party increased (Table 7). The opposite effect was observed for females and preferred social partners: as their numbers increased, male displays were less likely to be vocal (Table 7). We found an interaction effect between the directedness of a display and the dominance distance between the displaying male and the most dominant male in the party (Figure 9): during nondirected displays, higher-ranking males relative to the most dominant male in the party were less likely to be vocal whereas lower-ranking males were more likely to be vocal. During directed displays, the pattern was reversed: higher-ranking males relative to the most dominant male in the party were more likely to be vocal whereas lower-ranking males were less likely to be vocal. Finally, we found no effect of age of the displaying male (Table 7).

Table 7 Relationship between the production of display pant hoots and the investigated independent variables

Term	Estimate	SE	Lower CI	Upper CI	χ^2	P
Intercept	-1.309	0.287	-1.977	-0.750		
Dominance distance	-0.479	0.231	-1.016	0.003		
Number of males	0.400	0.196	-0.046	0.866	4.123	**0.042**
Number of females	-0.376	0.143	-0.697	-0.094	7.419	**0.006**
Number of PSP	-0.389	0.176	-0.792	-0.053	4.851	**0.028**
Age displayer	-0.021	0.233	-0.492	0.482	0.007	0.934
Directedness	0.751	0.241	0.223	1.269		
Dominance distance*Directedness	0.581	0.239	0.097	1.117	5.931	**0.015**

CI: confidence interval; PSP: preferred social partner. Significant results are depicted in bold.

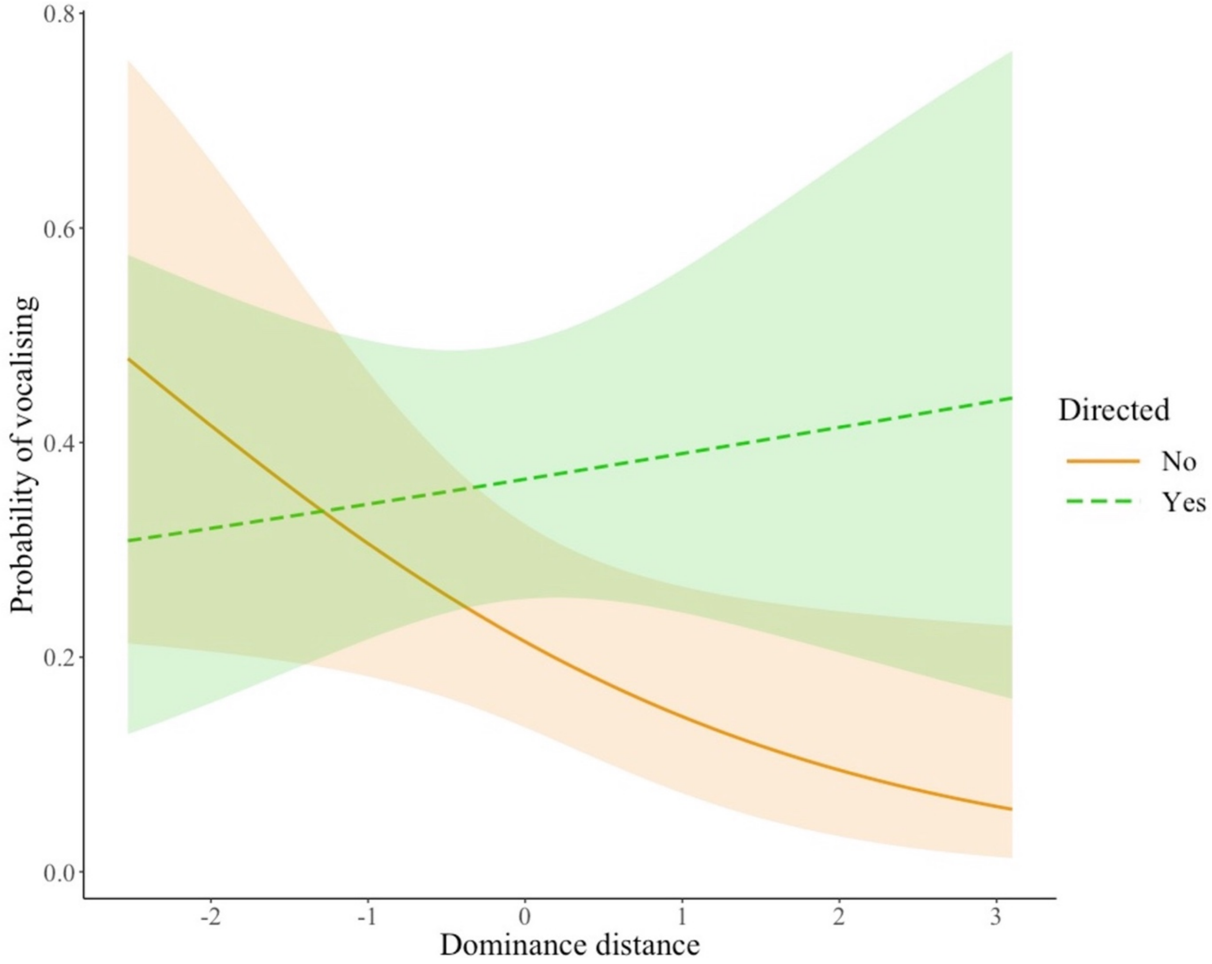

Figure 9 Likelihood of vocalizing depending on the interaction between the dominance distance and the directedness of a display. The fitted model line is presented with confidence bands for the fitted values based on standard errors (95%). Dominance distance values are z-standardized.

13.4.4. The Introduction Phase Model

In a second analysis, we investigated what factors best explained whether males produced an introduction phase in their pant hoots. The difference between the full and null models was significant (LRT: χ26 = 19.70, P* = 0.006). We found that displaying males were more likely to produce an introduction phase as the number of males in the audience increased. Directed displays were more likely to contain an introduction phase than nondirected ones (Table 10). Finally, the number of females, age of displaying male, dominance distance, and chorusing, had no effect (Table 10). As the variable ‘Number of PSP’ was colinear with the variable ‘Number of males’ we removed it from the model.

Table 8 Relationship between the production of the introduction phase and the investigated independent variables

Term	Estimate	SE	Lower CI	Upper CI	χ^2	P
Intercept	-0.132	0.407	-1.041	0.788		
Dominance distance	-0.195	0.298	-0.936	0.441	0.389	0.533
Number of males	0.713	0.323	0.082	1.544	4.833	**0.028**
Number of females	-0.100	0.274	-0.693	0.569	0.126	0.722
Age displayer	-0.212	0.303	-0.883	0.430	0.426	0.514
Directedness	1.538	0.467	0.611	2.656	11.236	**0.001**
Chorus	-0.477	0.527	-1.613	0.613	0.794	0.373

CI: confidence interval. Significant results are depicted in bold.

13.4.5. The Build-up Phase Model

In a third analysis, we investigated what factors best explained whether males produced a build-up phase in their pant hoots. We failed to find an impact of the test predictors on the probability of producing a build-up phase. The difference between the full and null models was not significant (LRT: $\chi^2_7 = 10.941$, $P^* = 0.141$).

13.4.6. The Climax Phase Model

In a fourth analysis, we investigated what factors best explained whether males produced the climax phase in their pant hoots. The difference between the full and null models was significant (LRT: $\chi^2_7 = 17.79$, $P^* = 0.010$). We found that males were more likely to produce a climax if they were lower ranking relative to the most dominant male in the party and if another individual joined in a chorus (Table 9). However, we did not find an effect of the number of males, number of females, directedness of displays, and age of displaying male (Table 9). The variable 'Number of PSP' was colinear with the variable 'Number of males' and therefore not considered.

Table 9 Relationship between the production of the climax phase and the investigated independent variables

Term	Estimate	SE	Lower CI	Upper CI	χ^2	P
Intercept	-1.643	0.417	-2.898	-0.914		
Dominance distance	-0.625	0.273	-1.322	-0.117	5.517	**0.019**
Number of males	-0.276	0.264	-0.972	0.230	1.140	0.286
Number of females	-0.205	0.295	-0.964	0.395	0.497	0.481
Age displayer	-0.244	0.231	-0.782	0.260	1.124	0.289
Directedness	0.228	0.452	-0.720	1.249	0.257	0.612
Chorus	1.540	0.510	0.609	2.918	9.517	**0.002**

CI: confidence interval. Significant results are depicted in bold.

13.4.7. The Let-down Phase Model

In a fifth analysis, we investigated what factors best explained whether males produced the let-down phase in their pant hoots. The difference between the full and null models was significant (LRT: $\chi^2_7 = 18.95$, $P^* = 0.010$). Here, males were more likely to produce a let-down if another individual chorused with the displaying male (Table 10). We found an interaction effect between the directedness of a display and the age of the displaying male (Figure 10): younger individuals were more likely to produce a let-down phase during nondirected displays, while older individuals were more likely to produce it during directed displays. We did not find a significant effect of the number of males, the number of females, and the dominance distance (Table 10). The variable 'Number of PSP' was colinear with the variable 'Number of males' and therefore removed from the model.

Table 10 Relationship between the production of the let-down phase and the investigated independent variables

Term	Estimate	SE	Lower CI	Upper CI	χ^2	P
Intercept	-2.430	0.537	-4.513	-1.659		
Dominance distance	-0.484	0.301	-1.377	0.144	2.633	0.105
Number of males	0.032	0.283	-0.729	0.677	0.012	0.911
Number of females	-0.177	0.321	-1.049	0.475	0.314	0.575
Age displayer	-0.838	0.419	-2.163	0.025		
Directedness	0.602	0.544	-0.395	2.275		
Chorus	1.784	0.569	0.746	3.610	10.250	**0.001**
Age displayer* Directedness	1.006	0.477	0.031	2.640	4.638	**0.031**

CI: confidence interval. Significant results are depicted in bold.

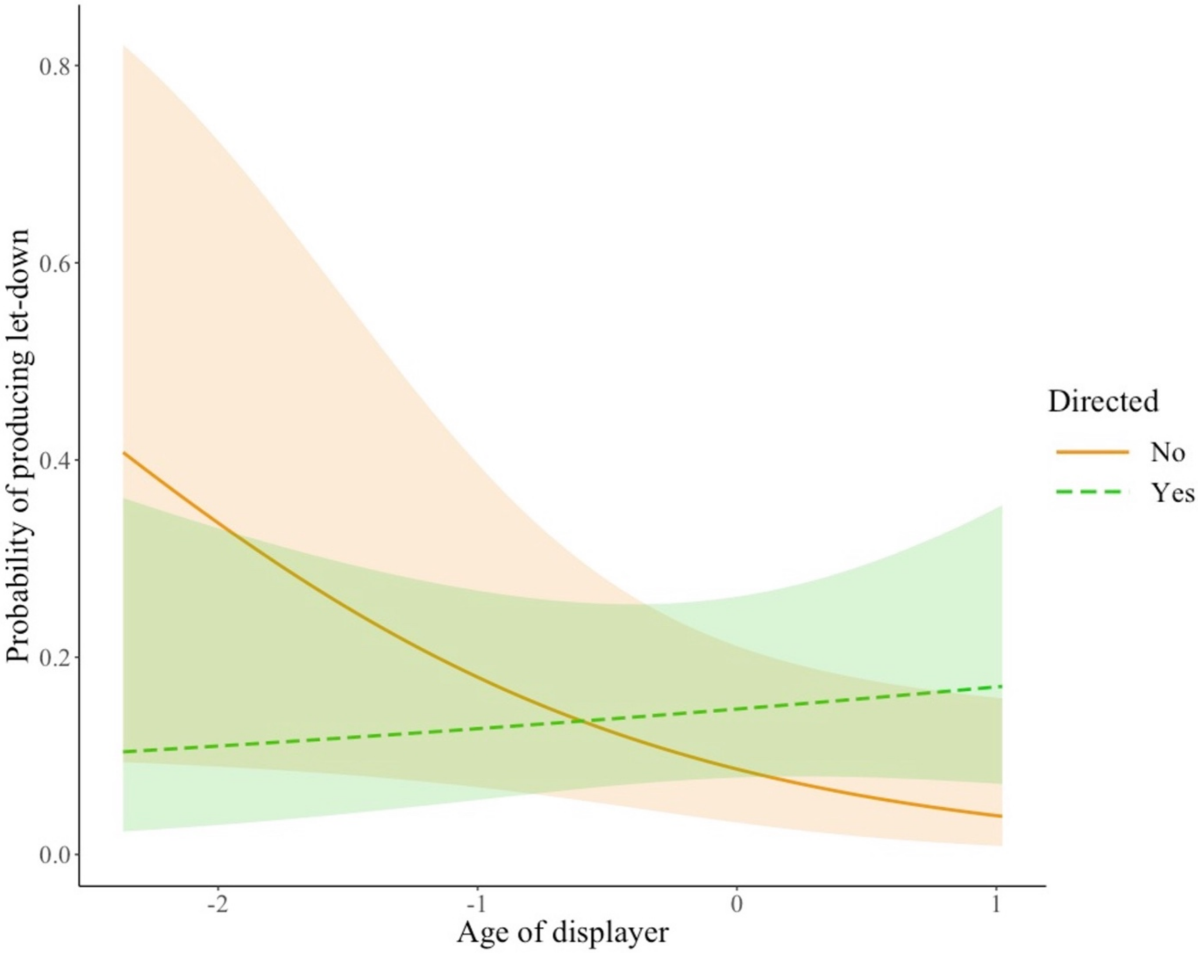

Figure 10 Likelihood of producing a let-down phase depending on the interaction between the age of the displaying male and the directedness of a display. The fitted model line is presented with confidence bands for the fitted values based on standard errors (95%). Age values are z-standardized.

13.4.8. The Drumming Model

In a final analysis, we investigated which factors best explained whether males accompanied their vocal and nonvocal displays with drumming. The difference between full model and null model was significant (LRT: $\chi^2_6 = 54.35$, $P^* < 0.001$). Here, males were more likely to drum as the number of males present in the party decreased (Table 6). We found an interaction effect between age and directedness (Figure 11). Specifically, older males were more likely to drum during directed displays, while the pattern was opposite for younger males (Figure 11). We found no effect of dominance distance and of the number of females (Table 6). The 'Number of PSP' was colinear with 'Number of males' and therefore removed from the model.

Table 11 Relationship between the production of drumming and the investigated independent variables.

Term	Estimate	SE	Lower CI	Upper CI	χ^2	P
Intercept	-0.007	0.155	-0.324	0.332		
Dominance distance	-0.091	0.141	-0.394	0.178	0.413	0.520
Number of males	-0.542	0.151	-0.876	-0.259	12.080	**0.001**
Number of females	-0.011	0.123	-0.262	0.241	0.008	0.927
Age displayer	-0.300	0.188	-0.696	0.068		
Directedness	-1.215	0.233	-1.757	-0.801		
Age displayer* Directedness	0.674	0.240	0.203	1.229	8.298	**0.004**

CI: confidence interval. Significant results are depicted in bold.

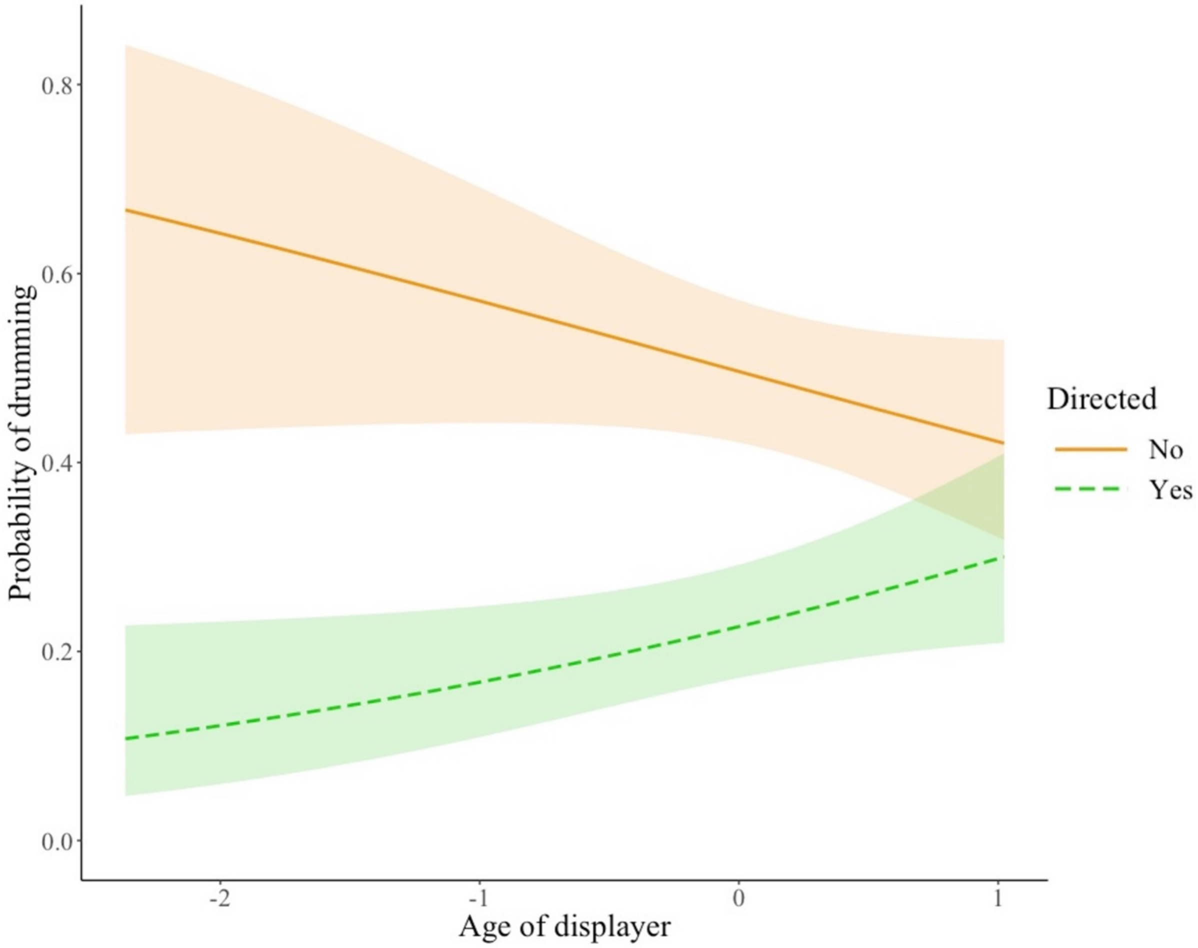

Figure 11 Likelihood of drumming depending on the interaction between the age of the displaying male and the directedness of a display. The fitted model line is presented with confidence bands for the fitted values based on standard errors (95%). Age values are z-standardized.

13.5. Discussion

The aim in this study was to investigate whether audience features such as the number of males, females, and preferred social partners, as well as the displaying male's social status, predict the production of pant hooting, including each of its four phases, and drumming, during displays. We also considered the displaying male's age, whether displays were directed at another individual, and whether pant hoots were given as part of a chorus. During directed displays, higher-ranking males were more likely to pant hoot than lower-ranking males. For nondirected displays, the pattern was reversed. Males were more likely to pant hoot in the presence of small numbers of preferred social partners and females. Regarding the structure of pant hooting, whether males produced the introduction depended on the number of other males in the audience and on whether the display was directed. We found that the climax was mainly produced by lower-ranking males and during chorusing. Let-down was mainly produced by younger males during nondirected displays and during chorusing. Finally, drumming was more likely to occur in the absence of other males and to be produced by older males during directed display, while the opposite was the case for nondirected displays.

Males were less likely to produce display pant hoots as the number of females increased. Previous studies have also reported effects of the presence of females but in opposite directions. In the Mahale group, males did not increase pant hoot rates in the presence of oestrous females (Mitani & Nishida, 1993), whereas in the Kanyawara group they did so in the presence of (parous) oestrous females (Fedurek et al., 2014). Given that pant hoots were mostly recorded during feeding and travelling in previous studies, it is possible that audience effects on pant hoots vary based on the context of production. Considering that females are frequent targets of displays, often as part of sexual coercion (Muller & Mitani, 2005; Smuts & Smuts, 1993), it is unlikely that display pant hoots function to attract females. Instead, suppressing pant hoots during displays may be a strategic decision that some males take, for example, to avoid alienating females or to conceal their identity and location to distant competitors (Fichtel & Manser, 2010), a pattern also seen in other species (e.g. lions: Grinnell & McComb, 2001). In line with our observation, in Budongo Forest, chimpanzee males preferentially use low-amplitude gestures during consortships, presumably to keep their mating efforts concealed (Hobaiter & Byrne, 2012).

Similar to the presence of females, males were less likely to produce display pant hoots when their preferred social partners were in the audience. A possible interpretation is that displaying males were trying to attract their partners to support them during competitive display episodes. The introduction and climax phases are individually distinctive, suggesting that the identity of the caller is revealed to receivers provided they produce one of these two phases (Fedurek, Zuberbühler, et al., 2016; Kojima et al., 2003; Mitani et al., 1996). In our analyses it was not possible to investigate whether introduction and climax phases were affected by the number of preferred partners, due to collinearity problems. However, in other studies, it has been concluded that males use pant hoots to maintain spatial contact between conspecifics, especially with social partners (Wrangham & Smuts, 1980), and call more when their social partners are absent in the party but nearby (Mitani & Nishida, 1993).

Males tend to stop pant hooting once reunited with group members (Fedurek et al., 2014). It is important to point out that in this study we only analysed display pant hoots and that pant hoots produced in travelling and feeding contexts may operate under different social mechanisms. Generally, however, the notion of long-distance calls as a way to promote cohesion has been established in other social animal species, such as bonobos (*Pan paniscus*: White et al., 2015), elephants (*Loxodonta africana*: Leighty et al., 2008), and lions (McComb et al., 1994). An alternative interpretation is that the presence of social partners in the audience could represent a form of support to the displaying male. In their absence, males would benefit from making their displays more intimidating by producing a pant hoot, similarly to how lower-ranked males displayed in the presence of more dominant males (see below).

