MEANING AND FUNCTION OF WILD OLIVE BABOONS, *PAPIO ANUBIS*, COMMUNICATION

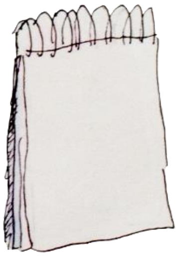
For the degree of PhD in Biology

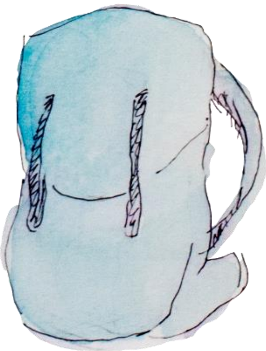
By Yaëlle Bouquet
Institute of biology
University of Neuchâtel

Thesis defended the 21rst of September 2018

Prof. Klaus Zuberbühler, University of Neuchâtel - Supervisor
Prof. Redouan Bshary, University of Neuchâtel - Internal examiner
Prof. Stuart Semple, University of Roehampton - External examiner
Dr Eloïse Déaux, University of Neuchâtel – Internal Examiner

UNIVERSITÉ DE
NEUCHÂTEL





UNIVERSITÉ DE
NEUCHÂTEL

Faculté des Sciences
Secrétariat-décanat de Faculté
Rue Emile-Argand 11
2000 Neuchâtel – Suisse
Tél : + 41 (0)32 718 21 00
E-mail : secretariat.sciences@unine.ch

IMPRIMATUR POUR THESE DE DOCTORAT

La Faculté des sciences de l'Université de Neuchâtel autorise l'impression de la présente thèse soutenue par

Madame Yaëlle BOUQUET

Titre:

“Meaning and function of wild olive baboons, *Papio anubis,* communication”

sur le rapport des membres du jury composé comme suit:

- Prof. Klaus Zuberbühler, directeur de thèse, Université de Neuchâtel, Suisse
- Prof. Redouan Bshary, Université de Neuchâtel, Suisse
- Prof. Stuart Semple, University of Roehampton, United Kingdom
- Dr Eloïse Déaux, Université de Neuchâtel, Suisse

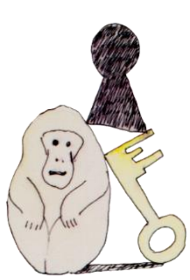
Neuchâtel, le 22 novembre 2018

Le Doyen, Prof. P. Felber

P. Fel

A mes merveilleux grands-parents:

Grand-maman,
Collet,
Paul
et Majijo



Résumé

Cette thèse examine deux vocalisations produites par les babouins olives, les cris de copulation et les grognements sociaux. Dans la première partie de ma recherche, j'ai analysé la fonction des cris de copulation à la fois en termes de leur paterne de production et de leur structure acoustique. Dans la deuxième partie, je me suis intéressée aux grognements sociaux émis par les femelles en investiguant leur fonction et leur mécanisme de production.

Les cris de copulation sont relativement communs chez les primates. Acoustiquement, ce sont souvent des vocalisations bruyantes et rythmiques, émises durant ou juste après une monte. Plusieurs hypothèses ont été proposées pour déterminer la fonction de cette vocalisation, y compris la compétition spermatique, le choix de la femelle et la compétition mâle-mâle. Cependant, malgré beaucoup de travail empirique, la fonction des cris de copulation est encore largement débattue.

Une autre vocalisation intéressante est le grognement. Ces cris sont tonals, harmoniques, individuellement distincts et émis durant les interactions sociales rapprochées. Ils ont été minutieusement étudié chez les babouins chacmas, une espèce étroitement apparentée aux babouins olives. Ces recherches ont brossé un tableau détaillé des mécanismes permettant leur production ainsi que leur fonction. Le principal but de cette étude était d'investiguer le rôle des grognements sociaux chez les babouins olives afin de tirer des conclusions plus générales sur le rôle de telles vocalisations durant les interactions sociales et sur la cognition des primates.

Ma recherche sur les babouins olives sauvages a été effectuée sur deux sites : A Gashaka Gumti National Park au Nigéria et au Kibale National Park en Ouganda. Dans trois études distinctes, j'ai premièrement examiné la fonction de la production des cris de copulation. J'ai construit différents modèles selon trois hypothèses fonctionnelles : La compétition spermatique, le choix de la femelle et la compétition mâle-mâle. En utilisant une approche fondée sur la théorie de l'information, les modèles ont été testés les uns par rapport aux autres et classés en fonction de leur probabilité de concordance par rapport aux données.

Dans une deuxième étude, j'ai examiné la variation dans la structure acoustique temporelle des cris de copulation, en utilisant à nouveau l'inférence multi-modèle. J'ai effectué deux séries d'analyses. Dans la première série, j'ai redéployé les modèles utilisés dans la première étude mais, cette fois, en se concentrant sur la structure acoustique des cris de copulation comme variable dépendante. Dans la deuxième série, j'ai peaufiné les modèles en ajoutant les différents antécédents d'accouplement des femelles.

Dans la dernière étude, j'ai examiné différentes variables dyadiques (la dominance relative ou la force des liens) afin d'investiguer sur quelles caractéristiques de leur relation les femelles babouins comptent quand elles émettent des grognements. J'ai également examiné si les grognements facilitaient les interactions sociales amicales et la manipulation de jeunes enfants.

J'ai trouvé que la compétition spermatique était l'explication la plus probable pour la production des cris de copulation. Il y a quelques évidences en faveur du choix de la femelle tandis que la compétition mâle-mâle semble peu probable. Concernant la structure acoustique des cris de copulation, j'ai trouvé que la compétition spermatique était la meilleure explication pour une caractéristique temporelle, le nombre d'éléments produits lors de la vocalisation. A nouveau, j'ai aussi trouvé quelques évidences pour l'hypothèse du choix de la femelle en considérant la durée moyenne des inter-éléments comme variable dépendante. Quand les antécédents copulatoires des femelles ont été ajouté aux modèles, toutes les trois hypothèses fonctionnelles ont reçu du soutien, ce qui suggère que les femelles peuvent, en plus de la compétition spermatique, suivre des stratégies d'accouplement socialement plus complexes. Finalement, j'ai trouvé qu'aucun des modèles testés ne prédisaient la production des grognements. Cependant, la présence ou l'absence de jeunes enfants change le classement relatif des modèles de dominance et d'amitié. Quand des enfants sont présents, le modèle d'amitié se classe en premier, alors que quand les enfants sont absents, c'est le modèle de dominance. J'ai finalement démontré que les grognements en soi ne facilitaient pas la manipulation des enfants ni les interactions sociales ultérieures, ce qui suggère que cette vocalisation est déployée afin de réguler les interactions sociales dont l'issue pourrait être incertaine.

Globalement, ma recherche montre que les femelles babouins olives semblent utiliser la compétition spermatique comme stratégie d'accouplement. Cependant, j'ai trouvé quelques évidences en faveur des autres hypothèses, ce qui suggère que les cris de copulation pourraient être multifonctionnels. Concernant les grognements sociaux, j'ai trouvé que la présence ou l'absence de jeunes enfants avait une influence sur comment les femelles babouins émettaient leurs grognements. Comme conclusion générale, ces découvertes démontrent que, bien que les cris de copulation et les grognements sociaux sont des vocalisations acoustiquement simples, leur production est certainement sous un contrôle cognitif considérable, puisque ces vocalisations sont produites de manière flexible afin de maximiser les bénéfices des interlocuteurs dans des environnements sociaux-écologiques en constant changement.

Mots-clés: Cris de copulation, grognements sociaux, inférence multimodale, théorie de l'information, hypothèse de la compétition spermatique, hypothèse du choix de la femelle, hypothèse de la compétition mâle-mâle, babouins olives, communication

General abstract

The thesis examines two vocalizations uttered by olive baboons, copulation calls and social grunts. In the first part of my study, I analysed the function of copulation calls both in terms of their production pattern and in terms of their acoustic structure. In the second part, I focussed on the social grunts given by females, investigating their function and mechanism of production.

Copulation calls are relatively common in primates. Acoustically, they are often loud, rhythmic vocalizations given before, during or just after a mount. Several hypotheses have been proposed for the function of this vocalization, including sperm competition, female choice and male-male competition. However, despite much empirical work, the function of copulation calls is still much debated.

Other interesting call given during close-range social interactions, are the tonal, harmonic and individually distinct grunts. This vocalisation has been thoroughly investigated in chacma baboons, a closely related species of olive baboons, which has produced a detailed picture of the mechanisms underlying their production as well as their function. The main goal in this study was to investigate the role of grunts in olive baboons, to draw more general conclusions about the role of such vocalisations in primate social interactions and cognition.

My research on wild olive baboons was carried out at two field sites, in Gashaka Gumti National Park, Nigeria and in Kibale National Park, Uganda. In three separate studies, I first investigated the function of copulation call production. I built different models according to three functional hypotheses: sperm competition, female choice and male-male competition. Using an information theoretic approach, the models were tested against each other and ranked according to their likelihood to fit the data.

In a second study, I investigated the variation in the temporal acoustic structure of copulation calls, again using multi-model inference. I conducted two sets of analyses. In a first set, I redeployed the models developed in the first study but this time focussing on the copulation calls' acoustic structure as the dependent variable. In a second set, I refined the models by additionally taking into account the different females' mating histories.

In the final study, I evaluated different combinations of dyadic variables (i.e. relative dominance or bonds strength) to investigate what relationship features female baboons relied on when they utter their grunts during approaches. I further examined whether grunts facilitated friendly social interactions and infant handling.

I found that sperm competition was the most likely explanation for the production of copulation calls. There was some evidence for female choice while male-male competition seemed very unlikely. Considering the acoustic structure of copulation calls, I found that sperm competition was the best explanation for one temporal feature, the number of elements produced during calling. Again, I also found partial support for the female choice hypothesis when considering the mean duration of inter elements, an acoustically salient structural feature, as the dependent variable. When the females' copulatory history was added to the models, all three functional hypotheses received some support, suggesting that females can, in addition to sperm competition, additionally follow socially more complex mating strategies. Finally, I found that none of the tested models predicted grunts production. However, the presence or absence of young infants changed the relative ranking of the friendship and dominance models. With infants present, the friendship model ranked top, whereas in the absence of infants, it was the dominance model. I finally demonstrated that grunting by itself did not facilitate infant handling or subsequent friendly interactions, suggesting that this call is deployed to regulate social interactions whose outcome may be unclear.

Overall, my research shows that female olive baboons seem to employ sperm competition as a mating strategy. However, I found some support for the other functional hypotheses, which suggests that copulation calls could be multifunctional. For the social grunts, I found that the presence or absence of infants has an influence on how female baboons utter their grunts. As a general conclusion, these findings demonstrate that, although that copulation calls and grunts are acoustically simple vocalizations, their production is most likely under considerable cognitive control as calls are uttered in flexible ways to maximise the callers' benefits in ever changing socio-ecological environments.

Keywords: Copulation calls, social grunts, multimodel inference, information theory, sperm competition hypothesis, female choice hypothesis, male-male competition hypothesis, olive baboons, *Papio anubis*, communication

Table of contents

1 General introduction 1

1.1.1 The costs of group living 1

1.1.2 Dominance as counter strategy 1

1.1.3 Social bonds as counter strategy 2

1.1.4 Social communication 2

1.2 Why do primates produce signals during mating? 3

1.2.1 Sexual signals 3

1.2.2 Copulation Calls 3

1.2.3 Functional hypotheses of copulation calls 4

1.2.4 Female choice, sperm competition, male-male competition hypotheses 6

1.2.5 Multifunctional female copulation calls? 6

1.3 Why do primates produce signals during encounters? 7

1.3.1 Close-range social signals 7

1.3.2 Social grunts in baboons 7

1.3.3 Grunts to facilitate friendly interactions 8

1.3.4 Grunts to facilitate infant handling 8

1.3.5 Dominance and social bonds as drivers of grunt production 9

2 General methods 11

2.1.1 Study species 11

2.1.2 Sexual behaviour 12

2.1.3 Friendship 13

2.1.4 Communication 13

2.1.5 Study sites 14

2.1.6 Data analyses 15

3 Research questions 17

4 Comparing functions of copulation calls in wild olive baboons (*Papio anubis*) using multi-model inference 19

4.1 Abstract 20

4.2 Introduction.. 21

4.2.1 The male-male competition hypothesis.. 21

4.2.2 The sperm competition hypothesis... 22

4.2.3 The female choice hypothesis 23

4.3 Material and Method 24

4.3.1 Study site and subjects... 24

4.3.2 Data collection... 24

4.3.3 Behavioural analyses 26

4.3.4 Model formulation and statistical analysis 26

4.4 Results 29

4.4.1 Multi model inference.. 29

4.5 Discussion 30

4.6 Acknowledgements... 34

4.7 Appendix... 35

5 Wild female olive baboon, *Papio anubis*, modify the acoustic structure of copulation calls to maximise reproductive success...................................37