We found multiple dominance effects in our data, in particular in determining whether a displaying male also produced a pant hoot. Here, calling was common in males that were lower ranking than other party males, but only in nondirected displays. For higher-ranking males, we found the opposite pattern. Dominance also impacted the phase structure of pant hoots, with lower-ranking males being more likely to produce a climax than higher-ranking males. Lower-ranking males may follow this strategy as a way to make their displays more impressive or intimidating while avoiding more dangerous directed display. In a similar way, chimpanzees and bonobos incorporate the use of objects, such as dragging and throwing, to amplify their displays (Nishida et al., 1999; Schamberg et al., 2017). Given that previous studies have come to the conclusion that higher-ranking males not only pant hoot more often (Fedurek et al., 2014; Mitani & Nishida, 1993) but also produce more climax phases (Fedurek, Slocombe, et al., 2016; Fedurek, Zuberbühler, et al., 2016; Riede et al., 2007), in contrast to what we found in this study, it would be relevant to extend our analyses to pant hoots given in feeding and travelling contexts. The comparison with bonobos is interesting: males produce ‘contest hoots’, a multiphase call that can also be produced in directed or nondirected ways, to challenge other males and dominant females (Genty et al., 2014). In this sense, the vocal component of chimpanzee displays might have a similar function to bonobo contest hoos. On the other hand, more dominant males may be able to afford the costs associated with signalling during more severe displays, similar to how older males drummed more during severe displays. Note that, in previous studies, dominance was represented as an ordinal or categorical rank, an absolute measure of dominance, while in our study we used a relative measure of dominance, potentially producing different results. Alternatively, given that previous studies only considered calls produced in travelling or feeding contexts, the patterns found in this study may be characteristic of displays.

In our study, similarly to the use of pant hoots during displays, males were also less likely to accompany displays with drumming as the number of males in the party increased. This is in contrast to a previous study (Babiszewska et al., 2015), where the authors did not include the display context, suggesting that drumming is affected by the audience in different ways depending on context. However, in line with their conclusions, our results do not support the hypothesis that drumming was used by dominant males to assert social status. Instead, it was mainly used by young males during nondirected displays and by older males during directed displays. Given that younger males are often subject to aggression (Pusey, 1990; Sabbi et al., 2021), drumming during directed displays may be too costly for them. Interestingly, dominance distance, but not age, affected vocal production during directed displays and the effect of males in the audience on pant hoot production was the opposite to drumming. Consequently, although both vocal and nonvocal acoustic signals allow distant community members to identify and locate signallers during travelling (Babiszewska et al., 2015; Mitani & Nishida, 1993), their functions are likely to be context dependent. Note that buttress trees are common in the Budongo forest (Eleuteri, 2019) and males usually encountered multiple trees during a display event; thus, it is unlikely that tree availability affected drumming. More research is needed to investigate the function of drumming during displays.

We could not test factors influencing the production of the build-up phase, probably because modulation by the audience could not be reliably assessed due to its presence in most display pant hoots. However, given that a significant proportion of display pant hoots were build-up-only calls, which, in contrast to the introduction and the climax, do not primarily signal the identity of the caller (Fedurek, Zuberbühler, et al., 2016), it is unlikely that receivers can extract the identity of displaying males from this component alone. Considering that drumming in male chimpanzees lacks individual acoustic signatures when produced during displays, but not when produced during travelling (Eleuteri et al., 2022), the frequent use of build-up-only calls as well as drumming in displays may prevent signallers from revealing their identity to out-of-sight competitors and eavesdroppers while still benefiting from the use of impressive acoustic signals. On the other hand, our results showed that the presence of climax and let-down phases was associated with chorusing. Because the chorused call from a member in the audience always followed the pant hoot from the displaying male, the presence of a specific phase influenced chorusing rather than the other way around. Since let-downs always follow climaxes in the structure of pant hoots (Fedurek, Zuberbühler, et al., 2016; Notman & Rendall, 2005), it is unlikely that they promote chorusing. Instead, chorusing was likely to be associated with climax production. Signalling caller's identity via this call phase may increase the likelihood of others chorusing a display pant hoot. Males flexibly modify the climax phase to prolong and coordinate chorusing, which reflects short-term bonds (Fedurek, Machanda, et al., 2013; Fedurek, Schel, et al., 2013). Consequently, joining the displaying male's call in a chorus can either be used as a form of support to the displaying male by nearby social partners or to promote coalition formation against other males (e.g. Fedurek, Machanda, et al., 2013).

Males were more likely to produce the introduction phase during directed display pant hoots and as the number of males increased. Because the introduction is associated with the caller's identity and is considered a low-amplitude call component (Fedurek, Zuberbühler, et al., 2016), it could be used to recruit others to join the display. However, given that the inclusion of the introduction was not affected by the number of social partners or by chorusing, and since most display pant hoots were not joint, it is unlikely that this phase was used as an invitation to join. In contrast with previous studies from Gombe and Kanyawara where display pant hoots were rarely directed (Goodall, 1986; Muller, 2002), we observed that around half of the displays were. Vocal signals, in particular those including the introduction phase, were typically produced at the onset of directed displays (A.S. personal observation), which could allow receivers to avoid confrontation costs (Laidre & Johnstone, 2013; Zahavi, 1975). As an example, songbirds produce low-amplitude songs during aggressive encounters (Dabelsteen et al., 1998), which indicate an incoming attack (Akçay et al., 2011; Searcy et al., 2006). Indeed, in captive chimpanzees, ‘hooting’ during displays has been interpreted as a warning and predictor of aggression (De Waal & Hoekstra, 1980), while bonobo ‘contest hoots’ indicated incoming aggression (De Waal, 1988). Thus, low-amplitude calls may be used to attract attention from nearby conspecifics or alert conspecifics about an incoming directed display. Because the loud climax phase was similarly produced in directed and nondirected displays and was not produced in the absence of specific individuals (e.g. social partners), our study does not support the idea that its main function is to communicate to distant audiences. Instead, we suggest that males can afford to use a long-distance signal for short-distance communication and that by doing so they signal confidence or dominance. Consequently, pant hoots composed of long- and short-distance phases play an important role in short-distance communication and are likely to be directed at nearby individuals too.

Although we were not able to investigate the proximate processes underlying vocal production, our study is consistent with the view that chimpanzee vocal production is flexibly adjusted to highly variable social contexts. While the structure of primate vocalizations is largely constrained (Fischer & Hammerschmidt, 2020), callers do have a certain degree of control over when and which call types they produce (Seyfarth et al., 2010; Townsend et al., 2020). Because vocal production can be modulated according to fine details of the composition of the audience during high-arousal events (e.g. aggression: Slocombe & Zuberbuhler, 2007; copulation: Townsend et al., 2008; feeding: Fedurek & Slocombe, 2013; snake encounter: Crockford et al., 2012), arousal processes do not preclude but contribute to vocal flexibility (Cheney & Seyfarth, 2018; Dezecache et al., 2013; Seyfarth & Cheney, 2003; Snowdon, 2009). Our results, showing audience-based vocal flexibility during a high-arousal context, support this view. The primary concern in our study was not to explore the proximate mechanisms driving call production, while important, but rather to explore ultimate functions of vocal production. Since obtaining data on wild animals’ internal states is notoriously difficult, to study the extent to which arousal levels drive vocal production new methods such as infrared thermography might be beneficial (Ioannou et al., 2014; Tattersall, 2016).

Acoustic flexibility can be increased through changes in the acoustic structure of repertoire calls as well as through combinations of different call types (Engesser & Townsend, 2019; Zuberbühler, 2018; Zuberbühler & Lemasson, 2014). In chimpanzees, despite their relatively small repertoire with a fixed number of distinct call types (Slocombe & Zuberbühler, 2010), the capacity to convey multiple information and to elicit several specific responses from receivers is likely to be enhanced through the use of multicomponent vocal structures such as pant hoots. Our study supports the idea that pant hoots are in fact combinatorial structures (Crockford, 2019; Zuberbühler, 2020), for example by demonstrating production of two phases in isolation and as part of multiphase structures. In addition, we have shown that compositional structures that include different phases are affected differently according to the social context, corroborating the idea that different phases are associated with different types of information (Fedurek, Zuberbühler, et al., 2016). However, further testing is necessary to confirm the syntactic-like properties of this call. Because in primates call receivers show more flexibility in vocal behaviour than call producers (Seyfarth et al., 2010; Seyfarth & Cheney, 2003), future studies should focus on the perspective of receivers when investigating the function of complex vocal structures.

The production of vocal and nonvocal signals, including that of acoustically distinctive components in a complex call, is influenced by specific social factors, such as the composition of the audience. Our findings underscore the view that primate vocal structures are flexible and vary in response to fine social factors. Our analyses were limited to the presence or absence of a particular phase within a pant hoot sequence, without taking into consideration specific multiphase combinations and their potential communicative value. Future research should help clarify whether such combinations add to the flexibility of chimpanzee communication. Our study adds to the growing body of evidence that complex vocal structures enhance the communicative potential of vocal signals in species with limited vocal repertoires and allow the signalling of multiple types of information while targeting multiple audiences.

14. General discussion

14.1. Summary of key empirical findings

14.1.1. The earliest vocal sequences

Chimpanzees make frequent use of pant hoot vocalisations to mediate interactions with nearby and distant group members (Goodall, 1986; Marler & Hobbett, 1975). Early observations suggest that individuals start producing pant hoots during infancy, but only do so rarely (Marler & Tenaza, 1977; Pusey, 1990). However, the absence of systematic studies on the ontogeny of pant hoots makes it is unclear whether they are capable of producing this key social call since birth. Chapter two was aimed at clarifying this by looking at the first spontaneous utterances produced by a newborn chimpanzee.

Using a combination of qualitative and quantitative methods of call classification revealed that newborn chimpanzees are capable of producing different call types as part of vocal sequences (Figure 4). These vocalisations did not seem to be used to attract the attention of the mother or to be randomly produced. Furthermore, while they did not qualify as a form of babbling, they shared some similarities with protophone-like sounds produced by infant bonobos, and were likely used as a form of vocal practice or exploration. Notably, some of the newborn calls matched closely with pant hoots (Figure 2). However, the newborn calls lacked two out of four phases, were composed by shorter units, and contained fewer panted units when compared to adult pant hoots. Therefore, the newborn produced a rudimentary version of pant hoots that is yet to fully develop. Overall, my results support the idea that primate vocal repertoires are largely present from birth and that acoustically more complex vocal structures such as pant hoots and call combinations undergo ontogenetic processes.

14.1.2. Ontogeny of vocal usage and responses

While my findings suggest that pant hoots are likely part of chimpanzees' vocal repertoire since birth (Soldati, Muhumuza, et al., 2022), they are very rarely used by immature individuals (Marler & Tenaza, 1977). This is in stark contrast with the fact that they are the most frequently used call by adults and serve multiple social functions across different behavioural contexts (Fedurek et al. 2014; Marler & Tenaza, 1977). How do immature chimpanzees develop this vocal behaviour? In the third Chapter, I investigated the factors mediating the ontogeny of pant hoot usage and responses to others' pant hoots in infant and juvenile individuals.

Immature chimpanzees were rarely observed producing spontaneous pant hoots, the majority of which were produced by juveniles and all of them by males (Table A11). However, immature individuals responded to the pant hoots of others more frequently with two key behaviours, i.e., head movement towards the call and vocal response, and that individual and social factors drove the ontogeny of these responses (Table 6 and Table 7). More specifically, older individuals and the offspring of more gregarious mothers were more likely to both move their head and respond vocally. Immature individuals responded vocally more often in the presence of a larger number of nearby adult males and when their mother also responded vocally to the same call. Overall, immature males were more responsive than immature females. Furthermore, my results showed that the male offspring of more gregarious mothers were exposed more often to the pant hoots of others (Table A13; Figure A4). Taken together, my findings suggest that the ontogeny of vocal usage, responses, and to some extent comprehension, are mediated by social and individual factors in chimpanzees.

14.1.3. Flexible vocal displays

Pant hoots are arguably one of the most acoustically complex great ape vocalisations with their multi-phase structure. On top of that, they are flexibly used across several social contexts and each phase carry different social information reaching nearby audiences and some of which accessible to distant receivers (Fedurek, Machanda, et al., 2013; Fedurek, Zuberbühler, et al., 2016; Mitani & Nishida, 1993). Chapter four focused on testing the extent to which signallers use pant hoots flexibly during a high-arousal and understudied context of production, the display. More specifically, I tested whether the inclusion of each pant hoot phase as part of a vocal sequence is associated with different social contexts.

Mature males produced up to eight different pant hoot sequences (Figure 9) and called flexibly depending on the audience composition and the type of display (Soldati, Fedurek, et al., 2022). More dominant males were more likely to produce vocal displays during displays directed at a specific victim (Figure 10). In addition, males called more when fewer social partners and females were present nearby (Table 9). Flexibility extended to the inclusion or omission of a determined phase. The introduction was more likely to be used during directed displays and in the presence of larger male audiences (Table 10). The climax was used by less dominant males during non-directed displays and was associated with chorused calls from audience members (Table 11). Finally, the let-down was used by younger males during nondirected displays and was also associated with chorusing by the audience (Table 12). Overall, my findings support the idea that chimpanzees possess high levels of social awareness during vocal communication and flexibly adjust vocal output depending on the audience composition, even during high-arousal events. Furthermore, I showed that fine details of the social context affect the use of the individual components of vocal sequences.

14.2. Ontogeny of pant hoot production

Primate vocal ontogeny is the result of three separate processes: the development of production (i.e., a call’s acoustic structure), usage (i.e., context and order in which a call is used), and comprehension (i.e., association between a call and the world, as measured by their responses). Findings from my second chapter provided two main insights on the development of vocal production in chimpanzee pant hoots. First, pant hoots, are produced by newborns like most, if not all, chimpanzee calls. Therefore, even the most complex vocalisation is part of the vocal repertoire since birth, which supports the idea that chimpanzees have largely fixed repertoires like other primates (Hammerschmidt & Fischer, 2008, 2019). However, the second finding is that the pant hoots produced by the newborn were ‘rudimentary’, insofar as they resembled the correspondent adult pant hoots more than other call types but presented some notable differences. Some of these developmental changes are likely due to maturational processes such as the descent of the larynx (Nishimura et al., 2003), while others could be either individually or socially acquired. Although a systematic study on the ontogeny of vocal production of pant hoots is necessary to test these hypotheses, my preliminary observations on the pant hoots of immature chimpanzees can be informative. For instance, the vocal units produced by immatures appeared shorter in duration, graded more into each other between and within each phase, and were more likely to have a reversed V-shape when compared to mature pant hoots. The introduction and climax units produced by immatures gradually increased and then decreased in both fundamental and peak frequency thorough the entire vocal sequence (Figure 2 a, b, d), while in adults each phase tends to be acoustically distinct (Figure 1). Furthermore, the vocal sequences produced by immature individuals contained a larger number of units but fewer of these were followed by panted units when compared to mature pant hoots. While some of these developmental differences are likely the result of physical maturation, it cannot be excluded that external factors may also play a role.

A key transition in the social life of a chimpanzee takes place when they become socially independent from their mother (Goodall, 1986; Pusey, 1990). Because greater exposure and social interactions positively affected the ontogeny of vocal usage and responses, which also varied between sexes as presented in Chapter three, one possibility is that the ontogeny of vocal production is similarly affected by individual and social factors. While chimpanzees seem to be born with a head start in pant hoot production when compared to pant hoot usage or responses, my preliminary observations suggest that pant hoot production does not become fully adult-like at an earlier age than vocal usage and comprehension as in the case of the alarm calls of other primates (Seyfarth & Cheney, 1997) or chimpanzee greeting calls (Laporte & Zuberbühler, 2011). One possibility is that the ontogeny of socially used, acoustically complex, and long distance call types requires more time. Importantly, given that later emerging traits may be more prone to environmental influences, it cannot be excluded that socioecological factors play a role in the ontogeny of pant hoot production, even when call structures are largely innate and only subtle modifications are possible (Egnor & Hauser, 2004).

14.2.1. Study limitations and future directions

While I initially planned to also investigate the ontogeny of pant hoot production, one issue I encountered during data collection was the emigration of most sub-adult females, a low number of female infants and juveniles, and a low number of sub-adult males (Table A1). Because collecting data longitudinally was not possible for my thesis, I opted for a cross-sectional study. Tracking acoustic changes can be regarded as more challenging in great apes given that both chimpanzees and orang-utans calls decrease in consistency during ontogeny (Lameira et al., 2022; Taylor et al., 2021), while the opposite occurs in songbirds and marmosets for instance (Takahashi et al., 2015; Tchernichovski et al., 1999). Furthermore, given the high acoustic variability and strong individual signatures that characterise pant hoots, a large dataset from multiple individuals is necessary to systematically assess which factors drive ontogenetic changes in vocal production. To tackle these challenges, I created a collaborative dataset which includes pant hoots produced by immature chimpanzees of the Sonso community collected by researchers before and after my studies, which will also allow me to analyse data longitudinally. Investigating the ontogeny of pant hoots might be critical to resolve the inconsistent findings about the presence or lack of group dialects (see Crockford et al., 2004; Desai et al., 2022). In other animals, there are trade-offs when it comes to signals encoding both individual and group vocal identity (e.g., bats: Knörnschild et al., 2012, marmosets: Zürcher et al., 2021). While the end-result of socially learned vocalisations have been reported in adult great apes, the ontogenetic process that may be responsible for individual and community differences is largely unknown. Given the importance of auditory exposure during ontogeny of pant hoot usage and comprehension (Chapter three), one possibility that is yet to be directly tested is that chimpanzees acquire their group dialects through vocal convergence with the calls of their group members during a process that starts before adulthood, similarly to how adult social partners accommodate each other's pant hoot acoustic structures (Mitani & Brandt, 1994).

14.3. Ontogeny of pant hoot usage

In Chapter three I showed that immature chimpanzees use pant hoots less frequently when compared to mature individuals, both spontaneously and in response to other group members' pant hoots. Immature individuals experience one appropriate context for the use of pant hoots, i.e., exposure to others' calls and subsequent vocal responses, but reach adult-like levels of vocal usage only as they become sub-adults. Given their social dependence from the mother, immature individuals do not yet use pant hoots to coordinate and inform distant parties as mature chimpanzees do, which likely explain their infrequent use of spontaneous pant hoots. Thus, one possibility is that when the latter context of use becomes a central part of their social interactions, chimpanzees use pant hoots more frequently as a result.

In comparison, grunts start as one of the most used calls in young chimpanzees and their frequency of use declines over the years (Laporte & Zuberbühler, 2011). While both are socially used calls, pant grunts are simple short utterances used to mediate short-distance social interactions, while pant hoots are complex long calls used to mediate both short- and long-distance social interactions. Thus, these differences in the call form and function might explain the different developmental trajectories. Overall, however, the usage development of social calls appears to be slower than that of alarm calls, both in monkeys (Snowdon, 2009; Wegdell et al., 2019) and in great apes (Dezecache et al., 2019; Laporte & Zuberbühler, 2011), which is likely due to their less evolutionarily urgent function. Because all chimpanzees, regardless of social and vocal exposure, will end up using pant hoots both spontaneously and in response to others' calls, their development can be regarded as mediated by experience and social factors to a certain extent.

14.3.1. Ontogeny of vocal sequences

Little is known about how and when in ontogeny great apes learn to use vocal sequences. In Chapter three, I observed that the introduction, the build-up, and the climax phases were produced by infant and juvenile chimpanzees, while the let-down was only produced by sub-adults and adults. The first possibility is that the latter phase is only used by sub-adult and adult males because it necessitates physical maturation or extensive vocal practice, both of which peak as individuals become sexually mature (Pusey, 1990). However, this explanation is unlikely given that the let-down is acoustically very similar to the build-up, a phase that is regularly produced by immature individuals. Instead, a second possibility is that younger chimpanzees do not experience the appropriate context of use for this phase until later. In adults, the production of the let-down phase is associated with arrival at a feeding source (Notman & Rendall, 2005) and travelling (Fedurek, Zuberbühler, et al., 2016). Thus, given that immature individuals do not travel and feed independently from their mother, it is likely that they experience less pressure and benefits in using let-downs as part of their pant hoots. Interestingly, in Chapter four I found that mature males were more likely to include a let-down phase during nondirected vocal displays when younger, while they were more likely to do so during directed ones when older, suggesting that only more experienced signallers can afford to use this phase during more severe displays. Upon further inspection, it seems that male chimpanzees used both the build-up and the let-down phases more often during traveling and displays than during feeding or resting (unpublished data). Interestingly, the let-down is the least frequently used phase in Western chimpanzees (Crockford et al., 2004; Kalan & Boesch, 2018). Given that Eastern chimpanzees are less gregarious and live in larger groups compared to Western chimpanzees (Lehmann & Boesch, 2004, 2008; Wilson et al., 2014), they likely use pant hoots more frequently to remain in contact and recruit others to feeding events, further supporting the idea that let-downs are predominantly used for this function. Taken together, these observations support the idea that the let-down phase appears later in ontogeny due to the lack of appropriate context of production. However, this hypothesis requires confirmation through the systematic study of the ontogeny of pant hoot phases across multiple communities.