5.1 Abstract 38

5.2 Introduction.. 39

5.2.1 The sperm competition hypothesis... 39

5.2.2 The female choice hypothesis 39

5.2.3 The male-male competition hypothesis.. 40

5.2.4 Copulation calling in olive baboon females... 40

5.3 Materials and method 42

5.3.1 Study site and subjects... 42

5.3.2 Data collection... 42

5.3.3 Dominance hierarchy ... 42
5.3.4 Friendship ... 43
5.3.5 Sexual interactions ... 43
5.3.6 Acoustic analyses ... 43
5.3.7 Models and statistical analyses ... 44
5.4 Results ... 47
5.4.1 Analysis 1: Basic functional models ... 47
5.4.2 Analysis 2: Extended models ... 47
5.5 Discussion ... 50
5.5.1 Sperm competition as an evolutionary driver of primate vocal behaviour ... 50
5.5.2 Copulation calls multifunctional ... 52
5.5.3 Conclusions ... 53
5.6 Supplementary material ... 54
6 Causes and consequences of wild female olive baboons, *Papio anubis*, grunting calls ... 67
6.1 Abstract ... 68
6.2 Introduction ... 69
6.3 Materials and method ... 71
6.3.1 Study site and subjects ... 71
6.3.2 Data collection ... 71
6.3.3 Behavioural analyses ... 71
6.3.4 Models and statistical analyses ... 72
6.3.5 Analysis overview ... 72
6.3.6 Causes of grunt production ... 73
6.3.7 Consequences of grunt production ... 74
6.4 Results ... 76
6.4.1 Causes of grunt production ... 77
6.4.2 Consequences of grunt production ... 78

6.5 Discussion ... 82

6.5.1 Consequences of grunt production ... 82

6.5.2 Conclusions ... 83

6.6 Appendix ... 85

7 General discussion ... 91

7.1 Summary of findings ... 91

7.2 Sperm competition ... 92

7.3 Flexibility ... 93

7.4 Simple signals ... 94

7.5 Limitations and perspectives ... 95

7.5.1 Methodological considerations ... 95

7.5.2 Future research ... 95

7.6 Conclusions ... 97

8 General acknowledgments ... 99

9 Bibliography ... 101

1 General introduction

1.1.1 The costs of group living

In almost all primate societies, individuals spend most of their life interacting with other group members. However, individuals differ in terms of their age, reproductive state and competitive abilities, suggesting that group living may have different impacts on different individuals. With regards to reproduction, living in a group with several males and females facilitates finding mating partners but also increases intra and intersexual competition (Robinson, 1982). For instance, in Taï forest, Ivory Coast, alpha male chimpanzees, *Pan troglodytes verus*, have a reproductive success of 67% of all the mating but only if few other male competitors are in the group. If the number of competitors increases, the alpha male mating success drops to 38% (Boesch, Kohou, Néné, & Vigilant, 2006), highlighting the costs of group living for some group members but not others. Similarly, living in a group generally facilitates the location and defence of food resources but it also increases competition for food access within the group. For example, lower ranking female black spider monkeys, *Ateles chamek*, are routinely excluded from food patches, and this can have a severe impact on their reproduction (Symington, 1988). Group living is also beneficial in defence against predation, mainly because vigilance costs can be shared with other group members and this can lead to an increase in the probability of detecting predators early (Roberts, 1996). But at the same time living in groups also increase visibility and exposure to some predators, especially if they hunt by ambush (Zuberbühler & Jenny, 2002). Finally, living in close proximity to others will lead to diseases and parasites spreading more efficiently among individuals (Møller, Dufva, & Allander, 1993).

1.1.2 Dominance as counter strategy

A general finding in group living animals is that individuals try to minimise the costs of group living by developing different coping strategies to optimize their survival and fitness. One way to benefit from group living, while keeping the costs down, is to strive for dominance over other group members. High social rank offers a range of advantages in terms of access to mates, food and grooming partners, which have all have documented fitness benefits. Cowlishaw and Dunbar (Cowlishaw & Dunbar, 1991), for example, demonstrated that there is a positive relation between rank and mating success. For instance, female olive baboons prefer to mate with young, immigrant but high-ranking males, presumably to optimize the chance that these males will in the future care for and protect their offspring (Bercovitch, 1991). Similarly, high-ranking female chacma baboons, *Papio ursinus*, live longer (Silk et al., 2010), have shorter inter-birth intervals and their offspring grow faster than subordinates females (Cheney et al., 2004; Johnson, 2003). Dominant individuals also have greater access to food than subordinates, in almost any species studied. For example, dominant female long-tailed macaques, *Macaca fascicularis*, have higher food intakes than subordinates, while their offspring have lower mortality rates (van Noordwijk & van Schaik, 1987). Dominant female chimpanzees in Taï Forest have better access to monopolisable foods than lower-ranking individuals (Wittig & Boesch, 2003), which is likely to have fitness effects. In a meta-analysis, Schino (2001) showed that higher-ranking individuals receive more grooming than lower-ranking ones, presumably because they are more valuable as allies in future agonistic interactions.

1.1.3 Social bonds as counter strategy

Another strategy visible in some species is that individuals seek to develop personalised relationships with each other, as a way to optimise some of the cost/benefits of living in a group. Studies showed that female chacma baboons that are more integrated socially experience lower glucocorticoid levels and seem able to overcome social stressors better than other females (Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008; Wittig et al., 2008). Similarly, female chacma baboons with strong bonds are more protected from social conflicts and therefore feed more efficiently than others (Silk, Alberts, & Altmann, 2003). Furthermore, female chacma baboons who form strong and stable bonds have a higher survival rate and their offspring live longer than those with only weak relationships, independently of rank (Silk, Alberts, et al., 2003; Silk et al., 2009, 2010). Similarly, both male and female olive baboons develop "friendships" (see below) where males protect females and their infants from aggression by other group members (Smuts, 1985).

1.1.4 Social communication

Vocal communication is one of the mechanisms by which individuals can mediate their social interactions and deal with social life. Most vocalizations are given during agonistic, friendly or sexual interactions, during feeding or predation events, or during group movement. For instance, when encountering a predator, some primate species utter alarm calls, either to alert conspecifics or to deter the predator. A classic early study demonstrated that vervet monkeys, *Chlorecebus aethiops*, give three acoustically distinct alarm calls to three different predators. They elicit different escape response from the other group members, i.e., running in a tree for leopard alarm calls, descending to the ground for eagle alarm calls and standing bipedal for snake alarm calls (Seyfarth, Cheney, & Marler, 1980). While feeding or when discovering food, some primate species give acoustically distinct food calls. It has been argued that these calls serve to attract group members (e.g. Chapman & Lefebvre, 1990; Gros-Louis, 2004). Several suggestions have been made to explain the fitness benefits of this behaviour, either to attract mates, potential coalition partners (Krunkelsven, Dupain, Van Elsacker, & Verheyen, 1996) or kin (Hauser, 1993) in order to decrease predation risk through increased shared vigilance (Elgar, 1986) or to announce ownership to decrease risk of punishment from conspecifics (Hauser & Marler, 1993). Primates can also use vocalizations to initiate or coordinate group movements. For example, white-face capuchins, *Cebus capucinus*, utter trills to initiate troop movement towards a specific direction as visibility in tropical forests is low (Boinski & Campbell, 1995). Screams are an example of vocalization given during agonistic interactions. They are usually uttered by victims of the conflict and seem to function either to repel opponents due to the chaotic acoustic structures of this vocalization (Owren & Rendall, 2001) or to recruit more powerful individuals than the aggressor from the audience (Slocombe & Zuberbühler, 2007).

Although primate vocal repertoires appear to be relatively fixed and species-specific, primates have considerable control over how often to produce calls (Cheney & Seyfarth, 2018). For instance, female vervet monkeys utter more alarm calls in the presence of kin than when they are with non-related individuals (Cheney & Seyfarth, 1985). Red-bellied tamarins, *Saguinus labiatus*, emit food calls at higher rates when group members are out of sight than when they are present, suggesting a possible recruitment function (Caine, Addington, & Windfelder, 1995). Male Thomas langurs, *Presbytis thomasis*, give alarm calls only if a conspecific is present (Wich & Sterck, 2003). Townsend et al. (Townsend & Zuberbühler, 2009; Townsend, Deschner, & Zuberbühler, 2008) demonstrated that female chimpanzees take into account the surrounding audience composition while uttering copulation calls (i.e. audience effect). Females refrain from giving these vocalizations if higher-ranking females are in the nearby audience. Competition between females is high in chimpanzees. Consequently, uttering copulation calls strategically could be a way to prevent such competition.

Living in groups has important fitness consequences both in terms of increased benefits through cooperation among individuals and costs due to competition between individuals. Vocal communication is one mechanism that has evolved to allow primates to counterbalance these costs and to navigate through social life. In this thesis, we focus on two specific vocalizations: (1) Copulation calls that help animals dealing with reproduction and (2) close range social grunts that mitigate social competition.

1.2 Why do primates produce signals during mating?

1.2.1 Sexual signals

During their breeding cycle, female primates can produce a variety of signals, which appear under strong sexual selection (Andersson, 1994). These signals can be visual, such as the sexual swellings in primates, where females perineal skin changes in colour, size, turgidity and shape (Rowell, 1972). These exaggerated anogenital signals are found in Old World monkeys and in multifemale, multimale groups where females mate promiscuously (Maestripieri & Roney, 2005). Swollen females advertise their receptivity to the surrounding males but the function of female swellings remains unclear. For instance, Pagel (1994) argued that sexual swellings are indicators of the female quality, with the fittest females having the biggest swellings. Nunn (1999) proposed the “graded-signal hypothesis” which states that swellings indicate the probability of ovulation. Studies on olive baboons demonstrate that female swelling size contains information about the female ovulation and fertile time whereas the colour does not (Higham, MacLarnon, Ross, Heistermann, & Semple, 2008). Males use swelling size changes to decide when to consort but do not use this information to decide when to copulate (Higham, Semple, MacLarnon, Heistermann, & Ross, 2009). Male baboons use other signals to estimate female fertility and likely ovulation days. For example, rates of male olfactory inspections increase during the females’ fertile phase, suggesting that olfactory cues may inform males of when to copulate (Rigaill, Higham, Lee, Blin, & Garcia, 2013).

1.2.2 Copulation Calls

A prominent class of signals given in relation to mating is the copulation calls. Copulation calls are loud and rhythmic vocalizations given before, during or just after copulation. They are found in a wide range of species and, in some cases, both males and females call (Higham et al., 2012), whereas in some others only the male (Hsu, Lin, Chen, & Agoramoorthy, 2002; Manno et al., 2007) or the female vocalizes (Semple, 1998; Townsend, Deschner, & Zuberbühler, 2011). For instance, female African elephants, *Loxodonta africana,* give loud, low frequency post-copulatory calls just after being mounted. These calls can be repeated up to 30 min after the copulation, suggesting females advertise their receptive state to distant audiences (Poole, Payne, Langbauer, & Moss, 1988). Male peacocks, *Pavo cristatus*, utter loud “hoots” just before attempting to mate with females (Petrie, Marion, Halliday, Helen, & Chris, 1992; Petrie, Tim, & Carolyn, 1991). Playbacks experiments showed that these calls attract distant females (Yorzinski & Anoop, 2013). In little brown bats, *Myotis lucifugus*, males give copulation calls during mating to promote and maintain male-female contact as sexual encounters resemble aggressive ones (Barclay & Thomas, 1979).

1.2.3 Functional hypotheses of copulation calls

Copulation calls are well studied in primates, where they are mostly uttered by females and tend to co-occur with species in which females produce sexual swellings. Despite a lot of empirical work, the function of primates' copulation calls remains unclear. Several different hypotheses have been proposed but without a clear consensus. However, there is a general agreement that copulation calls have evolved to communicate to the males of the group, allowing them to gain information about the reproductive state of the female (Hamilton & Arrowood, 1978; Hauser, 1990; Pradhan, Engelhardt, van Schaik, & Maestripieri, 2006), but it is unclear in what ways this will also benefit the calling female.