14.4. Ontogeny of pant hoot responses

My findings from Chapter three showed that the development of chimpanzee behavioural and vocal responses to others' pant hoots is enhanced by social and vocal exposure and that their ontogenetic trajectory is slow and gradual throughout infant and juvenile periods. Despite this, more gregarious individuals and male individuals showed greater responsiveness, acquiring adult-like responses earlier in ontogeny than other individuals. Furthermore, the increasing social complexity of the behavioural contexts that immature individuals experience as they grow older seems to be reflected in their increased responsiveness to vocal stimuli. Therefore, the development of pant hoot behaviours cannot be explained by a single factor such as physical maturation but is instead the result of both individual and social factors and is reinforced by two maternal effects. First, mothers affected the rate of vocal responses by chorusing with the pant hoots of their offspring. Second, mothers affected the rate of behavioural and vocal responses through their association patterns by exposing their offspring more often to groups and adult males. In line with the idea that social events mediated by pant hoots require more social awareness and recognition of other individuals (e.g., Chapter four), adult-like comprehension and responses developed slower in pant hoots than in more conservative and urgent call types (Dezecache et al., 2019; Laporte & Zuberbühler, 2011). Despite this, social learning did not seem to be prerequisite for the development of comprehension and responses in chimpanzees, similarly to baboons (Fischer, 2008). On the other hand, social learning enhanced chimpanzees' vocal development of comprehension and responses, similarly to vervet and marmoset monkeys (Hauser, 1989; Takahashi et al., 2015). Thus, the vocal development of great apes should not be regarded as either entirely fixed or socially learned, but instead as the result of both. Whether the same can be said for the ontogeny of great ape vocal production, in line with recent findings on marmoset monkeys (Gultekin & Hage, 2018; Takahashi et al., 2017), is yet to be determined.

14.5. Social awareness and vocal flexibility

Many animal species produce distinct vocal signals in response to external events, however, these communicative behaviours typically mediate fundamental biological and social processes but signallers rarely produce them with awareness of others. My findings from Chapter four suggest that chimpanzees possess sophisticated social awareness when using pant hoot sequences as well as when using individual components of such vocal sequences. Chimpanzees use of pant hoots during displays was affected by several social factors, which included the number of and the relationships with audience members, as well as individual factors such as the age and the social status of the signaller. In addition, the effect of differences in the social fabric of the party co-varied together with the severity of a display, suggesting that signallers modulate vocal output depending on the signal function while simultaneously monitoring the social environment. Thus, signallers may strategically adjust the use and structure of pant hoots during dynamic and unpredictable social events that engage them on different levels of social relationships with audience members. Remarkably, all this occurs when signallers are engaged in establishing their dominance or challenging the social status of others, a behaviour that is key for their fitness and success as group members of a chimpanzee society (Muller & Mitani, 2005).

There were some differences when compared to previous studies on the audience effects associated with the production of feeding and traveling pant hoots (e.g., Fedurek et al., 2014; Kalan & Boesch, 2015; Mitani & Nishida, 1993). However, given that chimpanzees use vocal signals across multiple contexts for different functions (Schamberg et al., 2018), it is likely that drivers of pant hoots are to some extent context-specific. For instance, as presented in Chapter one, during feeding events males call more often in the presence of more females, particularly if females are in oestrous, while the opposite occurred during vocal displays. In addition, higher-ranking males called less often during displays compared to other behavioural contexts. These contextually related effects are likely due the fact that pant hoots are flexibly used for multiple social functions. Previous studies found that pant hoots' acoustic structures vary depending on the context of production, which are likely accessible to chimpanzee receivers (Fedurek, Zuberbühler, et al., 2016; Notman & Rendall, 2005). Preliminary results from my research suggest that these acoustic differences might also be detectable by experienced human listeners (see Annex 'Ongoing Research'). Thus, the acoustic structure of pant hoots likely allows distant or out-of-sight receivers to infer the context of production, information that can then affects their subsequent behaviours.

Overall, my results are in line with the hypothesis that vocal behaviours of social calls are more flexible when compared to more 'evolutionary urgent' vocalisations, such as alarm calls (Snowdon, 2009). While previous studies investigated the effects of the presence or absence of certain individuals on "when" to call instead of "how" to call (e.g., Schel, Machanda, et al., 2013; Townsend et al., 2008), I showed that audience effects also apply to the production of acoustically different components of a vocal sequence, suggesting that even the use of complex vocal signals is adjusted to the social context. Thus, my findings support the hypothesis that greater complexity in the social environment is associated with greater complexity in vocal communication (Freeberg et al., 2012), where natural selection has likely favoured advanced and sophisticated communication in species living in large communities characterised by frequent fusion-fission events.

14.5.1. Pant hoots and drumming

Studying communicative signals separately from other co-occurring signals has been the most popular approach in primatology so far (Slocombe et al., 2011). However, because both human and primate communication is inherently multi-modal, where gestures, vocalisations, and facial expressions can occur at the same time, this aspect of communication deserves more attention (Fröhlich et al., 2019; Fröhlich & van Schaik, 2018). In my thesis, I examined pant hoots and drumming signals separately, despite the fact that they can be produced together (Arcadi et al., 1998; Babiszewska et al., 2015). During travelling, drumming is used to coordinate movements between parties and carries information about the identity of the signaller (Babiszewska et al., 2015; Eleuteri, 2019), similar to pant hoots used during travelling (Chapter one). However, drumming does not carry information about the signaller's identity during displays (Eleuteri et al., 2022). When considering vocal displays, males included the climax phase, which carries information about the caller's identity over long distances, less frequently compared to other contexts (unpublished data; Fedurek, Zuberbühler, et al., 2016). Instead, the most frequently produced phase during displays was the build-up, which does not signal the caller's identity (Fedurek, Zuberbühler, et al., 2016). Thus, the study by Eleuteri et al. (2019) and my findings suggest that chimpanzees do not benefit from revealing their identity to distant individuals through acoustic signals during competitive and higher-risk social events. Furthermore, the function of these long distance acoustic signals varies according to the context and is affected by the audience. Is the multi-modal use of pant hoots and drumming similar in this regard? One hypothesis is that the information provided by the two signal modalities is redundant but increases the likelihood that the message reaches receivers (Partan & Marler, 2005), which may be especially beneficial in forest habitats where acoustic signals degrade over long distances (Brown & Waser, 2017). Alternatively, the information provided by the two signal modalities is nonredundant and different or complementary information reaches receivers at the same time (Partan & Marler, 2005), which would be in line with the 'multiple information hypothesis' (e.g., Freeberg, 2006).

14.6. Relevance to human language evolution

Some scholars view the primate vocal systems as innate, constrained, lacking volitional control, and sharing more similarities with human emotional and more ancestral vocalisations such as cries and laughter than spoken language (Hammerschmidt & Fischer, 2008; Owren et al., 2011; Rendall, 2021; Tomasello, 2008). However, over the last few decades an increasing number of comparative studies on primate vocal behaviours provided evidence that language and primate vocal systems should be considered as part of a continuous and gradual evolutionary process rather than being fundamentally different (Fitch & Zuberbühler, 2013; Lameira et al., 2022; Townsend et al., 2020; Zuberbühler, 2017). It follows that some primate vocalisations might represent intermediary forms between acoustically simple and innate ancestral calls and the complex and socially learned human languages. These vocalisations would be more likely to be found in species biologically closer to humans where they likely underwent similar selection pressures. Chimpanzee pant hoots represent promising candidates in the search for such intermediary forms. Indeed, given that my work showed that chimpanzees use complex pant hoot sequences flexibly and that their ontogeny is also socially mediated, pant hoots might represent an example of intermediary form that potentially evolved from ancestral vocalisations (e.g., screams) which increased in acoustic complexity over time (e.g., screams accompanied by introduction and build-up phases) while being used as a social tool to navigate group interactions. One hypothesis is that animals referred to as the 'canonical vocal learners' (i.e., marine mammals, songbirds, and bats) demonstrate greater communicative complexity and the ability to learn signals because they are highly mobile and less regularly in contact with group members (Snowdon, 2009). Given that all four great ape species use similar long distance vocalisations (bonobos: Schamberg et al., 2016; gorillas: Salmi & Doran-Sheehy, 2014; orangutans: Spillmann et al., 2010), future studies can test this hypothesis by investigating whether less mobile and more cohesive great ape species such as gorillas use less complex vocalisations that are not socially learned.

14.6.1. Socially-mediated vocal learning

Social learning is regarded one of the unique features of language acquisition (Tomasello, 2008). In humans, social interactions and early experiences with caregivers play a major rule in the development of infant vocalisations (Kuhl, 2004). While primate studies contributed significantly to our understanding of language evolution, they critically overlooked the importance of ontogenetic processes (Griebel et al., 2016; Oller et al., 2016a). My findings are line with the idea that primates have a largely fixed vocal repertoire since birth, however, they also showed that vocal ontogeny can be socially mediated. Thus, social and vocal feedback play a role in the vocal development of humans and a limited number of non-human primates. While the ontogeny of vocal usage and comprehension were enhanced by social exposure and maternal feedback, at this stage I can only speculate about the ontogeny of vocal production. Nevertheless, evidence from primate studies remains overall more limited compared to the vocal learning capacities of songbirds and humans.

Because usage, production, and comprehension are uniquely affected by social or individual factors, scholars recently proposed to abandon the dichotomous "haves and have-nots" approach when determining whether a species has the vocal learning capacity and suggested instead to use continuous (Arriaga & Jarvis, 2013; Petkov & Jarvis, 2012) or 'multi-level' frameworks (Fischer & Hammerschmidt, 2020). Some scholars further argued that establishing vocal learning via evidence of learning novel calls through imitation is too restrictive and greatly limits our consideration of the diverse vocal learning behaviors displayed by non-human primates (Martins & Boeckx, 2020). With accumulating evidence from numerous animal species, Janik and Knörschild noted that "it becomes apparent that vocal production learning is not an all or nothing skill but that it can influence vocal behaviour to different degrees" (2021, p. 7). Finally, a continuous view of vocal learning capacities represents a better fit for the hypothesis that language emerged through a continuous evolutionary process.

14.6.2. Arousal-driven and intentional vocal communication

Arousal plays a role in the vocal communication of both human and non-human primates (Barrett & Bliss-Moreau, 2009; Kever et al., 2015; Marler et al., 1992). Instead, the capacity to use and understand communicative intentions seems to be unique to humans (Scott-Phillips, 2015; Tomasello, 2008). However, the traditional view that chimpanzee communication driven by arousal cannot be used flexibly or intentionally is becoming increasingly problematic given the accumulating evidence in favour of intentional use of gestures and vocalisations (Byrne et al., 2017; Crockford et al., 2012) as well as the presence of advanced cognitive abilities associated with the Theory of Mind (Krupenye & Call, 2019). Given that the use of vocal sequences composed by different call types is rare among primates (Girard-Buttoz, Zaccarella, et al., 2022) and even rarer is the use of syntactic-like structures (Leroux & Townsend, 2020), if chimpanzee calls are reflexive, one would expect more acoustically simple vocalisations during higher arousal contexts. Instead, in Chapter four I showed that males produced up to eight different vocal structures during displays and that the phase composition of pant hoots produced in this context varied more than in more relaxed contexts (i.e., feeding, resting) (unpublished data). Thus, the presence of arousal processes did not preclude vocal flexibility. Furthermore, approximately half of the vocal displays were directed at victims and both the entire call and each phase were affected by the presence and composition of the audience and provoked vocal responses in nearby individuals, which meet one of the four criteria used to assess first-order intentionality in vocal communication ('social use'; Townsend et al., 2017). However, measuring the other three intentionality markers is particularly challenging in vocalisations, mainly due to the fact that vocalisations are not typically directed at a specific receiver, unlike gestures (Townsend et al., 2017). For instance, I was not able to record whether signallers monitored or manipulated the attentional state of receivers before vocalising (Townsend et al., 2017). A recent study found that wild chimpanzees use short-distance contact calls intentionally to promote social cohesion, particularly between social partners (Bouchard & Zuberbühler, 2022a). Pant hoots, the other contact call used by chimpanzees, seem to be produced in goal-directed ways to communicate with distant group members, especially social partners (Mitani & Nishida, 1993). My findings on display pant hoots suggest that they are not exclusively used to maintain contact with distant receivers, opening the possibility that they may be used intentionally to communicated with nearby receivers. Sensitivity to the presence and composition of the audience and the use of directed vocal displays in chimpanzees suggest that precursors of intentional vocal signals may have evolved before the appearance of modern spoken language. Nevertheless, further work is necessary to clarify the extent to which human and primate emotions and intentional signals are alike in order to formulate testable hypotheses (Ben Mocha & Burkart, 2021; Demuru et al., 2022; Graham et al., 2020; Kret et al., 2020).

14.6.3. Are pant hoots call combinations?

Chimpanzees have received the most attention among the great apes with regard to their vocal behaviour (Slocombe et al., 2011), however, much less is known about the combinatorial aspect of vocal sequences used by great apes when compared to monkeys' combinatorial abilities (Leroux & Townsend, 2020). Chimpanzees produce several distinct vocal sequences composed of different call types that are ordered in non-random ways (Girard-Buttoz, Zaccarella, et al., 2022; Leroux et al., 2022), but whether these call combinations are meaningful for receivers or instead represent a the read-out of contextual changes is unclear. A significant number of vocal sequences are composed of pant hoot phases combined with other pant hoot phases or call types (Crockford & Boesch, 2005; Girard-Buttoz, Zaccarella, et al., 2022; Leroux et al., 2022), although if and how these phases are combined has not been systematically investigated. Given that primates, like most animals capable of combining calls, are largely limited to the use of two call types as part of vocal sequences (Miyagawa & Clarke, 2019), the multi-component structure of pant hoots might represent a rare case of complex combinatorial call. In my thesis the syntactic-like aspect of pant hoots was not the main focus, however, observations from Chapter four provide promising insights for further investigations on their combinatorial properties. More specifically, my findings revealed that two out of four phases were produced both in isolation and in combination with one or more other phases and were acoustically identical to the same phase produced in combination. These two features are considered as 'prerequisites' when assessing whether calls are combinatorial or not (Suzuki & Zuberbühler, 2019; Zuberbühler, 2019). In Chapter four, I found that the production of three phases was driven by unique social factors which, together with the fact that each phase is associated with different socio-ecological information (Fedurek, Zuberbühler, et al., 2016), suggest that pant hoot phases are used flexibly to achieve different goals. Furthermore, by combining these components, signallers could potentially transmit both more specific and multiple information to different receivers, which ultimately might function as a social tool to navigate more unpredictable interactions. A recent chimpanzee study found that greater combinatoriality occurred during socially challenging situations supporting the social complexity hypothesis (Leroux et al., 2022). Findings from my thesis are in line with this hypothesis and suggest that pant hoots are more sophisticated vocal structures than previously assumed.

However, two main limitations in my work need to be addressed in order to assess whether pant hoots qualify as call combinations. First, the multi-phase sequences might have been random co-occurrences. Here, it's worth noting that the order of phase production I observed followed the same 'stereotypical' order established in the literature, which results in a maximum of 15 unique structures (Table A23). Of these, chimpanzees produced eight structures during displays and upon further inspection of calls produced during other contexts I found the same eight structures with an additional one (I-C-L). Thus, the multi-phase structures followed a specific order of production and not all structures were observed, suggesting that they are unlikely to be randomly produced. One way to ascertain this would be to use collocation analyses, a method typically used in linguistics to calculate the probability of word occurring together, which has been recently adopted in the study of marmoset and chimpanzee vocal communication (Bosshard et al., 2022; Leroux et al., 2021). The second limitation was that I did not test how the audience composition affected specific multi-phase structures. Vocal output can be analysed on three levels based on the presence or absence of 1) a pant hoot; 2) one of four phases; 3) a specific multi-phase call. Investigating the first and second level allowed me to compare effects on the entire call and on each phase to gain insights on the function of distinct phases. The third level, key to understand the meaning or function of a combinatorial structure, is yet to be explored and only by adopting all three levels one can assess whether a signal possesses combinatorial properties. Nevertheless, inspection of the data revealed the combination of introduction and build-up phases to be a promising candidate. These two phases were produced in isolation and combined together as a two-phase structure. This type of combination of a call encoding the identity of the caller (introduction) together with another call encoding the context of production (build up, typically produced during displays) is akin to the combinations found in a series of mammalian species, including Diana monkeys (Cercopithecus diana: Coye et al., 2016) and Banded mongooses (Mungos mungo: Jansen et al., 2012). Whilst speculative at this point, the pant hoot could represent a rare example of hierarchical structuring in non-human animal calls.

14.6.3.1. Vocal learning of combinatorial calls

Investigating the combinatorial aspect of pant hoots is not only relevant to improve our understanding of syntactic-like precursors of human language in our closest living relatives, but also to study how population differences in the use of vocal sequences might result from usage learning. Earlier studies compared acoustic differences of pant hoots by different chimpanzee communities and found the presence of dialects, likely as a result of social learning (Crockford et al., 2004; Mitani et al., 1992). However, re-assessments found that these small acoustic differences are likely the result of individual, environmental, or group cohesion differences (Desai et al., 2022; Mitani et al., 1999). While current evidence suggests that the acoustic structure of pant hoots is highly similar across chimpanzee communities and sub-species (Desai et al., 2022), whether this is true for the arrangement of pant hoot phases and the context in which they are produced is an interesting unexplored avenue for future studies on vocal usage learning and might potentially provide insights on the evolution of culturally learned languages.

14.7. Final conclusion

To conclude, the key findings of my thesis suggest that the vocal ontogeny of chimpanzees is affected by a combination of innate, individual, and social factors. Pant hoots are produced since birth but likely undergo ontogenetic changes and their usage and comprehension development is enhanced by social and maternal effects. Finally mature individuals are capable of adjusting both entire vocal sequences and each component according to fine changes in the social context. Thus, my studies suggest that a limited number of repertoire calls and limited vocal production learning capacities do not preclude chimpanzees from using complex calls in flexibly ways. Overall, the vocal behaviours of both signallers and receivers were affected by multiple socio-ecological factors. The ontogeny of these more complex socially used calls is slower when compared to the ontogeny of calls used for more urgent functions, likely due to the fact that interactions mediated by pant hoots require more social awareness. Consequently, the ontogeny of pant hoots is also more subject to the influence of external factors, including social and vocal exposure. These social calls might be especially important in animal societies where social awareness allows individuals to navigate dynamic relationships and unpredictable interactions.

Social factors play an important role in the vocal ontogeny of a variety of animal species and findings from my thesis support the idea that the vocal ontogeny of primates should not be regarded as fundamentally different from that of songbirds and human. Instead, both monkey and great ape vocal ontogeny should be seen as part of a continuous and gradual evolutionary process that potentially led to the emergence of spoken language in the human lineage. Finally, my studies further corroborates the importance of the comparative approach when investigating primate vocal behaviours and their underlying social awareness in the natural environment to achieve a better understanding of their communication systems as well as to further elucidate the evolution of language.

15. Appendices

15.1. Appendix 1 – Supplementary material for: The ontogeny of vocal sequences: insights from a newborn wild chimpanzee (*Pan troglodytes schweinfurthii*)

15.1.1. The STRANGE framework

We evaluated the scope for bias in our study subjects by using the STRANGE framework to mitigate and report potential sampling biases in our study (Rutz & Webster, 2021; Webster & Rutz, 2020). The Sonso community is of typical size for wild chimpanzees (*P.t. schweinfurthii*, *P.t. troglodytes*, and *P.t. verus* communities range from 7-144 individuals with a median 42; East African sub-species (*P.t. schweinfurthii*) range is 18-144 with a median 49; Wilson et al. 2014). Sonso have a typical female-biased sex ratio among mature individuals of 1:1.7 males per females (*P.t. schweinfurthii* communities mean of 1:1.7; Wilson et al. 2014). Of relevance to perinatal behaviours, the Sonso community experience higher levels of infanticide compared to other chimpanzee communities (Lowe et al., 2020).