Several hypotheses have been proposed to explain the function of female copulation calls (see Table 1). For instance, at the proximate level, copulation calls can be viewed as an orgasm-like reaction (Hamilton & Arrowood, 1978). This hypothesis is inconsistent with the fact that, in some species, copulation calls occur after the mount, when the female is physically separated from the male (Pfefferle, Brauch, Heistermann, Hodges, & Fischer, 2008; Semple, 2001). In the ultimate domain, another hypothesis states that copulation calls strengthen the consort couple bond (Hamilton & Arrowood, 1978). Following this hypothesis, pair-bonded species (i.e. gibbons) should be more likely to give copulation calls than promiscuous species (i.e. baboons, macaques), which is not the case. Aich et al. (Aich, Moos-Heilen, & Zimmermann, 1990) argued that females utter copulation calls to advertise their fertility to males. This hypothesis is coherent with the fact that females are more likely to call when they are fully swollen. However, females also vocalize during other swellings stages and even during the detumescence phase, demonstrating that this hypothesis is not sufficient to explain calling pattern. Another hypothesis states that copulation calls are directed towards the surrounding females to promote breeding synchrony (Viljoen, 1977, for non-primates). Therefore, seasonal breeders (e.g. Japanese macaque, *Macaca fuscata*) should be more likely to call than non-seasonal ones (e.g. baboons) as seasonal breeders are more likely to be synchronous. Baboons exhibit as much copulation calls as Japanese macaques, which contradicts this hypothesis (Pradhan et al., 2006).

Table 1: Hypotheses for the utterance of female primates copulation calls

Hypothesis	**Reference**
Nonadaptive by-product of sexual intercourse	(Hamilton & Arrowood, 1978)
Nonadaptive phenomenon maintained by phylogenetic inertia	(Henzi, 1996)
Self-stimulates the occurrence of ovulation	*(Cheng, 1992, for non-primates)*
Promote synchronization of male and female orgasm	*(Hamilton & Arrowood, 1978)*
Strengthen the pair bond	*(Hamilton & Arrowood, 1978)*
Honest signals with which females advertise their reproductive status	(Aich et al., 1990)
Honest signals with which low-ranking females advertising their sexual motivation	(Gouzoules, Gust, Donaghey, & St. Andre, 1998)
Advertise mating to other females and inhibit breeding synchrony	(Hohmann & Herzog, 1985)
Advertise mating to other females and promote breeding synchrony	(Viljoen, 1977, for non-primates)
Advertise the presence of a male partner and reduce female harassment	(O'Connell & Cowlishaw, 1994)
Incite male competition and increase the probability of mating with dominant males	(Hamilton & Arrowood, 1978)
Incite male sperm competition to ensure that sons will inherit the best sperm (sexy son)	(O'Connell & Cowlishaw, 1994)
Incite multiple male mating to reduce paternity certainty and the risk of infanticide	(O'Connell & Cowlishaw, 1994)
Announce paternity certainty to promote paternal investment	(Henzi, 1996)
Encourage mate guarding by the consort male	(Todt, Hammerschmidt, Ansorge, & Fischer, 1995)

Taken from (Maestripieri & Roney, 2005) *Italic: Proximate hypotheses*

1.2.4 Female choice, sperm competition, male-male competition hypotheses

Amongst the various functional hypotheses that have been put forward, there are three that deserve serious attention, mainly because they directly follow from predictions made by sexual selection theory: the female choice hypothesis, the sperm competition hypothesis and the male-male competition hypothesis.

The female choice hypothesis states that the consorted female calls to encourage mate guarding by a preferred male (i.e. high-ranking or friend) (Maestripieri & Roney, 2005; Todt et al., 1995). This way, the consort female concentrates paternity in one single high-ranking male or friend, who might provide paternal care for the offspring or at least be tolerant with them (Buchan, Alberts, Silk, & Altmann, 2003). The call is directed towards the consort male but surrounding non-consort males can also hear the copulation call and therefore it forces the consort male into mate guarding. Female Guinea baboons, *Papio papio*, are more likely to utter copulation calls if they mate with highly successful males (i.e. males who copulate with more than one female), although likelihood also increases with the number of male partners (Maestripieri, Leoni, Raza, Hirsch, & Whitham, 2005).

Under sperm competition hypothesis, the consort female calls to advertise her receptivity to attract and mate with as many males as possible, independently of their ranks or their friendship status, to obtain the best or most compatible sperm for her own genotype (O'Connell & Cowlishaw, 1994). Consequently, her sons will also inherit competitive sperm (Keller & Reeve, 1995). For instance, female chacma baboons produce longer copulation calls with adult than with juvenile males and if ejaculation has occurred (O'Connell & Cowlishaw, 1994).

The male-male competition hypothesis states that the consort female utters copulation calls to induce direct competition between males by attracting non-consorting males to physically displace, which will then increase the probability that the consort female mates with another competitively stronger male (Hamilton & Arrowood, 1978). A study on Japanese macaques, *Macaca fuscata*, provided some evidence for this hypothesis as males are more likely to interrupt the ongoing mating if the consort female calls (Oda & Masataka, 1995). In yellow baboons, *Papio cynocephalus*, female identity, mating male rank and swelling state are encoded in female copulation calls, but the occurrence of ejaculation is not (Semple, 2001; Semple, McComb, Alberts, & Altmann, 2002). This information could allow males to know which female is mating and how close she is from ovulation. They could also deduce the competitive strength of the consorting male and hence decide whether or not to take over the consortship.

1.2.5 Multifunctional female copulation calls?

In some studies, researchers found that copulation calls could be multifunctional. For instance, in female long-tailed macaques, *Macaca fascicularis*, copulation calls do not contain information about female swelling stages but about mating male rank, whether the females are mate-guarded or not and whether male ejaculation occurred. These vocalizations seem to be bi-functional: First, females increase sperm competition and paternity confusion by signalling ejaculation and mate-guarding, which determines whether surrounding males are attracted. Second, by giving information about mating male rank, low ranking males should avoid interrupting copulation with dominants, as subordinates would not displace high ranking individuals. Therefore, females bias paternity towards those high ranking males (Engelhardt, Fischer, Neumann, Pfeifer, & Heistermann, 2012). Semple et al. (Semple & McComb, 2000) found that when females Barbary macaques, *Macaca sylvanus*, give copulation calls, they inform the surrounding males about their swelling states but not the occurrence of ejaculation, and argued that hiding ejaculation could be a female strategy to reduce male infanticidal tendencies. However, in a more recent study, Pfefferle et al. (Pfefferle, Brauch, et al., 2008) did not manage to corroborate these results. Instead, they found that females seem to influence the occurrence of ejaculation by calling or not and by adjusting call onset. In addition, if males hear a playback of female's copulation calls, the time between two copulations decreased in comparison to playback of a control stimulus (Semple, 1998), suggesting evidences for sperm competition hypothesis. Semple et al. (Semple, 1998) discovered that if two males hear recording of female copulation calls, only the highest ranking individual approach the speaker, suggesting some support for the male-male competition hypothesis. In eastern chimpanzees, *Pan troglodytes schweinfurthii*, females utter more copulation calls when mating with higher-ranking males, presumably because being found copulating with lower-ranking individuals expose females to aggression (i.e. female choice hypothesis) (Townsend et al., 2008). Townsend et al. (Townsend et al., 2011) found that female chimpanzees do not encode whether they are fertile or not in their copulation calls but inform the audience about their identity. The authors suggest that females conceal their ovulation period to prevent monopolization from dominants and thereby increasing paternity confusion. In addition, giving information about mating female identity may be useful as chimpanzees live in forested habitats that offer low visibility and given their fission-fusion social system.

In conclusion, despite much research the function of female copulation calls in primates is still debated, with no clear pattern having emerged. However, it seems likely that, as different species faces different selective pressures, copulation calls have evolved for different reasons, suggesting that each species needs to be tested separately.

1.3 Why do primates produce signals during encounters?

1.3.1 Close-range social signals

During social interactions, animals can exchange different type of signals. For gestures, these signals are usually referred as "greetings". For instance, male olive baboons often exchange ritualized sexual gestures, such as mounting or penis diddling, during encounters (Smuts & Watanabe, 1990). These greetings take different forms depending on the age of the individuals involved. Greetings between two young males are tense and often interrupted or actively resisted whereas old males greetings are usually completed and reciprocated demonstrating their cooperative relationship. A possible function of these signals could be to negotiate important aspects of their relationships. Male Guinea baboons also exchange intense greeting involving sexual gestures. Whitham et al. (Whitham & Maestripieri, 2003) suggested that these greetings function to test bonds between individuals as they can obtain honest information about their partners by exchanging costly signals (i.e. penis diddling). Spider monkeys, *Ateles geoffroyi*, greet by embracing each other after a fusion event. Dias et al. (Dias, Luna, & Espinosa, 2008) suggested that this behaviour reduces tension between individuals of different party.

1.3.2 Social grunts in baboons

During close-range interactions, baboons give tonal, harmonically and individually distinct vocalizations labelled grunts (Owren, Seyfarth, & Cheney, 1997; Ransom, 1981; Rendall, 2003). This vocalization is well studied in chacma baboons. For instance, a playback experiment demonstrated that chacma baboons could infer if they were the target of a grunt. Females are more likely to move away and to look during a shorter period of time towards the speaker if they heard a threat-grunt (i.e. unidirectional vocalization given from dominants towards subordinates) after being threated than after being groomed (Engh, Hoffmeier, Cheney, & Seyfarth, 2006). Grunts also appear to reconcile opponents after agonistic interactions. Cheney et al. (Cheney, Seyfarth, & Silk, 1995b) demonstrated that subordinate female chacma baboons that have be involved in a fight responded less strongly to their former aggressors threatening screams if dominants grunted to them than if they did not. Several studies analysed grunt acoustic structures. For instance, Rendall et al. (Rendall, Seyfarth, Cheney, & Owren, 1999) studied baboons grunts given in two different situations: Move and infant grunts. They found that these two types of grunt are acoustically distinct for the baboons. However, they also discovered that animals were sensitive to the caller rank and identity. In some cases, the contextual cues also helped the recipient to behave accordingly. In a more recent study, other researchers also analysed the same grunt types but added two other contexts: Foraging and social grunts. They also verified for audience effect (i.e. whether the grunt is directed at a recipient or not) and individual identity. They discovered that even if the overall production specificity was low and that the variation in caller arousal was controlled, foraging, social interaction and infant grunts but not the move grunt could be statistically distinguished from each other. They found that individual identity affected the acoustic structure but that audience effect was absent (Meise, Keller, Cowlishaw, & Fischer, 2011). Ey et al. (Ey, Rahn, Hammerschmidt, & Fischer, 2009) discovered that olive baboons utter longer grunts and at higher rate in forest than in open habitat, suggesting a certain degree of plasticity of this vocalization with regard to the environment.

1.3.3 Grunts to facilitate friendly interactions

One function of grunting is the facilitation of friendly interactions. When two individuals come in close proximity, there can be some ambiguity on what will happen next (Silk, Kaldor, & Boyd, 2000). Thus, baboons' social grunts seem to facilitate subsequent friendly interactions and to signal benign intent following reunion. For instance, dominant female chacma baboons are less likely to supplant subordinates and more likely to engage in friendly interactions, such as grooming, if they grunt while approaching than if they do not (Cheney et al., 1995b). Another study on female chacma baboons showed that individuals are more likely to grunt towards sisters and non-kin (i.e. with whom they have less predictable relationships) than towards mothers and daughters (i.e. with whom they have closest bonds). Dominant females are also more likely to grunt towards subordinates. Taken together, these results suggest that baboons utter grunts to render approach outcomes more predictable and to signal benign intent (Silk, Seyfarth, & Cheney, 2016).