Table A1 List of all individuals from the Sonso community. Main subjects are in bold. Asterisks represent (potentially) emigrated females

ID	Sex	Age category	Year of birth
AC	F	Infant	2017
AN	F	Adult	1990
BG	F	*	2004
CD	F	Young adult	2003
DL	F	Young adult	2002
DB	F	Infant	2018
DR	F	Young adult	2004
ER	F	Infant	2019
EV	F	Young adult	2004
FA	F	Sub-adult	2006
FH	F	Juvenile	2013
FL	F	Adult	1979
FK	M	Adult	1999
GF	M	Juvenile	2013
GH	F	Infant	2020
GL	F	Adult	1976
GR	F	*	2006
HD	M	Infant	2017
HM	F	Juvenile	2013
HR	F	Sub-adult	2009
HT	F	Adult	1978

HW	M	Adult	1993
IN	F	Adult	1999
IS	F	Infant	2017
JA	F	Infant	2018
JB	M	Juvenile	2011
JL	F	Adult	1990
JN	F	Adult	1984
JS	M	Sub-adult	2006
KA	F	Adult	1998
KB	F	*	2007
KC	M	Sub-adult	2006
KH	**F**	**Sub-adult**	**2008**
KF	**M**	**Juvenile**	**2014**
KG	F	Adult	1998
KJ	M	Juvenile	2013
KL	F	Adult	1979
KO	M	Juvenile	2014
KP	F	*	2008
KQ	M	Infant	2016
KS	M	Adult	2003
KT	**M**	**Adult**	**1993**
KU	**F**	**Adult**	**1979**
KV	M	Juvenile	2014
KW	F	Adult	1981
KX	F	Sub-adult	2007
KY	F	Adult	1983
MB	M	Sub-adult	2009
MI	F	Sub-adult	2007
MK	F	Adult	1980
ML	F	Adult	1975
MS	M	Adult	1992
MZ	M	Infant	2015
NB	F	Adult	1962
OK	F	Adult	1996
OZ	M	Juvenile	2014
PS	M	Adult	1998
RF	F	Sub-adult	2007
RH	F	Adult	1965
RM	F	Young adult	2002
RS	F	Adult	1997
SM	M	Adult	1993
ST	F	*	2007
TJ	F	Adult	1984

TW	F	Sub-adult	2010
UP	F	Adult	1999
ZD	M	Young adult	2001
ZL	M	Adult	1995

Table A2 List of external experts who qualitatively categorised the calls with the wild chimpanzee communities they have worked with and examples of studies they conducted on vocal behaviours

Name	Experience	Work examples
Crockford C.	Sonso and Tai chimpanzees	(Crockford, 2019; Crockford et al., 2004, 2018; Crockford & Boesch, 2003, 2005)
Hobaiter C.	Bossou, Bugoma, Sonso, and Waibira chimpanzees	(Fröhlich and Hobaiter 2018; C. Hobaiter et al. 2017; Hobaiter and Byrne 2011, 2014; Rodrigues et al. 2021)
Laporte M.	Sonso chimpanzees	(Bouchet, Laporte, et al., 2013; Laporte & Zuberbühler, 2010, 2011)
Matsuzawa T.	Bossou and Nimba chimpanzees	(Matsuzawa, 1999, 2009; Matsuzawa et al., 2006; Myowa-Yamakoshi et al., 2004; Okamoto et al., 2002)
Mitani J.	Mahale and Ngogo chimpanzees	(Marler and Mitani 1988; Mitani et al. 1996; Mitani and Brandt 1994; Mitani and Gros-Louis 1998; Mitani and Nishida 1993; Mitani and Stuht 1998)
Slocombe K.	Sonso and Kanyawara chimpanzees	(Slocombe & Zuberbühler, 2005a, 2005b, 2010; Slocombe & Zuberbuhler, 2007; Watson et al., 2015a)
Townsend S.	Sonso chimpanzees	(Leroux and Townsend 2020; Schel et al. 2013; Townsend et al. 2008, 2018; Townsend et al. 2011)

Table A3 List of acoustic parameters extracted from the call units. We indicate the number of call unit (Nr.), the type of call according to our qualitative classification (Type), the cluster number resulted from cluster analysis (C-A), whether the unit is part of a sequence (Seq.: N = No (single call), Y = Yes (numbers group together units that are part of the same sequence)), whether the unit is part of a combination (Combo), and whether the unit is followed by an inhaled unit (Inhaled). F0 values are in Hz

Nr.	Type	C-A	Seq	Combo	Inhaled	Duration (s)	Start F0	Middle F0	End F0	Max F0	Min F0
1	Grunt	1	N	No	No	0.052	70.2	86.3	93.9	99.6	94.1
2	Grunt	1	Y-1	No	No	0.043	221.1	232.1	232.1	232.1	221.1
3	Grunt	1	Y-1	No	No	0.120	124.9	130.1	123.9	131.6	124.9
4	Whimper	1	Y-2	No	No	0.054	237.4	237.2	232.1	237.4	232.1
5	Whimper	1	Y-2	No	No	0.090	231.2	237.3	238.1	238.1	231.2
6	Whimper	1	Y-3	Yes	No	0.064	313.8	313.6	308.7	313.6	308.7
7	Bark	2	Y-3	Yes	No	0.068	538.1	515.3	483.2	538.9	483.2
8	Bark	2	Y-3	Yes	No	0.114	553.7	558.7	553.6	561.3	553.6
9	Grunt	1	Y-3	Yes	No	0.048	211.7	206.6	211.7	211.7	206.6
10	Phase 1	3	Y-4	Yes	Yes	0.346	298.5	334.1	313.2	339.3	313.2
11	Phase 1	3	Y-4	Yes	Yes	0.304	318.9	344.1	308.7	354.7	308.7
12	Phase 1	3	Y-4	Yes	Yes	0.351	354.6	370.2	334	370.2	334
13	Phase 1	3	Y-4	Yes	No	0.296	344.4	364.8	359.7	369.9	344.4
14	Phase 1	3	Y-4	Yes	Yes	0.320	339.2	390.3	354.7	395.4	339.2
15	Phase 2	3	Y-4	Yes	Yes	0.310	324	451.6	426	466.9	324
16	Phase 2	3	Y-4	Yes	Yes	0.311	339	533.2	446.4	548.5	339
17	Phase 2	3	Y-4	Yes	Yes	0.271	345.2	563.8	497.5	565.8	340.2
18	Phase 2	3	Y-4	Yes	Yes	0.252	375	523	502.6	594.4	375
19	Phase 2	3	Y-4	Yes	No	0.292	364.8	574	446.4	579.1	364.8
20	Phase 2	3	Y-4	Yes	No	0.299	364.9	543.4	436.2	553.6	364.9
21	Phase 2	3	Y-4	Yes	No	0.292	344.4	543.4	482.2	545.6	344.4
22	Phase 2	3	Y-4	Yes	No	0.298	380.1	568.9	441.3	568.9	380.1
23	Phase 2	3	Y-4	Yes	No	0.193	375	420.9	410.7	457.7	375
24	Phase 2	3	Y-4	Yes	No	0.151	405.6	436	497.5	466.9	405.6
25	Squeak	2	Y-4	Yes	No	0.096	502	977.1	1013	1038	502
26	Grunt	1	Y-4	Yes	No	0.051	303	303.6	298.5	308.7	303
27	Phase 1	3	Y-5	Yes	Yes	0.470	272.9	278	267.8	278	267.8
28	Phase 1	3	Y-5	Yes	Yes	0.384	293.4	318.9	298.5	324	293.4
29	Phase 1	3	Y-5	Yes	Yes	0.276	318.9	369.9	390.3	380.3	318.9
30	Phase 2	3	Y-5	Yes	Yes	0.295	313.8	431.9	354.6	451.6	313.8
31	Phase 2	3	Y-5	Yes	Yes	0.320	339.1	507.7	426	517.9	339.1
32	Phase 2	2	Y-5	Yes	Yes	0.294	400.5	783.2	574	788.3	400.5
33	Phase 2	2	Y-5	Yes	Yes	0.362	441.3	931.2	609.7	1018	441.3
34	Phase 2	2	Y-5	Yes	No	0.246	507.6	864.9	829.3	946.6	507.6

35	Phase 2	2	Y-5	Yes	No	0.308	487.3	1013	655.7	1013	487.3
36	Phase 2	2	Y-5	Yes	No	0.347	457.2	834.3	548.5	849.6	457.2
37	Phase 2	2	Y-5	Yes	No	0.315	395.1	706.7	487.3	706.7	395.1
38	Squeak	2	Y-5	Yes	No	0.209	313.9	722	859.2	1013	313.9
39	Grunt	1	Y-5	Yes	No	0.053	359.1	349.5	313.8	359.1	313.8
40	Whimper	1	Y-6	No	No	0.075	278	272.9	262.6	278	262.6
41	Whimper	1	Y-6	No	No	0.079	267.8	313.8	293.4	313.8	267.8
42	Whimper	1	Y-6	No	No	0.139	262.7	318.9	312.2	312.2	262.7
43	Whimper	1	Y-6	No	No	0.197	181.1	186.4	150.5	186.4	150.5
44	Grunt	2	N	No	No	0.054	502.1	472	487.3	512.8	472
45	Whimper	1	Y-7	Yes	No	0.096	257.6	298.5	288.3	298.5	257.6
46	Hoo	3	Y-7	Yes	No	0.535	298.5	329.1	313.8	329.1	298.5
47	Hoo	3	Y-7	Yes	No	0.350	308.7	359.7	354.6	359.7	308.7
48	Hoo	3	Y-7	Yes	No	0.311	344.4	345	334.2	345	334.2
49	Hoo	3	Y-7	Yes	No	0.291	339.3	340	342.2	342.2	339.3
50	Hoo	3	Y-7	Yes	No	0.242	364.8	349.5	400.5	400.5	349.5
51	Hoo	3	Y-7	Yes	No	0.094	373.2	375	373.2	375	373.2
52	Grunt	1	N	No	No	0.069	256.7	262.7	252.5	262.7	252.5
53	Phase 1	3	Y-8	No	No	0.362	329.1	329.1	308.7	329.1	308.7
54	Phase 1	3	Y-8	No	No	0.351	334.2	348.2	339.3	348.2	334.2
55	Phase 1	3	Y-8	No	No	0.334	318.9	359.7	313.8	380.1	313.8
56	Phase 1	3	Y-8	No	No	0.314	329.1	395.4	410.7	410.7	329.1
57	Phase 1	3	Y-8	No	No	0.297	359.7	451.6	395.4	461.4	359.7
58	Phase 1	3	Y-9	No	No	0.222	400.5	400.5	446.5	446.5	400.5
59	Phase 1	3	Y-9	No	No	0.215	392.8	515.2	525.5	525.5	392.8
60	Phase 1	3	Y-9	No	No	0.340	331.8	382.6	352	423	331.8
61	Phase 1	3	Y-9	No	No	0.269	328.4	382.1	372.4	382.1	328.4
62	Phase 1	3	Y-9	No	No	0.287	331.3	392.8	454.1	454.1	331.3
63	Phase 1	3	Y-9	No	No	0.234	331.5	341.8	362.6	362.6	331.5
64	Phase 1	3	Y-9	No	No	0.191	424.3	505.2	484.6	505.2	424.3
65	Phase 1	3	Y-9	No	No	0.397	423.5	484.5	463.3	494.8	423.5
66	Phase 1	3	Y-9	No	No	0.315	311.1	392.8	372.4	392.8	311.1
67	Phase 1	2	Y-9	No	No	0.290	484.1	556.3	536.5	589.1	484.1
68	Phase 1	2	Y-9	No	No	0.324	535	637.6	596	637.6	535
69	Phase 1	3	Y-9	No	Unk	0.366	392.3	454	433.6	454	392.3
70	Phase 1	3	Y-9	No	Unk	0.411	372	512.3	515	545.2	372

Table A4 Summary of responses from external experts on the classification of the vocal structures resembling pant hoot calls and on the age of the caller. The numbering order of experts does not match with the order presented in Table A2

Expert n°	Call description	Age of caller
1	Hooting (similar to the build-up phase of a pant hoot).	Young adult or juvenile
2	Start of a pant hoot.	Young individual
3	Attempt at a pant hoot or whimpering.	Juvenile
4	Poor attempt at a pant hoot (with elements reminiscent of introduction and climax phases).	Infant
5	Pant hoot.	Young individual
6	Pant hoot-like (with elements reminiscent of introduction and let-down phases).	Young individual
7	Loud and unusual whimpers.	Immature or juvenile

Table A5 Stability measures calculated for each K value using four methods. Lower values indicate higher stability

		Number of clusters (K)					
		2	3	4	5	6	7
Method	**APN**	0.019	0.061	0.049	0.035	0.062	0.047
	AD	276.051	209.170	167.674	146.862	135.026	119.820
	ADM	10.770	29.447	14.130	11.520	12.794	7.838
	FOM	89.934	69.386	53.407	49.416	46.503	42.499

Table A6 Maximum and minimum mean silhouette values calculated for each number of clusters. Higher consistency of a cluster solution is represented by a smaller range of values

	Number of clusters (K)					
	2	3	4	5	6	7
Max. value	0.374	0.450	0.395	0.403	0.399	0.343
Min. value	0.356	0.355	0.327	0.258	0.222	0.169
Range	0.018	0.095	0.069	0.145	0.177	0.174

Table A7 Number of calls and percentages of call types within cluster

	Grunt	Bark	Hoo	Phase 1	Phase 2	Squeak	Whimper
Cluster 1	7 (46.7%)	-	-	-	-	-	8 (53.3%)
Cluster 2	1 (7.7%)	2 (15.4%)	-	2 (15.4%)	6 (46.1%)	2 (15.4%)	-
Cluster 3	-	-	6 (14.3%)	24 (57.1%)	12 (28.6%)	-	-

Table A8 List of all individuals considered for the comparison with pant hoots

ID	*Age category*	*Nr. pant hoots*	*Nr. vocal units*
GF	Juvenile	2	8
JB	Juvenile	3	11
JS	Subadult	3	16
KC	Subadult	3	15
KF	Infant	3	17
KJ	Juvenile	3	11
KS	Subadult	2	10
KT	Adult	3	12
KV	Infant	3	12
MB	Juvenile	2	8
MB	Subadult	3	14
MS	Adult	3	15
MZ	Infant	4	20
PS	Adult	2	8
ZL	Adult	3	12
Total		42	189

Table A9 Vocal usage rate of each pant hoot phase

	Introduction	Build-up	Climax	Let-down
Infants	0.38	0.24	0.38	0
Juveniles	0.20	0.35	0.45	0
Subadults	0.38	0.21	0.38	0.03
Adults	0.42	0.08	0.42	0.08

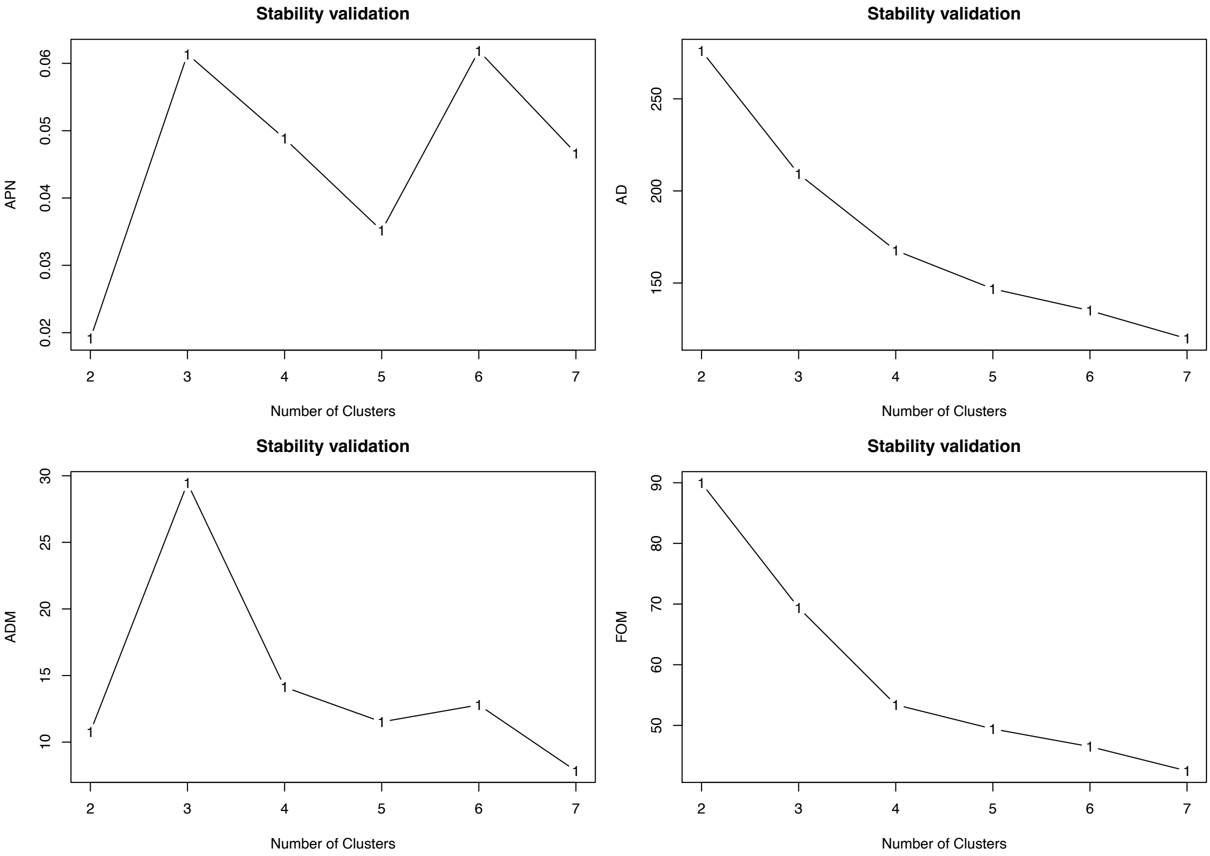

Figure A1 Graphical representation of the four measures of stability (APN, AD, ADM, FOM) based on the number of clusters. Lower values indicate higher stability.

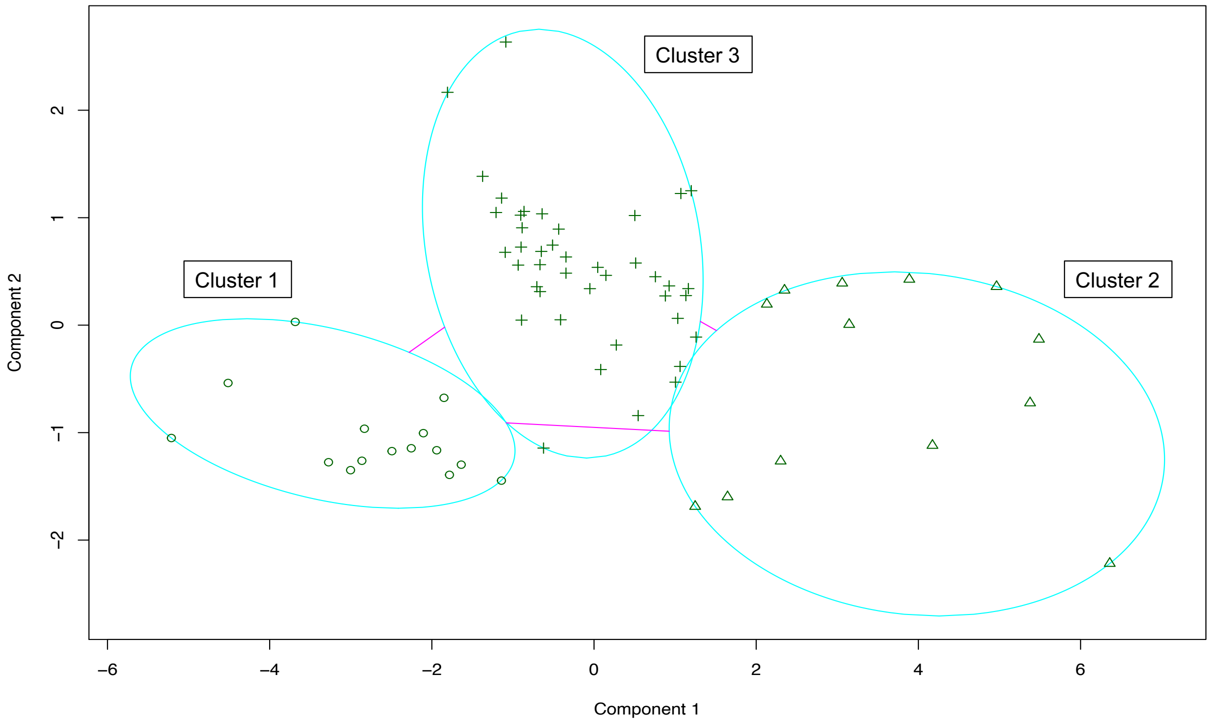

Figure A2 Territory plot representing the three-cluster separation obtained from the best-fitting model. Components 1 and 2 explain 85.73% of the point variability. Data points are represented by different shapes based on their cluster group (circles: Cluster 1; crosses: Cluster 2; triangles: Cluster 3).

15.1.2. Report of the birth event

15.1.2.1. Before birth

We first established contact with KU on the morning of the 20th of November 2019 at 07:30am. KU was first observed resting in a nest in a large tree (*Ficus Mugusa*) adjacent to the research station. In the same party, 12 other chimpanzees were present, including three adult male and four adult female chimpanzees and two of KU's offspring (KF and KH). Since the start of the day, KU performed a series of actions that were recognised as unusual, which included repeatedly standing in the nest on all four, staring immobile in one direction for several seconds, and laying down. KU added new branches to the first nest in which she was found on four separate occasions before resuming resting. At 7:47 she moved out of the nest and fed on figs. Her genital area appeared larger than usual. At 8:05 she built another nest (2nd) close to where she was feeding and alternated laying down, sitting, adding branches, and feeding. At 9:02 she left the nest decisively and descended the tree, slowly followed by her youngest son (KF). She reached a branch extremity and constructed a smaller nest (3rd) where she spent a short amount of time. She then moved on another branch and built a larger nest (4th), to which she added branches on multiple occasions. She moved one hand close to her genitals, where we noted presence of flies and residues of faeces, and she swung her hand as if to chase flies away. KF joined her in the nest, groomed her briefly, and they then groomed each other. At 9:45, she "cupped" one hand over her vagina and put a finger inside. The genital area looked more swollen than before. In the meantime, the males had left the party and joined a group feeding approximately 50 m away. At 9:55 she inspected her vagina a second time and then decisively left the tree to move into an already built nest (5th) in the adjacent tree (*Margariteria discordia*) at a height of approx. 12 m from the ground. Although the nest was already larger than the previous ones, she added more branches. The males then left the feeding area vocalising and reached another feeding tree approx. 300 meters away. At 10:09 she uttered a series of soft groaning sounds which resembled vocalisations that conspecifics produce during grooming (personal observation). The groans were soft and temporally separated by a few seconds.