1.3.4 Grunts to facilitate infant handling

Grunting often occurs before infant handling and therefore may facilitate this behaviour (Silk, Rendall, Cheney, & Seyfarth, 2003). Females are strongly attracted to young infants; they want to touch, nuzzle, smell and carry them (Altmann, 1980). Infant handling is a heterogeneous phenomenon and several functional explanations have been put forward but without clear consensus (Maestripieri, 1994). For instance, infant handling in Barbary macaques, *Macaca sylvanus*, seems to have evolved as a non-adaptive by-product of a strong selection for mother-offspring bonding (Paul & Kuester, 1996). This hypothesis seems to apply to female chacma baboons, as they are attracted to other infants if they have young infants of their own and their interest in other infants declined when their own infants grow old (Silk, Rendall, et al., 2003). Manson (Manson, 1999) proposed that infant handling in white-faced capuchins, *Cebus capucinus*, functions to test bonds between females, as females are more likely to handle the infants of females with whom they groomed or formed aggressive coalitions. Rhesus macaques, *Macaca mulatta*, form stronger bonds with related individuals who handled them when they were infants (Dunayer & Berman, 2017).

Grunting seems to facilitate access to young infants. Silk et al. (Silk, Rendall, et al., 2003) demonstrated that female chacma baboons are more likely to handle other females infants if they grunt prior to approaching than if they do not. This is true especially if the approached females are low-ranking, suggesting benign intent (Silk et al., 2016). In stumptailed macaques, *Macaca arctoides*, females who grunt while approaching mothers are less likely to receive aggressions (Bauers, 1993).

1.3.5 Dominance and social bonds as drivers of grunt production

Beside the multitude of suggested functions, grunt production seems to be driven by different mechanisms, such as expressing dominance or social bonds (i.e. friendship). Several studies demonstrated that primates express their hierarchical status by uttering grunts. For instance, subordinate olive baboons give unidirectional fear-barks towards dominants (Ransom, 1981). Similarly, subordinate chimpanzees, *Pan troglodytes*, utter pant grunts when they encounter a more dominant individuals (Goodall, 1986). These vocalizations seem also to be dependant of the surrounding audience with females that are more likely to pant grunt to other males if the alpha male is absent, suggesting that these calls are inhibited socially (Laporte & Zuberbühler, 2010). For friendship, a research on chimpanzees demonstrated that individuals are more likely to give rough grunts (i.e. indicating a valuable food source) when arriving with friends at a food trees (Slocombe et al., 2010).

2 General methods

2.1.1 Study species

Baboons (genus *Papio*) are widespread in Africa and the Arabian Peninsula. Six distinct species are recognized: Chacma (*Papio ursinus*), Guinea (*Papio papio*), yellow (*Papio cynocephalus*), Kinda (*Papio kindae*), hamadryas (*Papio hamadryas*) and olive baboons (*Papio anubis*). Zinner et al. (Zinner, Buba, Nash, & Roos, 2010) challenged the traditional view of five baboon species (excluding the hamadryas) by conducting a study on faecal mitochondrial DNA collected across all geographical range of baboons in Africa. They found eight distinct haplogroups instead of five, which demonstrates a different pattern between morphology-based baboon taxonomy and mitochondrial DNA data. Except for the hamadryas and the Guinea baboons, all the species have the same social structure with female phylopatry and male emigration when reaching sexual maturity. Hamadryas and Guinea baboons have a multi-levels social system with one male unit being the smallest and more stable unit consisting of one leader male, one to several females and their offspring and sometimes one or several followers for the hamadryas (Kummer & Kurt, 1963). Guinea baboons also have one-male unit but this unit is less stable than the hamadryas and multi-males and multi-females form the next social level, called "gangs" comprising between 50 to 70 individuals (Maciej, Patzelt, Ndao, Hammerschmidt, & Fischer, 2013; Patzelt et al., 2011).

Olive baboons belong to the Cercopithecidae (cheek pouch monkeys) family. They received their name from the greenish colour of their fur. They are also called Anubis baboons, in reference to the Egyptian god Anubis, represented with a dog-like head and associated with mummification and after life. They can be found both in savannah and forest environments and range the widest of all the baboon taxa. They are found all across equatorial Africa and occupy 25 countries from Sierra Leon to Ethiopia (Groves, 2001). There are hybridization zones between olive and yellow baboons in Kenya (Alberts & Altmann, 2001) and between hamadryas and olive in Ethiopia (Nagel, 1973). Olive baboons live in multi-male, multi-female groups, called troops. Troops can range from 30 to more to 90 individuals, with between 5 and 16 males and between 7 to 30 females (Ransom, 1981; Rowell, 1966; Strum & Western, 1982). Both male and females have a linear dominance hierarchy with males being dominant over females, with a strong sexual dimorphism with males usually twice the size of the females (Males: 24kg- 33kg; Females: 15kg (Strum, 1991)). Females are the philopatric sex and males leave the group when they reach sexual maturity, between 6 and 9 years old, to avoid inbreeding (For the different age classes, see Table 2). Usually, young new immigrants rank above older individuals, which leads to a male hierarchy that follows age. Females form matrilines, which are groups of individuals revolving around female kinship (i.e. mother, daughters and their offspring). When females give birth to a daughter, she will rank just below her mother.

Table 2: Age classes

Age	Classification	Characteristics
0 - 3 months	Black infant	Black fur, skin is pink. Close association with mother and nursing
3 - 24 months	Infant	Fur is turning yellow and skin black. Close association with mother. Occasional nursing
2 - 4 years	Juvenile female	Fur is olive. Skin is completely black. Not in association with mother for lengthy period. Fully weaned
2 - 6 years	Juvenile male	
4 - 6 years	Subadult female	Gradually grows to size of adult female. Red genital swelling. Menarche
6 - 9 years	Subadult male	Lengthier mantle and shoulder hairs. May spend time away from the troop
6 - 8 + years	Adult female	Considered as female when they conceive their first infant. Long enlarged nipples
9 + years	Adult male	Long hairs around neck and shoulder. Large canine. Twice the size of adult female

Adapted from (Lowe, 2014; Ransom, 1981)