Figure A3 a) KU7 moments after birth, holding on to his mother KU's belly with the umbilical cord still attached to his body, b) KU holding a branch in her mouth and detaching more to add to the nest, c) KU feeding on the placenta, d) KU7 on KU's belly two days after birth

15.1.2.2. After birth

At 10:12 KU licked her hands and arms wet from a liquid of transparent red colour. At this point, because of her body posture, we could not see the bottom half of her body. A few seconds afterward, we noticed she was carrying her newborn (KU7) on her belly. The newborn moved his arm and grabbed her belly hair. At 10:19 KU to add further branches with her newborn KU7 clinging onto her belly (Online Resource 3). KU7 appeared wet and of dark grey colour and was carried on the mother's belly ventrally with the umbilical cord still attached but separated from the mother (Figure A3a). KU supported and kept KU7 close to her belly with one hand while adding branches (Figure A3b). KU7 was only intermittently visible due to his positioning on KU's belly while inside the nest. At 10:39 (roughly 30min after birth) we heard the first vocalisations produced by KU7. Although we could not see his face, the vocalisations did not appear to be in response to an external event and we did not observe any change KU's behaviour. At 10:43, KF moved slowly downward from the Ficus tree, joined KU in the nest, and saw KU7 for the first time at 10:44. He observed for a long time his mother in the nest sitting on the edge and seemed to be staring at KU7, though he did not react in any remarkable way or produce any vocalisations. At 10:54 KH joined them in the nest. Both KH and KF were staring at KU from different edges of the nest. KF was seen entering a few times. KF and KH looked calm, inquisitive, and never alarmed or aroused. At 11:22, KH and KF groomed each other and then played together close to the nest. They both moved back in the nest and KH produced a short scream after KU made a sudden movement and grunted at her. Both KH and KF moved a few meters away. It is possible that KH and KF made abrupt movement to the KU7, movements not tolerated by KU. At 11:44, KU was observed feeding on the placenta (Figure A3c, Online Resource 4). At 11:53 she was still feeding on the placenta and on part of the umbilical cord (Online Resource 5). She urinated once from the nest. KF and KH alternated grooming and playing outside of the nest. At 12:27 KU moved out of the nest, came down stopping at 2 different heights of the tree, and monitored the surroundings. She never appeared affected by our presence. We followed her and her offspring as they reached the ground from a distance. After approximately 100m they then entered under an area with impenetrable dense vegetation. They did not produce any sound for the rest of the day. We left the forest at 16:30. KU was seen again with KU7 on the 22nd of November (Figure A3d) and no unusual behaviour from other present chimpanzees was recorded that day since she joined a large group including all adult males. KU7 looked healthy and was sexed male but was not observed vocalising on that day.

15.1.2.3. Death

On the 26th of November, the first and second authors observed KU carrying the lifeless body of KU7. The corpse did not show any sign of aggression and looked as if he died within the previous 24h (personal observation). The next day, a strong smell emanated from the corpse. While carrying the dead infant, KU spent a great amount of time with the main group of adult males and was groomed by most, in particular by KT (her oldest son) and by the beta and alpha males. During this period both KH and KF followed their mother. KU was never observed grooming the dead body. When moving on the ground she carried the corpse in one hand and when climbing or moving in trees the corpse was placed in a sort of "pocket" formed by the fold of her inner leg. On the 27th, KU was seen without the dead infant. On the 1st of December all adult males except KT and ZL showed signs of arousal as she joined the group. Some adults mounted and kissed KU, and all of them except for KT inspected and sniffed her genitals. Most of the males proceeded to groom her extensively and regularly checked her genitals. Other males played and groomed with KF.

15.1.3. Discussion – Birth event

KU gave birth while adult males were feeding in her vicinity. This is at odds with females' tendency to isolate as parturition approaches, a strategy likely meant to prevent male infanticide (Nishie & Nakamura, 2018; Palombit, 2012), and even more odd considering that infanticide is an important risk in the Sonso community (Lowe et al., 2020). KU is a central Sonso female who has been subject of extensive sexual attention from males during the last oestrous before the pregnancy (personal observation). It is possible that males were particularly confused about paternity in her case, which resulted in the absence of infanticide when they encountered the newborn (e.g. Zamma and Shabani 2012).

The absence of responses from conspecifics was noteworthy considering that the vocalisations of the newborn were audible up to at least 30m away, within earshot of all individuals in the neighbouring tree, and potentially of certain males. This is particularly surprising given that chimpanzees are known to react strongly to unknown chimpanzee calls (Herbinger et al., 2009; Wilson et al., 2001) and the infanticide risk is higher in this community (Lowe et al., 2020). The mother did not attempt to stop the newborn from vocalising and did not move away as soon as the vocalisations were produced, even if a pant hoot vocalisation can inform receivers of the caller's location and identity (Fedurek, Zuberbühler, et al., 2016; Kojima et al., 2003). Only the offspring of KU approached and inspected the newborn (as in Goodall and Athumani 1980; Kiwede 2000) and did so after the first vocalisations were uttered. KU did not appear affected by the nearby research station or our presence. In addition, another female had been observed giving birth in the same tree close to camp (Kiwede, 2000). Thus, it is possible that researchers witnessed these extremely rare events because of how well habituated Sonso chimpanzees are.

15.2. Appendix 2 – Supplementary material for: Social and individual factors mediate chimpanzee vocal ontogeny

15.2.1. Study subjects

Table A10 List of all individuals from the Sonso community

ID	Sex	Age category start	Age category end	Year of birth
AC	F	Infant	Infant	2017
AN	F	Adult	Adult	1990
BC	F	Adult	†	1976
BG	F	Sub-adult	*	2004
CD	F	Young adult	Young adult	2003
DL	F	Young adult	Young adult	2002
DB	F	Infant	Infant	2018
DR	F	Sub-adult	Young adult	2004
ER	F	Infant	Infant	2019
EV	F	Sub-adult	Young adult	2004
FA	F	Sub-adult	Sub-adult	2006
FH	F	Juvenile	Juvenile	2013
FL	F	Adult	Adult	1979
FK	M	Young adult	Adult	1999
GF	M	Juvenile	Juvenile	2013
GH	F	Infant	Infant	2020
GL	F	Adult	Adult	1976
GR	F	Sub-adult	*	2006
HD	M	Infant	Infant	2017
HM	F	Juvenile	Juvenile	2013
HR	F	Juvenile	Sub-adult	2009
HT	F	Adult	Adult	1978
HW	M	Adult	Adult	1993
IN	F	Young adult	Adult	1999
IS	F	Infant	Infant	2017
JA	F	Infant	Infant	2018
JB	M	Juvenile	Juvenile	2011
JL	F	Adult	Adult	1990
JN	F	Adult	Adult	1984
JS	M	Sub-adult	Sub-adult	2006
KA	F	Adult	Adult	1998
KB	F	Sub-adult	*	2007
KC	M	Sub-adult	Sub-adult	2006
KH	F	Sub-adult	Sub-adult	2008
KF	M	Infant	Juvenile	2014
KG	F	Adult	Adult	1998

KJ	M	Juvenile	Juvenile	2013
KL	F	Adult	Adult	1979
KO	M	Infant	Juvenile	2014
KP	F	Sub-adult	*	2008
KQ	M	Infant	Infant	2016
KS	M	Sub-adult	Adult	2003
KT	M	Adult	Adult	1993
KU	F	Adult	Adult	1979
KV	M	Infant	Juvenile	2014
KW	F	Adult	Adult	1981
KX	F	Sub-adult	Sub-adult	2007
KY	F	Adult	Adult	1983
KZ	M	Adult	†	1995
MB	M	Juvenile	Sub-adult	2009
MI	F	Sub-adult	Sub-adult	2007
MK	F	Adult	Adult	1980
ML	F	Adult	Adult	1975
MS	M	Adult	Adult	1992
MZ	M	Infant	Infant	2015
NB	F	Adult	Adult	1962
OK	F	Adult	Adult	1996
OZ	M	Infant	Juvenile	2014
PS	M	Young adult	Adult	1998
RF	F	Sub-adult	Sub-adult	2007
RH	F	Adult	Adult	1965
RM	F	Young adult	Young adult	2002
RN	M	Infant	†	2018
RS	F	Adult	Adult	1997
RY	M	Infant	†	2013
SM	M	Adult	Adult	1993
SQ	M	Adult	†	1991
ST	F	Sub-adult	*	2007
TJ	F	Adult	Adult	1984
TW	F	Juvenile	Sub-adult	2010
UP	F	Adult	Adult	1999
ZD	M	Young adult	Young adult	2001
ZF	M	Adult	†	1982
ZL	M	Adult	Adult	1995

F: female; M: male. Study subjects are in bold.

† Subjects that died during the study period.

* (Potentially) emigrated females.

Table A11 List of study subjects

ID	Mother ID	Age (years)	Sex	Head movement	Vocal responses	Spontaneous pant hoots	Focal duration (h)	Gregariousness
DB	DL	1	F	11 (N = 24)	1 (N = 38)	0	11.3	18.39
GF	GL	6	M	13 (N = 22)	13 (N = 33)	1	10.0	6.87
HM	HT	6	F	16 (N = 34)	6 (N = 46)	0	13.9	10.75
HR	HT	9	F	9 (N = 12)	1 (N = 21)	0	8.5	10.75
IS	IN	1	F	14 (N = 47)	1 (N = 56)	0	15.4	18.26
JB	JL	8	M	20 (N = 45)	2 (N = 57)	0	21.2	5.60
KJ	KW	5	M	11 (N = 22)	2 (N = 31)	4	16.2	9.35
KO	KL	4	M	22 (N = 31)	4 (N = 42)	0	8.3	8.14
KQ	KA	3	M	17 (N = 38)	1 (N = 48)	1	11.7	20.69
MB	ML	9	M	30 (N = 36)	12 (N = 50)	3	20.1	8.66
MZ	ML	3	M	6 (N = 28)	3 (N = 36)	0	13.4	8.66
OZ	OK	4	M	23 (N = 47)	1 (N = 62)	0	14.1	15.81
TW	TJ	9	F	6 (N = 16)	4 (N = 34)	0	6.5	7.92
Total			F = 5 M = 8	198 (N = 402)	51 (N = 554)	9	170.6	

Age was calculated at the start of the study. M: male; F: female. We report the number of head movements and vocal responses recorded with, in brackets, the total number of occurrences.

Table A12 List of mature individuals

ID	Sex	Head movement	Vocal responses	Spontaneous pant hoots	Focal duration (h)	Gregariousness
DL	F	42 (N = 62)	8 (N = 86)	5	19.5	18.39
EV	F	36 (N = 40)	4 (N = 56)	5	9.2	13.39
FK	M	80 (N = 143)	38 (N = 182)	33	30.0	24.42
HT	F	25 (N = 46)	14 (N = 59)	1	14.6	10.75
HW	M	48 (N = 67)	8 (N = 84)	24	32.8	29.17
IN	F	66 (N = 99)	19 (N = 194)	4	17.8	18.26
JN	F	8 (N = 18)	9 (N = 36)	5	9.2	22.19
JS	M	58 (N = 98)	12 (N = 123)	17	27.0	19.11
KC	M	55 (N = 81)	13 (N = 109)	3	20.6	26.18
KH	F	23 (N = 28)	2 (N = 42)	1	8.7	5.82
KL	F	8 (N = 20)	1 (N = 28)	0	13.0	20.69
KS	M	24 (N = 40)	10 (N = 52)	6	13.7	16.34
KT	M	79 (N = 127)	25 (N = 146)	38	34.6	19.71
KW	F	0 (N = 2)	3 (N = 3)	1	10.0	9.35
KX	F	12 (N = 20)	2 (N = 36)	3	9.9	9.11
KZ	M	32 (N = 45)	6 (N = 56)	5	9.4	12.63
ML	F	21 (N = 35)	4 (N = 66)	6	11.8	8.66
MS	M	78 (N = 114)	22 (N = 147)	31	33.9	24.34
NB	F	18 (N = 36)	7 (N = 48)	3	13.3	24.10
OK	F	32 (N = 54)	15 (N =71)	0	12.3	15.81
PS	M	47 (N = 67)	8 (N = 95)	19	25.5	25.86
SM	M	44 (N = 63)	14 (N = 77)	6	29.0	19.93
SQ	M	9 (N = 22)	7 (N = 32)	4	11.2	13.38
ZD	M	51 (N = 65)	8 (N = 88)	13	14.8	15.93
ZL	M	75 (N = 107)	19 (N = 141)	25	20.1	19.02
Total	F = 12 M = 13	971 (N = 1499)	278 (N = 2057)	258	451.9	

F: female; M: male. We report the number of head movements and vocal responses recorded with, in brackets, the total number of occurrences.

15.2.2. Offspring's exposure to pant hoots

To investigate whether the offspring's exposure to pant hoots is related to the gregariousness level of mothers, we created a linear model where the dependent variable was the number of pant hoots heard per hour of focal following (mean 3.36 ± 0.91) by the immature individuals (Table A11). We included the gregariousness of the mother as independent variable, the age of the offspring (years), and the sex of the offspring as control variables. As for the head movement and vocal response models, we initially considered the interaction between age, sex, and gregariousness. There was no collinearity between the examined independent variables (maximum VIF value: 1.72).

Table A13 Relationship between the offspring's exposure to pant hoots and the investigated independent variables

Term	Estimate	SE	Lower CI	Upper CI	T-value	P
Intercept	0.429	0.417	-0.534	1.391		
Gregariousness	-1.061	0.662	-2.587	0.464		
Age of offspring	-0.681	0.375	-1.547	0.185	-1.814	0.107
Sex of offspring	-0.335	0.513	-1.517	0.847		
Gregariousness**Sex***	1.711	0.658	0.195	3.228	2.602	**0.032**

CI: confidence interval. Interaction is represented by an asterisk between variables. Control variables are in italic. Significant results are depicted in bold.

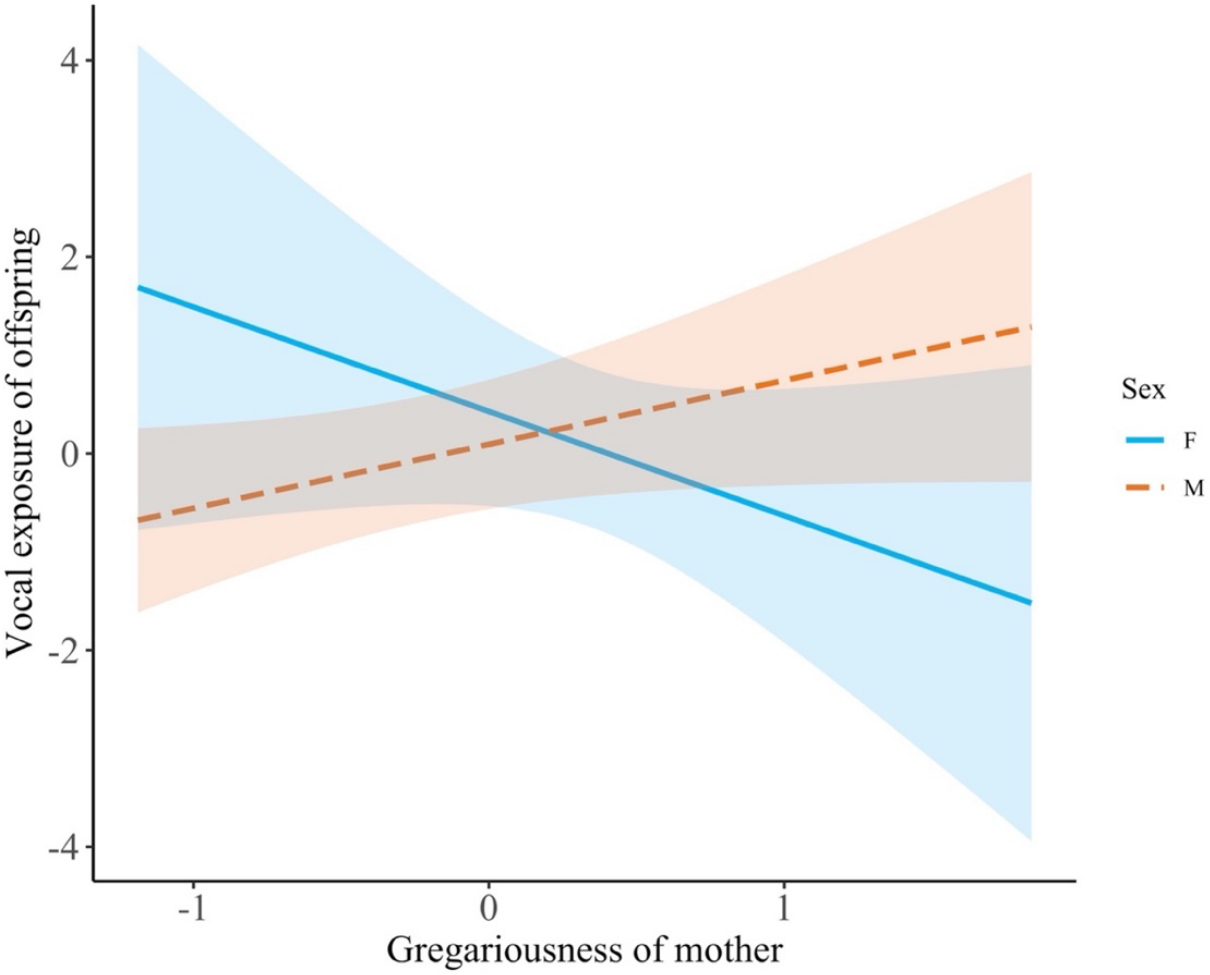

Figure A4 Vocal exposure to pant hoots of immature individuals depending on the gregariousness level of their mother (red: males, blue: females). The fitted model lines are presented with confidence bands for the fitted values based on standard errors (95%). Gregariousness and vocal exposure values are z-standardized.

Table A14 Relationship between whether or not mature or immature individuals moved their head towards a pant hoot and the investigated independent variables

Term	Estimate	SE	Lower CI	Upper CI	χ^2	Z-value	P
Intercept	0.524	0.246	0.212	1.010			
Age category	0.619	0.204	-0.080	0.633	7.592		**0.006**
Sex	0.279	0.178	-0.305	0.061	2.368		0.124
Gregariousness	-0.120	0.092	-0.567	-0.076	1.625		0.202
Call from within party	-0.326	0.124	-0.610	-0.212	6.767		**0.009**
Solo call	-0.412	0.099	0.212	1.010	17.179		**<0.001**
Number of females	-0.208	0.060	-0.324	-0.088	12.157		**<0.001**
Number of males	0.058	0.067	-0.081	0.190	0.748		0.387
Activity (feeding)	-0.317	0.120	-0.554	-0.079		-2.650	**0.008**
Activity (other)	-0.511	0.157	-0.829	-0.210		-3.248	**0.001**
Activity (social)	-1.257	0.165	-1.572	-0.921		-7.622	**<0.001**

CI: confidence interval. Control variables are in italic. Significant results are depicted in bold.

Table A15 Relationship between whether or not mature or immature individuals produced a vocal response to a pant hoot and the investigated independent variables

Term	Estimate	SE	Lower CI	Upper CI	χ^2	Z-value	P
Intercept	-2.821	0.319	-3.408	-2.127			
Age category	0.798	0.270	0.196	1.314	8.978		**0.003**
Sex	0.269	0.225	-0.188	0.716	1.410		0.235
Gregariousness	-0.082	0.116	-0.308	0.148	0.504		0.478
Call from within party	-0.242	0.163	-0.546	0.093	2.258		0.133
Solo call	-0.167	0.122	-0.405	0.073	1.876		0.171
Number of females	-0.266	0.084	-0.423	-0.091	10.756		**0.001**
Number of males	0.076	0.084	-0.086	0.247	0.814		0.367
Activity (feeding)	0.144	0.195	-0.230	0.547		0.736	0.462
Activity (other)	0.291	0.148	-0.004	0.576		1.966	**0.049**
Activity (social)	-0.219	0.251	-0.701	0.325		-0.875	0.382

CI: confidence interval. Control variables are in italic. Significant results are depicted in bold.

15.3. Appendix 3 – Supplementary material for: Audience sensitivity in chimpanzee display pant hoots

15.3.1. Study subjects

Table A16 List of all individuals from the Sonso community

ID	Sex	Age category start	Age category end	Year of birth
AC	F	Infant	Infant	2017
AN	F	Adult	Adult	1990
BC	F	Adult	†	1976
BG	F	Subadult	*	2004
CD	F	Young adult	Young adult	2003
DL	F	Young adult	Young adult	2002
DB	F	Infant	Infant	2018
DR	F	Subadult	Young adult	2004
ER	F	Infant	Infant	2019
EV	F	Subadult	Young adult	2004
FA	F	Subadult	Subadult	2006
FH	F	Juvenile	Juvenile	2013
FL	F	Adult	Adult	1979
FK	**M**	**Young adult**	**Adult**	**1999**
GF	M	Juvenile	Juvenile	2013
GH	F	Infant	Infant	2020
GL	F	Adult	Adult	1976
GR	F	Subadult	*	2006
HD	M	Infant	Infant	2017
HM	F	Juvenile	Juvenile	2013
HR	F	Juvenile	Subadult	2009
HT	F	Adult	Adult	1978
HW	**M**	**Adult**	**Adult**	**1993**
IN	F	Young adult	Adult	1999
IS	F	Infant	Infant	2017
JA	F	Infant	Infant	2018
JB	M	Juvenile	Juvenile	2011
JL	F	Adult	Adult	1990
JN	F	Adult	Adult	1984
JS	**M**	**Subadult**	**Subadult**	**2006**
KA	F	Adult	Adult	1998
KB	F	Subadult	*	2007
KC	**M**	**Subadult**	**Subadult**	**2006**
KH	F	Subadult	Subadult	2008
KF	M	Infant	Juvenile	2014
KG	F	Adult	Adult	1998

KJ	M	Juvenile	Juvenile	2013
KL	F	Adult	Adult	1979
KO	M	Infant	Juvenile	2014
KP	F	Subadult	*	2008
KQ	M	Infant	Infant	2016
KS	**M**	**Subadult**	**Adult**	**2003**
KT	**M**	**Adult**	**Adult**	**1993**
KU	F	Adult	Adult	1979
KV	M	Infant	Juvenile	2014
KW	F	Adult	Adult	1981
KX	F	Subadult	Subadult	2007
KY	F	Adult	Adult	1983
KZ	M	Adult	†	1995
MB	**M**	**Juvenile**	**Subadult**	**2009**
MI	F	Subadult	Subadult	2007
MK	F	Adult	Adult	1980
ML	F	Adult	Adult	1975
MS	**M**	**Adult**	**Adult**	**1992**
MZ	M	Infant	Infant	2015
NB	F	Adult	Adult	1962
OK	F	Adult	Adult	1996
OZ	M	Infant	Juvenile	2014
PS	**M**	**Young adult**	**Adult**	**1998**
RF	F	Subadult	Subadult	2007
RH	F	Adult	Adult	1965
RM	F	Young adult	Young adult	2002
RN	M	Infant	†	2018
RS	F	Adult	Adult	1997
RY	M	Infant	†	2013
SM	**M**	**Adult**	**Adult**	**1993**
SQ	M	Adult	†	1991
ST	F	Subadult	*	2007
TJ	F	Adult	Adult	1984
TW	F	Juvenile	Subadult	2010
UP	F	Adult	Adult	1999
ZD	**M**	**Young adult**	**Young adult**	**2001**
ZF	M	Adult	†	1982
ZL	**M**	**Adult**	**Adult**	**1995**

F: female; M: male. Study subjects are in bold.

†Subjects that died during the study period.

*(Potentially) emigrated females.

Table A17 List of study subjects with number of vocal, nonvocal and drum displays recorded

Individual	Age	Nonvocal displays	Vocal displays	Drum displays
Frank (FK)	19	48	24	15
Hawa (HW)	25	51	37	29
James (JS)	12	9	20	10
Klauce (KC)	12	10	1	5
Kasigwa (KS)	15	14	12	9
Kato (KT)	25	37	10	17
Mbotella (MB)	9	13	5	6
Musa (MS)	26	22	26	20
Pascal (PS)	20	20	19	18
Simon (SM)	25	21	10	11
Zed (ZD)	17	19	4	9
Zalu (ZL)	23	16	6	5
Total		280	174	154

Age (in years) was calculated at the beginning of the study.

Table A18 List of focal individuals with total focal duration (h) and number of separate focal following events

ID	Focal duration	Number of focal events
FK	30.0	12
HW	32.8	8
JS	27.0	7
KC	20.6	6
KS	13.7	6
KT	34.6	10
MB	20.1	7
MS	33.9	10
PS	25.5	10
SM	29.0	5
ZD	14.8	7
ZL	20.1	6
Total	302.1	94
Mean	25.2	8

15.3.2. Dominance distance

Table A19 Elo-ratings for each subject divided by three 6-month periods

ID	Period 1	Period 2	Period 3
FK	1797	1799	1920
HW	2150	2248	2200
JS	916	1107	1192
KC	860	927	961
KS	1173	1224	1087
KT	1408	1428	1452
MB	887	833	860
MS	1807	1943	1870
PS	1402	1397	1301
SM	1412	1549	1558
ZD	1228	1199	1191
ZL	1447	1508	1575

15.3.3. Preferred Social Partners Index

Long-term preferred social partners (PSP) were established using a modified social index from Gilby and Wrangham (2008) that was developed by Schel, Townsend, et al. (2013). Dyadic affiliative relationships were determined using a composite social index based on three different dyadic association measures for periods of 6 months (same as those used for dominance).

The first association measure is the simple ratio index (SRI), which represents the proportion of time that a dyad (chimpanzees ‘A’ and ‘B’) was observed in the same party:

$$SRI_{ab} = P_{ab} / (P_a + P_b - P_{ab})$$

where P_{ab} is the number of parties in which both A and B were together, while P_a is the number of parties in which A was present and P_b the number of parties containing B. The second association measure is based on nearest-neighbour data, which calculates the rate of spatial proximity between the focal individual (A) and another individual (B):

$$NN_{ab} = A_f B_g \text{ / focal duration A}$$

where $A_f B_g$ represents the number of 15 min scans in which A was the focal individual and B its nearest neighbour. The denominator is the total focal observation time of A. The third dyadic association measure is the grooming rate between the focal individual and another individual (B):

$\text{Grooming}_{ab} = A_f B_g$ / focal duration A

where $A_f B_g$ is the total duration of grooming between the focal individual A and another individual B. The direction of grooming was not considered, which means that receiving, giving and reciprocating grooming were all included. The denominator is the total focal time of A.

After each of the three measures was calculated for each individual, we divided it by the mean of the measures of all other dyads of individuals for a given period to standardize each value, following Gilby and Wrangham (2008). This was done to balance measures before combining them. We then combined the three measures in a composite friendship index (CFI) by averaging them together. For each individual, we calculated mean and standard deviation from all their dyadic composite friendship indexes. These were used to calculate standard z scores which better represent the magnitude and direction of a dyadic relationship and also control an individual's level of gregariousness to associate with others. The following score represents the strength of the bond between the focal individual and another individual relative to all his other bonds:

$(\text{CFI}_{ab}$ – mean $\text{CFI}_a)$ / SD of CFI_a

where CFI_{ab} is the friendship index between the focal individual A and another individual B. The mean CFI_a is obtained by averaging the CFI values between the focal individual A and all other individuals of the community. The denominator is the standard deviation of the CFI_a values. Finally, for each study subject the five highest-scoring individuals were considered preferred social partners (Table A5).

Table A20 List of the five highest scoring preferred social partners (PSP) for each study subject divided by the three 6-month periods

ID	Period	First PSP	Second PSP	Third PSP	Fourth PSP	Fifth PSP
FK	1	DL	HW	JN	SM	KZ
	2	JN	PS	HW	SM	OK
	3	HW	JN	KX	RS	MS
HW	1	MS	FK	ZF	SM	JN
	2	MS	KT	JS	ZL	PS
	3	MS	ZL	KT	PS	FK
JS	1	ZF	MS	HW	NB	KC
	2	SM	JN	HW	KT	DL
	3	JN	KX	KU	RS	MB
KC	1	KL	PS	NB	ZF	KZ
	2	KL	MS	IN	KS	HW
	3	KL	CD	PS	ZD	FK
KS	1	JL	HT	KU	KA	KG
	2	DR	EV	KU	KA	FK

	3	IN	OK	JN	CD	HW
KT	1	MS	OK	HW	HT	FK
	2	HW	FK	MS	EV	KC
	3	HW	RS	MS	OK	ZL
MB	1	HW	KZ	ZL	KC	ML
	2	ZD	KS	MS	ML	ZL
	3	ML	FK	PS	DL	HW
MS	1	NB	HW	PS	SQ	KU
	2	NB	HW	KC	FK	ZL
	3	NB	HW	PS	KT	ZL
PS	1	HW	MS	KC	KT	IN
	2	ZL	ZD	HW	FK	KS
	3	MS	KC	HW	SM	JN
SM	1	JN	HW	KT	SQ	NB
	2	HW	ZL	JN	ZD	MS
	3	HW	FK	KS	MS	KL
ZD	1	JN	FK	ZL	DL	KS
	2	ZL	SM	ST	KS	MS
	3	KU	JN	KX	ML	KT
ZL	1	HW	JN	MS	KT	ZF
	2	PS	ZD	MS	HW	DL
	3	HW	FK	MS	SM	ZD

15.3.4. Acoustic analyses

Table A21 Summary of the number of calls used for the acoustic analyses divided by individual, call type (Introduction, Build-up) and call structure (single = single calls, multi = multiphase pant hoots)

ID	Introduction single	Introduction multi	Build-up single	Build-up multi
FK	2	4	1	3
HW	2	4	5	10
JS	2	3	3	4
KT	1	3	1	3
PS	2	3	1	2
Total	9	17	11	22

Table A22 List of acoustic parameters used for the analyses for each phase

Acoustic parameter	Definition
Introduction phase	
F0 variation *	Mean variation in the F0 contour (Hz) divided by duration
% Time of max. intensity *	Percentage of the total element duration during which F0 was at its maximum
AM var	Mean variation per s of the intensity contour, calculated as the cumulative variation in amplitude divided by duration
AM rate	Number of complete cycles of amplitude modulation per second of intensity contour
Jitter *	Mean of absolute difference between frequencies of consecutive F0 periods divided by mean F0
Build-up phase	
Sound duration	Duration of the element (s)
F0 absolute slope *	The mean absolute slope of F0
Q75%	The frequency values at the upper limit of the third quartiles of energy, measured on a linear amplitude spectrum
% EFpeak	The percentage of the total duration where energy value of the frequency with the highest energy was maximum
Shimmer	The mean absolute difference between the amplitudes of consecutive F0 periods divided by the mean amplitude of F0

From Watson et al., 2018.

*Parameters that have been log-transformed to be normally distributed.

Table A23 List of possible phase combinations with number of observed cases (*N*)

Introduction	Build-up	Climax	Let-down	N
1	0	0	0	11
1	1	0	0	56
1	1	1	0	7
1	1	1	1	27
1	1	0	1	0
1	0	1	0	3
1	0	1	1	0
1	0	0	1	0
0	1	0	0	50
0	1	0	1	0
0	1	1	0	3
0	1	1	1	7
0	0	1	0	0
0	0	1	1	0
0	0	0	1	0
Total				164

15.3.4.1. Transition probabilities

We used transitional probabilities to model the sequences of possible states (i.e. pant hoot phases) derived from our sample, where the transition from one step to another is not dependent on the previous state. Probabilities were calculated by dividing the count for each transitional state by the total number of observations (Table A8). This model allowed us to predict transitions between phases including the start and the end of a sequence (Table A9), and to visualize transitions using an arc diagram (Figure 8).

Table A24 Matrix table of the transitional probabilities (%) between pant hoot phases

	Introduction (I)	Build-up (B)	Climax (C)	Let-down (L)	End (Z)
Onset (O)	63	37	0	0	0
Introduction (I)	0	55	2	0	7
Build-up (B)	0	0	27	0	65
Climax (C)	0	0	0	21	8
Let-down (L)	0	0	0	0	21

Each number represents the probability of change from one state to the next state, with the direction following the sequential order of pant hoot phases (I – B – C – L). For example, the probability that a pant hoot started with a build-up phase (O – B) was 37% (*N* = 60), and the probability that a pant hoot ended with a build-up phase (B – Z) was 65% (*N* = 106).

15.3.5. Pant hoot examples

In Figs A1-A5 we reduced the sampling frequency of the original recording from 44.1 kHz to 10 kHz to visualize a frequency resolution that makes the acoustic structure recognizable. Figures were extracted using Praat software (version 6.0.42, Boersma, 2001). We transformed calls with the Fourier function using a Hanning window function and 1024 time steps. Recordings of the calls are available as Supplementary material.

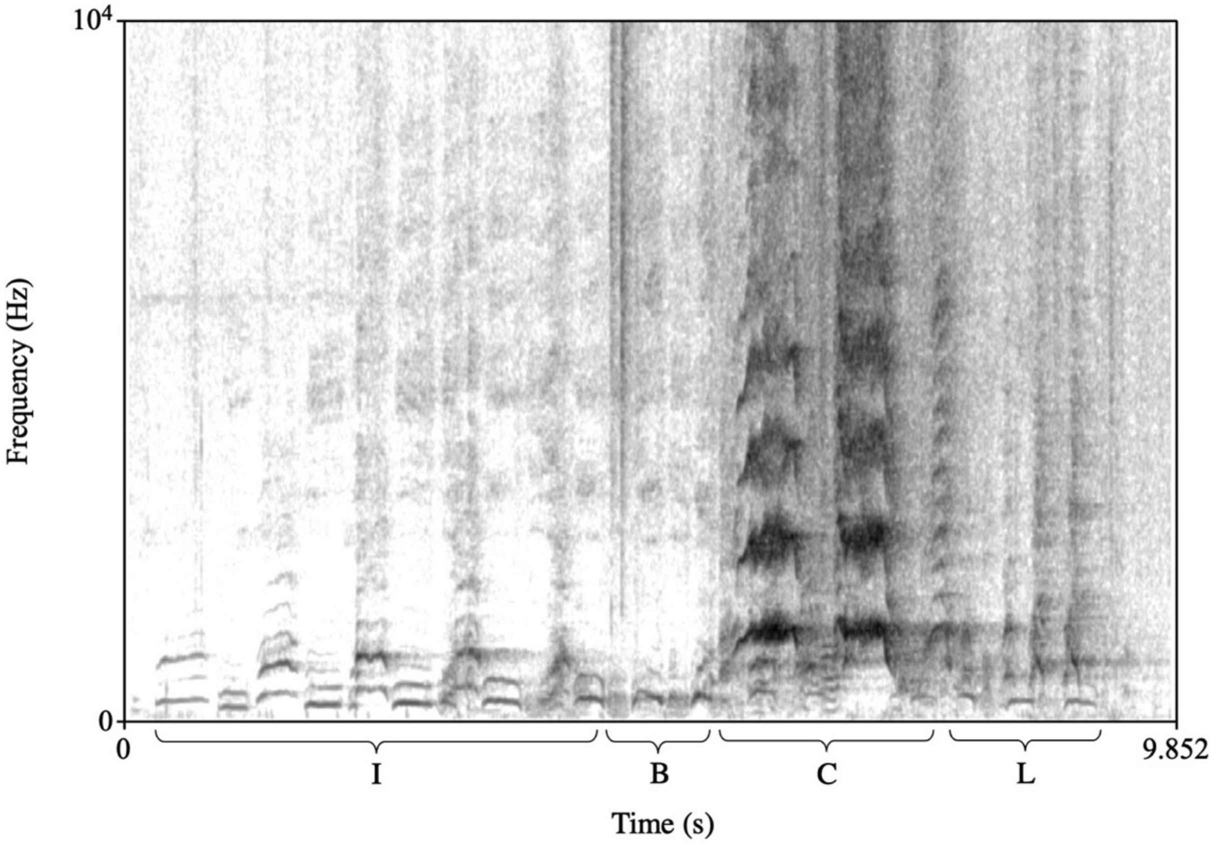

Figure A5 Acoustic spectrogram of a pant hoot produced by ZL during a display. The vocalization includes all four phases (I: Introduction, B: Build-up, C: Climax, L: Let-down).

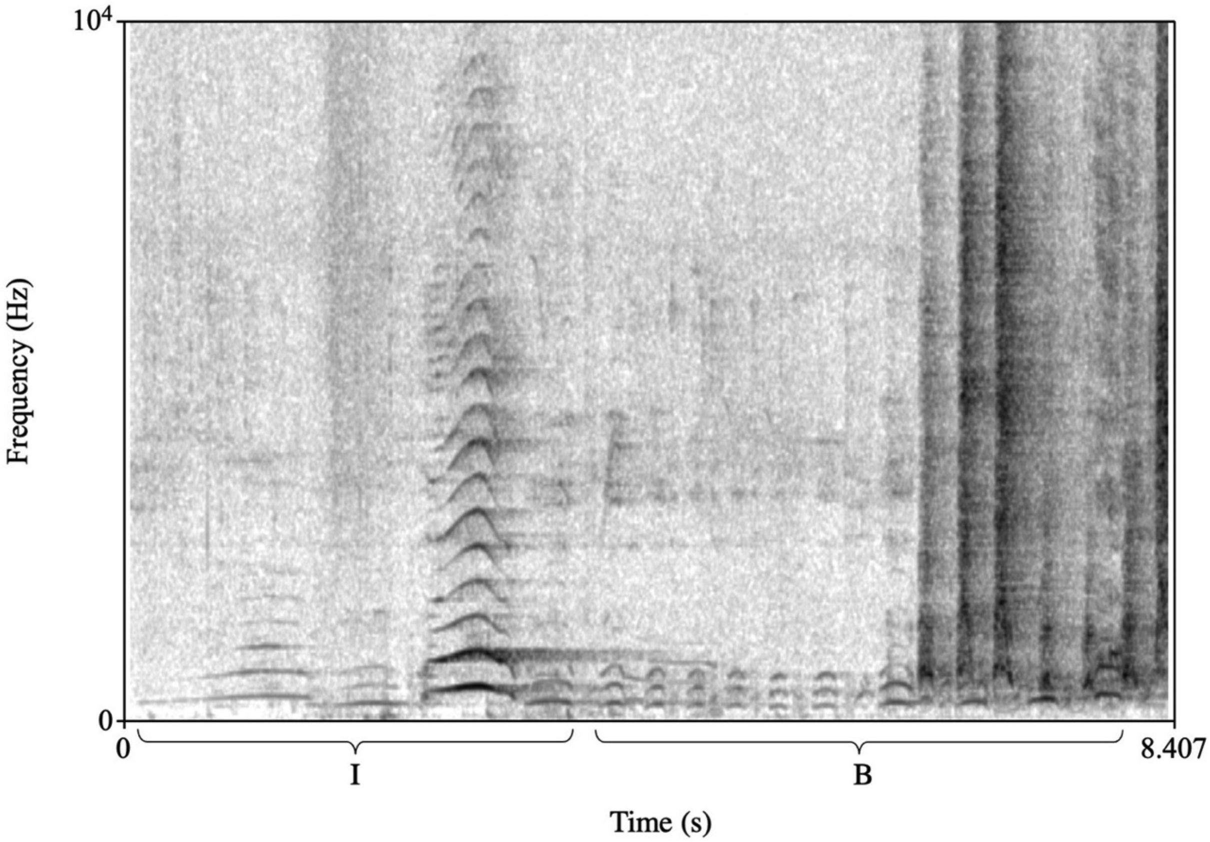

Figure A6 Acoustic spectrogram of a pant hoot produced by MS during a display. The vocalization includes two phases (I: Introduction, B: Build-up). Screams from the target audience of the display are co-occurring (higher pitch and amplitude) towards the end of the build-up.

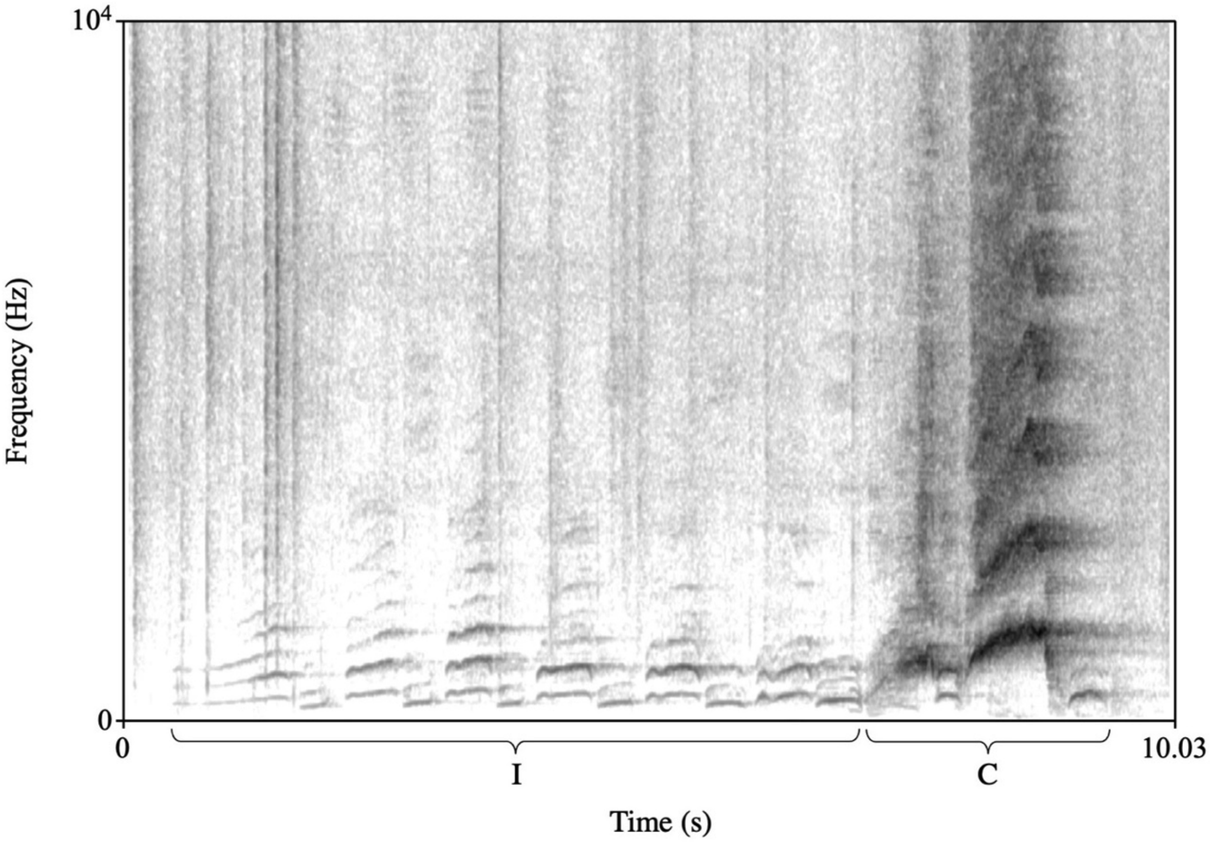

Figure A7 Acoustic spectrogram of a pant hoot produced by PS during a display. The vocalization includes two phases (I: Introduction, C: Climax).

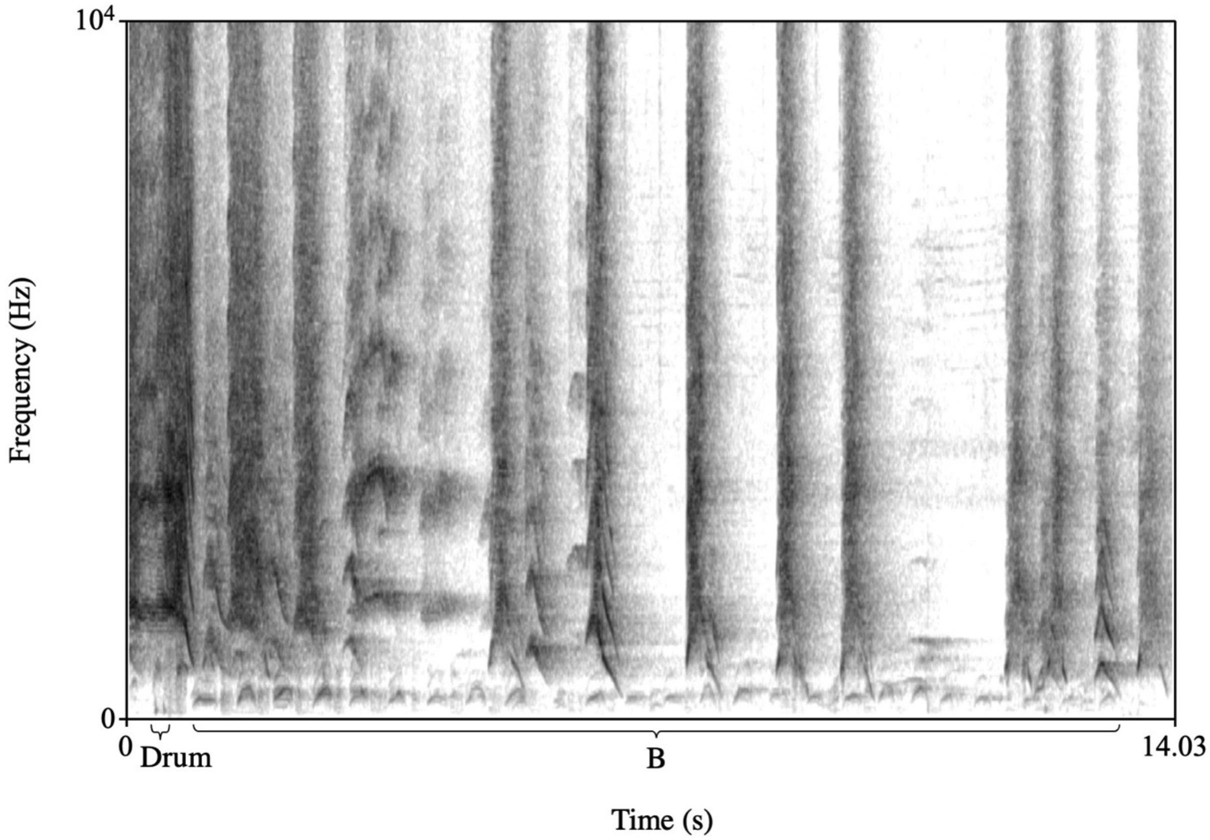

Figure A8 Acoustic spectrogram of pant hoot and drum display produced by MS. The vocalization includes one phase (B: Build-up) and drumming (Drum). Screams and barks from the target audience of the display are co-occurring (higher pitch and amplitude) throughout the call.

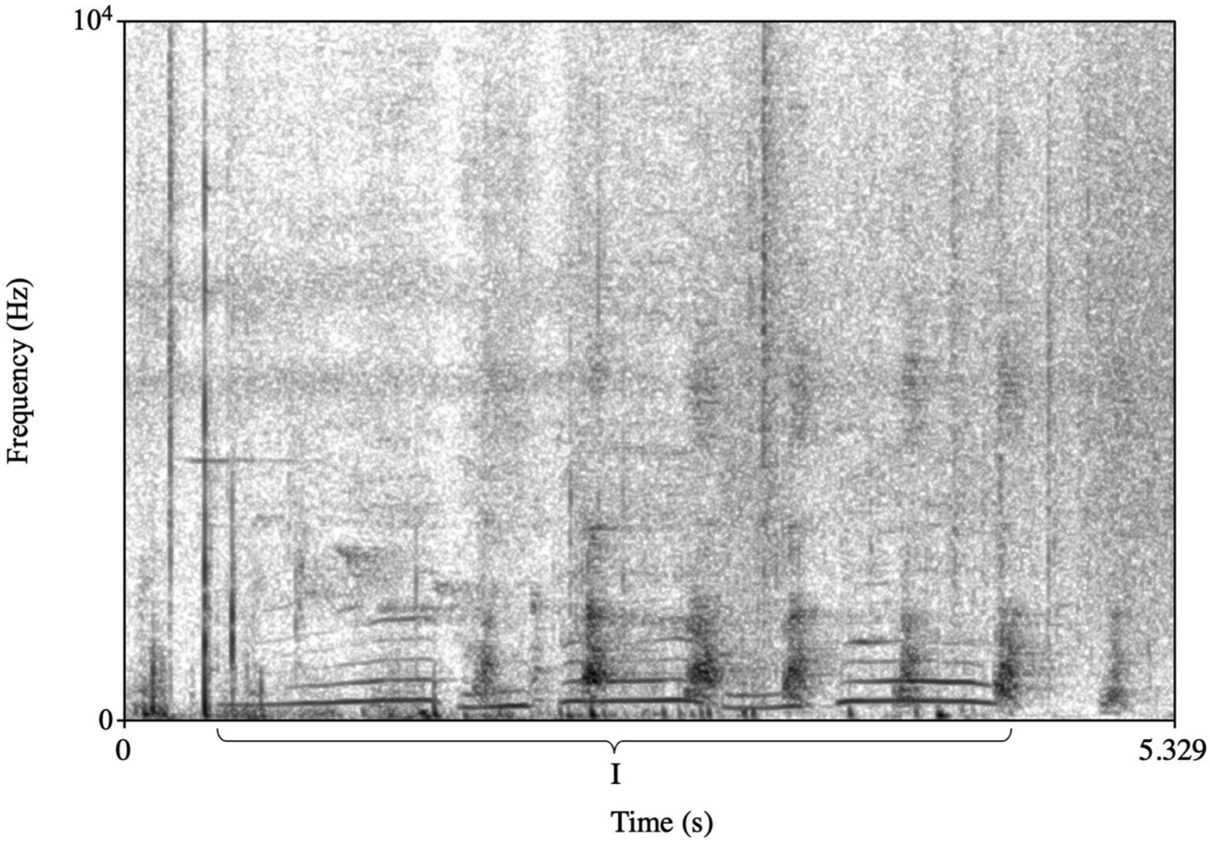

Figure A9 Acoustic spectrogram of a pant hoot produced by PS during a display. The vocalization includes one phase (I: Introduction). Pant grunts from the target audience of the display are co-occurring (noisy short call units) throughout the call.

15.4. Appendix 4 - Additional academic outputs

15.4.1. Ongoing research - Skin temperature changes in response to pant hoots

For my PhD thesis I initially planned to use infra-red thermography to collect observational data on the vocal behaviours of chimpanzees. However, the Covid-19 pandemic forced me to revisit my thesis empirical chapters during my second year of studies due to my reduced field time. For the first project I collected focal and opportunistic infra-red videos of adult chimpanzees resting or involved in social activities and noted all the surrounding social events, with a particular focus on the vocalisations heard by the subjects. The aim of the project was to investigate whether the vocalisations of socially relevant individuals, such as preferred social partners or dominant males, elicit faster or stronger arousal changes in receivers. As showed in Chapter 3, two most frequently observed responses are the movement of the head towards the source of a pant hoot or a vocal response. However, in approximately half of the instances mature receivers did not move the head and in five out six times they did not vocally responded after hearing the call. Giving that even in the absence of a visible response receivers can still process the information received, to better understand these "non-visible" responses I used non-invasive thermal imaging (Ioannou et al., 2014), where changes in skin temperature in specific body areas are linked to changes in arousal states. My hypothesis was that receivers underwent changes in their arousal state depending on the identity of the caller. For the second project I tested the same hypothesis by using playback experiments on isolated adult males. I exposed subjects to pant hoots from preferred and non-preferred social partners and recorded their responses with a thermal video camera. Because of the premature termination of my data collection period and overall challenges in finding isolated subjects for the experiments, I had to abandon the project. While both studies did not become empirical chapters in the thesis, I am currently using the data for Master students and future projects.

15.4.2. Ongoing research - Human listeners extract information from chimpanzee calls

Pant hoots are characterised by strong individual signatures and receivers are able to discern the identity of the caller. In addition, information such as the age, the social status, and the context of production are also encoded in the acoustic structure of pant hoots. Interestingly, some of this information is not accessible exclusively to chimpanzees. Based on personal communications with field researchers and anecdotes (e.g., Boesch, 1991), researchers and field assistants seem to be capable to identify callers that are out of sight and locate them in the forest, as well as potentially understand what callers are doing. However, whether humans can extract information reliably has not been investigated yet but is relevant for two main reasons. First, it would allow researchers to rely on the knowledge of field assistants or their own to collect additional behavioural data, particularly from the perspective of receivers. For instance, testing whether the identity of the caller is relevant for receivers and affects their subsequence behavioural and vocal responses. In addition, researchers would value the expertise of field assistants, which has been overlooked but critical in the field of primatology. Second, it would help us to better understand if and how humans might learn to extract information from the vocalisations of our closest living relatives. For this study, I asked field assistants (n = 6) and researchers during my data collection period (n = 4) to listen to pant hoot vocalisations that I recorded in the field and answer a series of question. In the first questionnaire, participants had to write the identity, the sex and the age category of the caller, as well as the presence of the climax phase and of drumming. In the second questionnaire, using new recordings, participants had to identify the identity, the sex and the age category of the caller, as well as the context of production. In order to provide a control group of human listeners who have not been exposed to chimpanzee vocalisations, I repeated the same experiment using an online questionnaire open to the public. I am currently analysing the data, however, preliminary results suggest that the skills of field assistants improve as they accumulate experience with the chimpanzees and are very reliable at discerning male and female callers as well as recognising the presence of climax and drum components, with the most experienced research assistant being able to also recognise the majority of adult callers. Researchers, who typically rely on their field assistants to locate chimpanzees, do not seem as skilled when it comes to identify the caller or other traits. Thus, human listeners seem to be able to extract information from chimpanzee pant hoots and improve on this ability thanks to greater exposure to their vocalisations.

15.4.3. Co-supervision of Master students

During my time at the University of Neuchâtel I co-supervised the research projects of three biology Master students together with Prof. Klaus Zuberbühler. During May 2018 – June 2020 I co-supervised Claire Barrault's thesis titled "Skin thermal changes in wild chimpanzees during threatening contexts and upon hearing neighbouring communities". Claire's thesis received a very good final grade (5.25/6). In addition to directly supervising and training Claire on the use of infrared thermography, I helped with the design of the study, the coding and extraction of thermal data from images, the statistical analyses, and the writing of the thesis and manuscript. Using infrared thermography during social feeding contexts, we showed that chimpanzees' nose skin temperatures are lower when they consume meat as compared to figs, consistent with the idea that feeding on more contested resources can be more stressful and dangerous. In addition, we found that their nose temperatures were affected by the audience composition, with lower temperatures during meat feeding associated with the presence of larger groups of males or of more dominant males in the proximity, and higher temperatures during fig feeding in the presence of more social partners. Thus, chimpanzees monitor and are affected by their surrounding social environment, which can be revealed by using new non-invasive methods even in the absence of 'visible' behaviours and responses. The output of this research has been published in *Philosophical Transactions of the Royal Society B: Biological Sciences* as:

Claire, B.*, Soldati, A.*, Hobaiter, C., Stephen, M., De Moor, D., Zuberbühler, K.*, Dezecache, G.* (2022). Thermal imaging reveals social monitoring during social feeding in wild chimpanzees. doi.org/10.1098/rtsb.2021.0302

During July 2019 – January 2021 I co-supervised Marion De Vevey's thesis titled "Investigation of the influence of social environment on wild male chimpanzees' emotions using infrared thermal imaging". Marion's thesis received the maximum grade (6/6). In addition to directly supervising her data collection, I helped with the design of the study, the coding and extraction of thermal data from images, the statistical analyses, and with the writing of the thesis and manuscript. We found that chimpanzees involved in competitive events had lower nose skin temperatures, which are typically associated with increased stress levels, whereas those involved in cooperative events had higher temperatures. In addition, we found that the presence of the alpha male reduced nose skin temperatures during cooperative events, whereas the presence of females increased the nose skin temperatures during competitive events. We showed that chimpanzees perceive social events depending on their cooperative and competitive nature and that these perceptions are modulated by audience effects. The output of this research has been published in *Scientific Reports* as:

De Vevey, M., Bouchard A., Soldati, A., Zuberbühler, K. (2022). Thermal imaging reveals audience-dependent effects during cooperation and competition in wild chimpanzees. doi.org/10.1038/s41598-022-07003-y

During October 2018 – July 2019 I co-supervised Lotus Emam's thesis titled "Social behaviours and transmission of tool-use among wild chimpanzees". Lotus successfully defended her work during an oral examination and her thesis was evaluated as good (16.3/20). I directly supervised her data collection, helped with the study design, statistical analyses, and writing of the thesis. We investigated the use of hand dominance across social and feeding contexts and showed that chimpanzees used the right hand more often during feeding behaviours and the left hand during grooming behaviours. We found that the use of the right hand is associated with goal-oriented actions, while the use of the left hand is associated with social events, in line with human cognitive processes.

15.4.4. Teaching

During my PhD, I taught two academic courses at the University of Neuchâtel for biology Bachelor students. During January - May 2019 I taught the APP3 Comparative Cognition course. I followed the students during a 2-week field course at the Budongo Conservation Field Station (Uganda). The students developed small research projects on the behaviour of animal species of the Budongo forest (e.g. bats, army ants, chimpanzees) and collected data. During September - October 2021 I taught a practical course (TP) in Ethology at University of Neuchâtel. This was a 6-week theoretical and practical course on animal behaviour. The students developed small research projects on animal behaviour with data collection at the Zoo of Basel.

15.4.5. External research projects

During my PhD, in addition to the work that I presented in the three empirical chapters, I collaborated on several projects on chimpanzee behaviours and communication, both vocal and gestural. In all of the following studies, unless specified otherwise, I contributed with data that I collected in the field, I was involved in the writing of the original manuscript and during the revisions, and I provided feedback on the design of the study. In the first study, we investigated whether drumming signals are individually distinctive, like pant hoots, and whether their usage is mediated by the audience composition. We found that the signaller's identity is encoded during traveling but not display contexts, suggesting a strategic inclusion or omission of information depending on the activity of the signaller. When chimpanzee travel, drumming is flexibly used as a long-distance acoustic signal to maintain contact by informing others about the identity and location of the signaller. When chimpanzees display, drumming is mostly used as a short-distance signal lacking signaller's identity to reduce competition and aggression from potential eavesdroppers. This study has been published in Animal Behaviour as:

Eleuteri, V., Henderson, M., Soldati, A., Badihi, G., Zuberbühler, K., & Hobaiter, C. (2022). The form and function of chimpanzee buttress-drumming. 10.1016/j.anbehav.2022.07.013

I also led a research project on a rare behavioural response of chimpanzee mothers to the death of their infants, typically referred to as 'dead infant carrying'. We used 40 years of combined long term data from two communities and three observations of particularly prolonged dead-infant carrying instances to evaluate current hypotheses. We also provided new evidence of potential 'substitute' object carrying after a mother carried her dead infant for almost three months. Our observations suggest that mothers are not unaware that their infants are dead but continue to carry them likely due to the strong maternal bond they share and potentially as a coping mechanism. The study has been published in Primates as:

Soldati, A., Fedurek, P., Crockford, C., Adue, S., Akankwasa, J. W., Asiimwe, C., Asua, J., Atayo, G., Chandia, B., Freymann, E., Fryns, C., Muhumuza G., Taylor, D., Zuberbühler, K., Hobaiter, C (2022). Dead infant carrying by chimpanzee mothers in the Budongo Forest. 10.1007/s10329-022-00999-x

Finally, I collaborated on a replication study on the use of referential gestures across different communities. We investigated whether 'big loud scratches' (BLS) gestures, which have been previously claimed to be referential (Pika & Mitani, 2006), are also used in this manner in four chimpanzee communities. We found that only in the site of the original study chimpanzees are more likely to receive grooming in the desired body part after using the BLS gesture. Instead, in another community the same signal is used to initiate, reengage, and request grooming. Our findings suggest a flexible use of this gesture depending on the social context. The study has been published in *Animal Behaviour* as:

Wilke, C.*, Lahiff, N. J.*, Badihi, G., Donnellan, E., Hobaiter, C., Machanda, Z., Mundry, R., Pika, S., Soldati, A., Wrangham, R., Zuberbühler, K., Slocombe, K.E. (2022) Referential gestures are not ubiquitous in wild chimpanzees: alternative functions for exaggerated loud scratch gestures. 10.1016/j.anbehav.2022.04.007

15.4.6. Public outreach

Here follows a list of online media outlets that covered some of the research articles I have published as co-author and first author during my PhD.

Thermal imaging reveals social monitoring during social feeding in wild chimpanzees

Soldati, A.*, Claire, B.*, Hobaiter, C., Stephen, M., De Moor, D., Zuberbühler, K.*, Dezecache, G.* (2022). *Philosophical Transactions of the Royal Society B: Biological Sciences*. doi.org/10.1098/rtsb.2021.0302

https://www.snf.ch/en/kemje0YHDY63AqKc/news/arguing-over-meat-finding-comfort-with-friends-the-emotions-of-the-great-apes

https://phys.org/news/2022-09-meat-comfort-friends-emotions-great.html

https://tabbed.info/science/details/29557/Chimpanzees-The-Emotions-of-the-Great-Apes

https://vejaonlline.com/the-feelings-of-the-good-apes/

https://www.theblog101.com/the-emotions-of-the-great-apes/

https://www.presseportal.ch/de/pm/100002863/100895714

Thermal imaging reveals audience-dependent effects during cooperation and competition in wild chimpanzees

De Vevey, M., Bouchard A., Soldati, A., Zuberbühler, K. (2022). *Scientific Reports*. 10.1038/s41598-022-07003-y

https://le-o.ch/2022/03/02/singes-mis-a-nus-a-la-camera-thermique/

https://www.unine.ch/unine/home/pour-les-medias/communiques-de-presse/les-emotions-des-chimpanzes-capt.html

https://pages.rts.ch/la-1ere/programmes/cqfd/17-05-2022

https://www.20min.ch/fr/story/des-cameras-thermiques-de-lunine-devoilent-les-emotions-des-primates-267035537758

https://www.lessentiel.lu/fr/story/touchez-le-nez-du-singe-pour-savoir-ce-qu-il-ressent-594102389742

The form and function of chimpanzee buttress-drumming

Eleuteri, V., Henderson, M., Soldati, A., Badihi, G., Zuberbühler, K., & Hobaiter, C. (2022). *Animal Behaviour*. 10.1016/j.anbehav.2022.07.013

https://www.thetimes.co.uk/article/the-times-view-on-chimpanzee-rhythms-drum-solo-9w073f8cj

https://www.bbc.com/news/science-environment-62809420

https://www.sciencetimes.com/articles/39790/20220907/chimpanzees-use-drumming-beats-communicate-each-even-when-kilometers-apart.html

https://www.dailymail.co.uk/sciencetech/article-11184843/Chimps-individual-drum-beats-send-messages-friends.html?ns_mchannel=rss&ns_campaign=1490&ito=1490

https://www.smithsonianmag.com/smart-news/chimpanzees-play-their-own-signature-drumbeats-to-stay-in-touch-180980727/

https://ukprimenews.com/science/chimps-have-individual-drum-beats-to-send-messages-to-their-friends/

https://dailynewsera.com/2022/09/06/chimps-have-individual-drum-beats-to-send-messages-to-their-friends/

https://newscinema.in/chimps-have-individual-drum-beats-to-send-messages-to-their-friends https://articlesecretstoday.com/chimps-have-individual-drum-beats-to-send-messages-to-their-friends/

https://techsardar.com/chimpanzees-drum-to-their-very-own-signature-beats/

https://businessmagazine24.com/chimps-show-off-their-signature-drum-beats/

https://jordantimes.com/news/features/roots-rock-chimpanzees-drum-their-own-signature-beats

https://www.rfi.fr/en/science-environment/20220906-roots-rock-chimpanzees-drum-to-their-own-signature-beats

https://www.ecowatch.com/chimpanzees-drumming-signatures.html

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Dead infant carrying by chimpanzee mothers in the Budongo Forest
Soldati, A., Fedurek, P., Crockford, C., Adue, S., Akankwasa, J. W., Asiimwe, C., Asua, J., Atayo, G., Chandia, B., Freymann, E., Fryns, C., Muhumuza G., Taylor, D., Zuberbühler, K., Hobaiter, C. (2022). Primates. 10.1007/s10329-022-00999-x

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https://www.miragenews.com/chimpanzee-mothers-may-grieve-loss-of-their-818501/

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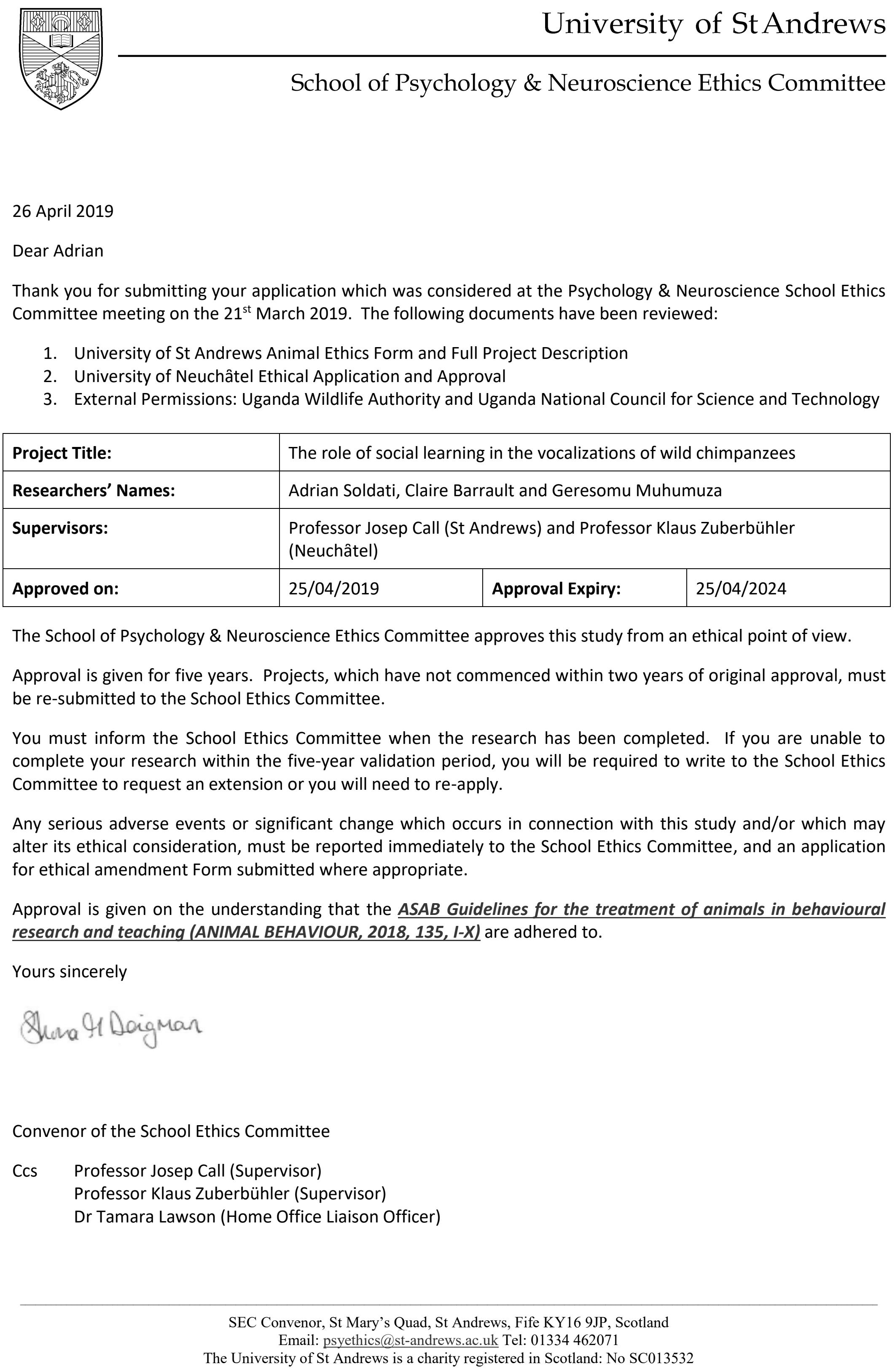
https://vervetimes.com/chimpanzee-mothers-may-grieve-loss-of-their-young/

15.5. Appendix 5 - Ethical approvals

15.5.1. University of St Andrews



University of St Andrews

School of Psychology & Neuroscience Ethics Committee

26 April 2019

Dear Adrian

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 21st March 2019. The following documents have been reviewed:

1. University of St Andrews Animal Ethics Form and Full Project Description
2. University of Neuchâtel Ethical Application and Approval
3. External Permissions: Uganda Wildlife Authority and Uganda National Council for Science and Technology

Project Title:	The role of social learning in the vocalizations of wild chimpanzees		
Researchers' Names:	Adrian Soldati, Claire Barrault and Geresomu Muhumuza		
Supervisors:	Professor Josep Call (St Andrews) and Professor Klaus Zuberbühler (Neuchâtel)		
Approved on:	25/04/2019	**Approval Expiry:**	25/04/2024

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for five years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five-year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an application for ethical amendment Form submitted where appropriate.

Approval is given on the understanding that the ***ASAB Guidelines for the treatment of animals in behavioural research and teaching (ANIMAL BEHAVIOUR, 2018, 135, I-X)*** are adhered to.

Yours sincerely

Shona H Doigman

Convenor of the School Ethics Committee

Ccs Professor Josep Call (Supervisor)
Professor Klaus Zuberbühler (Supervisor)
Dr Tamara Lawson (Home Office Liaison Officer)

SEC Convenor, St Mary's Quad, St Andrews, Fife KY16 9JP, Scotland
Email: psyethics@st-andrews.ac.uk Tel: 01334 462071
The University of St Andrews is a charity registered in Scotland: No SC013532

University of St Andrews | FOUNDED 1413

University Teaching and Research Ethics Committee

30 May 2019

Dear Adrian

Thank you for submitting your ethical application which was considered at the School of Psychology & Neuroscience Ethics Committee meeting on <*date*>; the following documents have been reviewed:

1. Ethical Application Form
2. Study Protocol
3. Participant Information Sheet
4. Participant Information and Consent Sheet
5. Questionnaire
6. Copy of linked University of St Andrews Animal Ethics application (approved: 25/04/2019)
7. External Permissions Documentation: Uganda National Council for Science and Technology, Uganda Wildlife Authority, University of Neuchâtel Ethical Application and Approval

The School of Psychology & Neuroscience Ethics Committee has been delegated to act on behalf of the University Teaching and Research Ethics Committee (UTREC) and has granted this application ethical approval. The particulars relating to the approved project are as follows -

Approval Code:	PS14304	Approved on:	27/05/2019	Approval Expiry:	27/05/2024
Project Title:	The role of social learning in the vocalizations of wild chimpanzees				
Researcher:	Adrian Soldati				
Supervisors:	Professor Josep Call (St Andrews) and Professor Klaus Zuberbühler (Neuchâtel)				

Approval is awarded for five years. Projects which have not commenced within two years of approval must be re-submitted for review by your School Ethics Committee. If you are unable to complete your research within the five year approval period, you are required to write to your School Ethics Committee Convener to request a discretionary extension of no greater than 6 months or to re-apply if directed to do so, and you should inform your School Ethics Committee when your project reaches completion.

If you make any changes to the project outlined in your approved ethical application form, you should inform your supervisor and seek advice on the ethical implications of those changes from the School Ethics Convener who may advise you to complete and submit an ethical amendment form for review.

Any adverse incident which occurs during the course of conducting your research must be reported immediately to the School Ethics Committee who will advise you on the appropriate action to be taken.

Cont.

School of Psychology & Neuroscience, St Mary's Quad, South Street, St Andrews, Fife KY16 9JP
Email: psyethics@st-andrews.ac.uk Tel: 01334 462071

University of St Andrews | FOUNDED 1413

School of Psychology & Neuroscience Ethics Committee

07 August 2020

Dear Adrian

Thank you for submitting your ethical amendment application.

The School of School of Psychology & Neuroscience Ethics Committee has approved this ethical amendment application:

Original Approval Code:	PS14304	**Original Approval Date:**	27/05/2019
Amendment Approval Date:	31/07/2020	**Approval Expiry Date:**	27/05/2024
Project Title:	The role of social learning in the vocalizations of wild chimpanzees		
Researcher:	Adrian Soldati	**Supervisor/PI:**	Professor Josep Call and Professor Klaus Zuberbuhler
School/Unit:	School of Psychology & Neuroscience		

The following supporting documents are also acknowledged and approved:

1. Participant Information Sheet and Consent Form

This approval does not extend the originally granted approval period. If you require an extension to the approval period, you can write to your School Ethics Committee who may grant a discretionary extension of no greater than 6 months. For longer extensions, or for any further changes, you must submit an additional ethical amendment application. For all extensions, you should inform the School Ethics Committee when your study is complete.

You must report any serious adverse events, or significant changes not covered by this approval, related to this study immediately to the School Ethics Committee.

Approval is given on the following conditions:

- that you conduct your research in line with:
    - the details provided in your ethical amendment application (and the original ethical application where still relevant)
    - the University's Principles of Good Research Conduct
    - the conditions of any funding associated with your work

Cont.

15.5.2. University of Neuchâtel

UNIVERSITÉ DE
NEUCHÂTEL

Commission d'éthique
de la recherche

Fbg de l'Hôpital 41
CH-2000 Neuchâtel

Neuchâtel, 26.02.2019

Monsieur Adrian Soldati
Université de Neuchâtel
Institut de Biologie
Rue Emile-Argand 11
2000 Neuchâtel

Re: "The role of social learning in the vocalizations of wild chimpanzees" – Revised research project assessment (ref. number. 38/2019-B)

Dear Mr Soldati,

We would like to thank you for your response sent on February 18, 2019 following our first evaluation of your research project. We also took into consideration the updated consent form, the rationale of the questionnaire part of the study as requested, and the updated version of the assessment and information form.

We took good note of your clarifications regarding which part of the project was supposed to receive ethical approval.

The questionnaire and description of the study look correct in accordance with the remarks we have made. For the part involving human participants, our opinion is that its main aim is to obtain experts' opinion on pant hoot of chimpanzees rather than conducting a research of which subjects would be those experts. This activity should be considered as a job and for this, they deserve, as suggested, a fair compensation according to SA laws.

According to the new documents submitted, we confirm that, in our opinion, there are no ethical objections to your research.

Please do not hesitate to contact me should you have any questions regarding the comments.

Yours truly,

Dominique Sprumont
Président de la commission d'éthique de la recherche de l'Université de Neuchâtel

Appendices

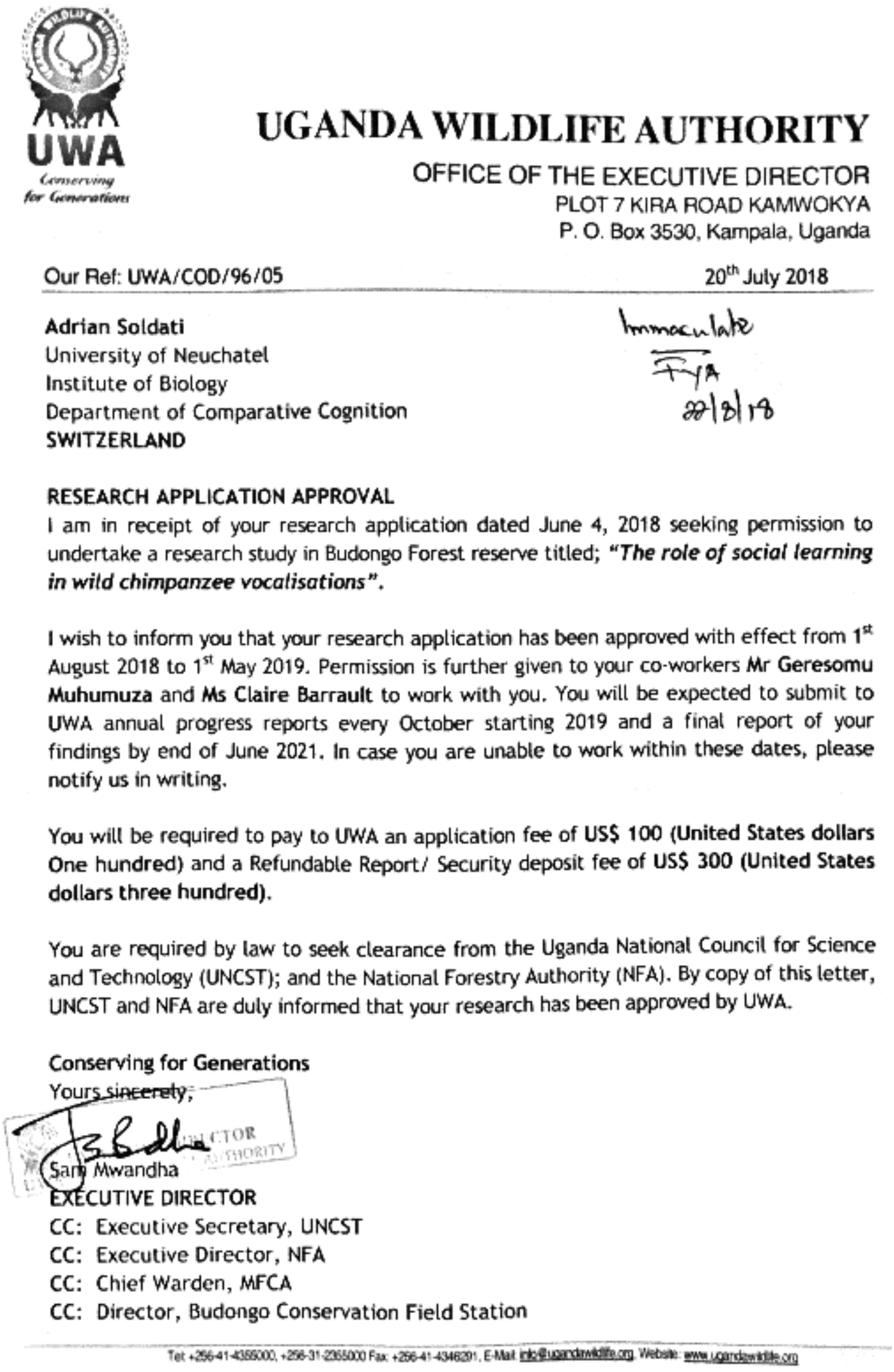
- CER assessment and information request, project 38 /2019-B

UNIVERSITÉ DE NEUCHÂTEL

**Commission d'éthique de la recherche
de l'Université de Neuchâtel**
Fbg de l'Hôpital 41
CH-2000 Neuchâtel
Tél : +41 (0)32 718 29 04
commission.ethique@unine.ch

www.unine.ch/unine/home/recherche/commission-ethique.html

15.5.3. Ugandan Wildlife Authority



UGANDA WILDLIFE AUTHORITY
OFFICE OF THE EXECUTIVE DIRECTOR
PLOT 7 KIRA ROAD KAMWOKYA
P. O. Box 3530, Kampala, Uganda

Our Ref: UWA/COD/96/05
20th July 2018

Immaculate
FYA
22/8/18

Adrian Soldati
University of Neuchatel
Institute of Biology
Department of Comparative Cognition
SWITZERLAND

RESEARCH APPLICATION APPROVAL

I am in receipt of your research application dated June 4, 2018 seeking permission to undertake a research study in Budongo Forest reserve titled; ***"The role of social learning in wild chimpanzee vocalisations".***

I wish to inform you that your research application has been approved with effect from **1st** August 2018 to 1st May 2019. Permission is further given to your co-workers **Mr Geresomu Muhumuza** and **Ms Claire Barrault** to work with you. You will be expected to submit to UWA annual progress reports every October starting 2019 and a final report of your findings by end of June 2021. In case you are unable to work within these dates, please notify us in writing.

You will be required to pay to UWA an application fee of **US$ 100 (United States dollars One hundred)** and a Refundable Report/ Security deposit fee of **US$ 300 (United States dollars three hundred).**

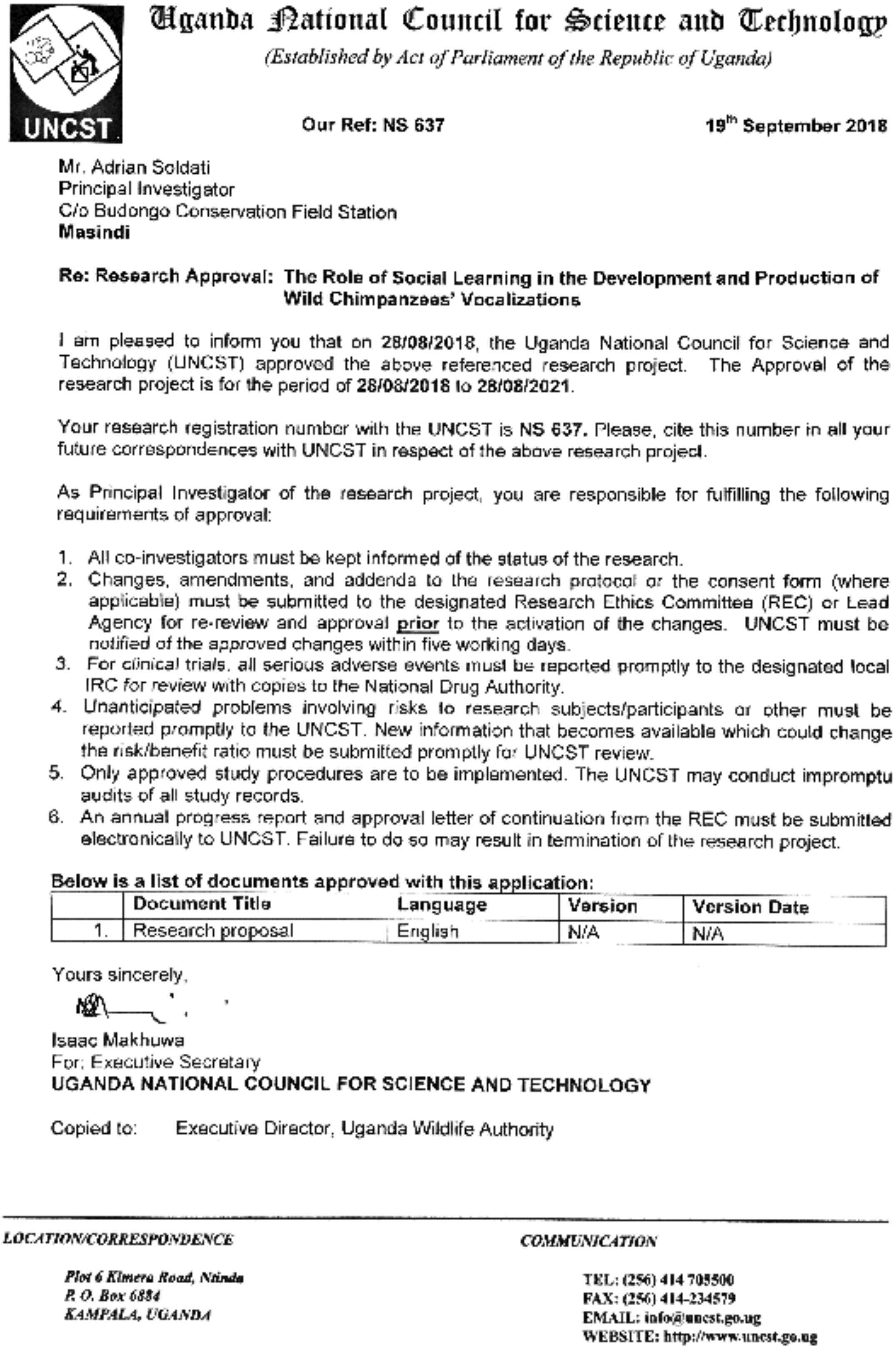
You are required by law to seek clearance from the Uganda National Council for Science and Technology (UNCST); and the National Forestry Authority (NFA). By copy of this letter, UNCST and NFA are duly informed that your research has been approved by UWA.

Conserving for Generations
Yours sincerely,

Sam Mwandha
EXECUTIVE DIRECTOR
CC: Executive Secretary, UNCST
CC: Executive Director, NFA
CC: Chief Warden, MFCA
CC: Director, Budongo Conservation Field Station

Tel: +256-41-4355000, +256-31-2355000 Fax: +256-41-4346291, E-Mail: info@ugandawildlife.org. Website: www.ugandawildlife.org

15.5.4. Ugandan National Council for Science and Technology



Uganda National Council for Science and Technology
(Established by Act of Parliament of the Republic of Uganda)
UNCST

Our Ref: NS 637 **19th September 2018**

Mr. Adrian Soldati
Principal Investigator
C/o Budongo Conservation Field Station
Masindi

Re: Research Approval: The Role of Social Learning in the Development and Production of Wild Chimpanzees' Vocalizations

I am pleased to inform you that on **28/08/2018**, the Uganda National Council for Science and Technology (UNCST) approved the above referenced research project. The Approval of the research project is for the period of **28/08/2018 to 28/08/2021**.

Your research registration number with the UNCST is **NS 637.** Please, cite this number in all your future correspondences with UNCST in respect of the above research project.

As Principal Investigator of the research project, you are responsible for fulfilling the following requirements of approval:

1. All co-investigators must be kept informed of the status of the research.
2. Changes, amendments, and addenda to the research protocol or the consent form (where applicable) must be submitted to the designated Research Ethics Committee (REC) or Lead Agency for re-review and approval **prior** to the activation of the changes. UNCST must be notified of the approved changes within five working days.
3. For clinical trials, all serious adverse events must be reported promptly to the designated local IRC for review with copies to the National Drug Authority.
4. Unanticipated problems involving risks to research subjects/participants or other must be reported promptly to the UNCST. New information that becomes available which could change the risk/benefit ratio must be submitted promptly for UNCST review.
5. Only approved study procedures are to be implemented. The UNCST may conduct impromptu audits of all study records.
6. An annual progress report and approval letter of continuation from the REC must be submitted electronically to UNCST. Failure to do so may result in termination of the research project.

Below is a list of documents approved with this application:

	Document Title	Language	Version	Version Date
1.	Research proposal	English	N/A	N/A

Yours sincerely,

Isaac Makhuwa
For: Executive Secretary
UGANDA NATIONAL COUNCIL FOR SCIENCE AND TECHNOLOGY

Copied to: Executive Director, Uganda Wildlife Authority

LOCATION/CORRESPONDENCE

Plot 6 Kimera Road, Ntinda
P. O. Box 6884
KAMPALA, UGANDA

COMMUNICATION

TEL: (256) 414 705500
FAX: (256) 414-234579
EMAIL: info@uncst.go.ug
WEBSITE: http://www.uncst.go.ug

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