2.1.2 Sexual behaviour

The females' reproductive cycles last between 30 and 40 days. They menstruate for 2-3 days and then begin to swell, reaching maximum swelling 10-15 days later. They remain fully swollen for 7-10 days and deflate for 3 days at which stage their swellings disappears. They remain flat between 10 and 14 days and start to menstruate again if they have not conceived. The ovulation occurs between 1 to 5 days prior to detumescence (Higham, Heistermann, Ross, Semple, & MacLarnon, 2008; Ransom, 1981; Smuts, 1985). If females do conceive, the gestation length is approximately six months and infants are dependant on their mother for a year (Smuts, 1985). Olive baboons are non-seasonal breeders with females mating with different males across their cycles, generating a high turnover in this species. Around the time of ovulation, females develop large swellings and males form consortships with them, i.e. shadowing and mating with them and aggressively repulsing mating attempts by other nonconsorting males (Bercovitch, 1988; Hausfater, 1975). Consortships can last from a few hours up to several days. Time budget wise, consort females have reduced feeding times, unlike males, suggesting heavier energetic costs for females during consort. Consort males frequently groom consort females who rarely reciprocate these grooming sessions (Bercovitch, 1983). As consort partners, females seem to prefer young, high ranking, new coming males although they do not have the highest mating success (Bercovitch, 1991). Nonconsorting males have adopted different strategies to gain access to the oestrous females: (1) Following the consort pair with one or several males shadowing the consorting couple and synchronizing their activities with the couple. Nonconsorting followers can interact with each other or with the consorting male (Danish & Palombit, 2014) It seems that "… the consort male becomes increasingly upset and excited by the presence of the follower male's persistent proximity" suggesting that following functions to inhibit copulations (Ransom, 1981, p.144). (2) As soon as the consort pair is copulating, nonconsorting males come running towards the couple, screaming and stamping as another strategy to inhibit the ongoing copulation (Ransom, 1981). (3) Nonconsorting males can form coalitions to displace the consorting male. Coalitionary males are usually older low to middle ranking males and target younger, higher ranking individuals (Bercovitch, 1988). These strategies are flexible with nonconsorting males being able to change between tactics within a day (Danish & Palombit, 2014).

2.1.3 Friendship

Female and male olive baboons can form long-lasting bonds called "friendship" which are characterized by close spatial proximity, high tolerance at food patches, high grooming bouts between the pair, traveling together and lower rates of aggression. Male friends also protect their female friend infants against predators and harassment from other baboons even if they are not necessarily the infant father. The average number of friends for one female is two, independently of the female age and rank status, whereas males tend to have between three and five female friends depending of their residence status in the troop (Long-term resident adult: mean = 5.2, median = 6; Young short-term resident: mean = 5.2, median = 6; Young adult and subadult natal resident: mean = 3.5, median = 2.5). Unlike mothers with infants, oestrous females seek contact with new immigrant males and often initiate consortship with them ending most of the time in friendship formation between the two individuals, especially if the female conceives, suggesting that female maximizes the probability that males will take care of her offspring. Friendship lasts through all the females cycle even though the time spending in proximity decreases when the female is in oestrous. Friendship stops when males emigrate to another troop or when females develop new friendship with younger immigrant males while cycling (Bercovitch, 1991; Smuts, 1985).

2.1.4 Communication

Olive baboons use visual, vocal and olfactory communication. In the vocal domain for example, adult males give loud vocalizations called "wahoos" given in a wide range of contexts such as during intergroup encounters, during dawn choruses and aggressive interactions with other males and when chasing females. These calls also contain acoustic cues about male age and dominance status, as well as male competitive abilities (Fischer, Kitchen, Seyfarth, & Cheney, 2004; Kitchen, Seyfarth, Fischer, & Cheney, 2003). Concerning visual communication, baboons can exchange a "come-hither face" during encounters, which is a friendly gesture consisting of flattering the ears against the skull and narrowing the eyes (Smuts, 1985). This signal is usually accompanied with lips smacking and social grunts (see above for social grunts) and allow individuals to come in close proximity (For a complete list of visual and vocal signals, see Ransom, 1981, p.90-105). In the olfactory domain, males can gain additional cues about the oestrous female receptivity state by sniffing the female swelling and sometimes even poking fingers into the female vaginal tract (Ransom, 1981; Rigaill et al., 2013).

2.1.5 Study sites

Gashaka Gumti National Park

A pilot study took place in Gashaka Gumti National Park (GGNP), Nigeria. The park is located at the North East of the country, near the border of the Cameroon (06°55'- 08°05'N and 11°11' - 12°13'E) and was founded in the early 70's. GGNP covers 6731 km^2 of Guinea savannah zone, with a mosaic of vegetation types, such as lowland forest, riverine galleries forest and woodlands of the southern Guinea savannah type, which is regularly burnt by humans (Adanu, Sommer, & Fowler, 2011). There is one dry season, which ranges from December to March and one wet season from April to November. More than 1000 plant species and 100 mammal species have been identified in the park (Dunn & Ejebare, 1999).

For research purposes, two troops of olive baboons, Gamgam and Kwano, have been habituated to human presence since 2000 and individually identified (Warren, Higham, MacLarnon, & Ross, 2011). We studied the Kwano troop from January to April and from August to December 2013 and from April to July 2014. The troop ranges from 28 to 35 individuals. Maternal kinship between the individuals is known.

Kwano baboons have several specificities. First, they live in smaller troops and females go through longer birth intervals in comparison to other olive baboon groups in Africa (Higham, Warren, et al., 2009; Ross, Warren, MacLarnon, & Higham, 2011). A possible explanation for these observations is the extreme climatic conditions these baboons are facing with high rainfall and temperature and associated limited resources. Second, researchers showed that Kwano baboons consume African black plums, *Vitex doniana*, which is a natural contraceptive. Therefore, females do not express swellings and, consequently, do not form consortship with males. However, the negative effects of this plant consumption could be counter balanced by the wide-range of medical properties attributed to this plant genus (Higham, Ross, Warren, Heistermann, & MacLarnon, 2007).

We had to abandon this field site due to the rise of the jihadist organization Boko Haram and the propagation of Ebola sickness.

Kibale National Park, Uganda

The main data collection took place in West Uganda, in Kibale National Park (0.13 - 0.41°N; 30.19 - 30.32°E), near the Congolese border. The park measures 766km^2 and is a moist, evergreen forest, transitional between lowland rain forest and montane forest (Chapman, Chapman, Wrangham, Isabirye-Basuta, & Ben-David, 1997). Kibale National Park is called the primates capital of the world as 13 different primate species live in the forest. There are also 350 tree, 372 bird and 71 mammal species. There are two rainy seasons (from March to May and to September to December) and two dry ones (from December to February and from June to August).

We studied the Kabasinguzi troop from May to December 2015. This baboon group is under constant observations since 2009 (Johnson, Swedell, & Rothman, 2012) and all the individuals are individually identifiable. During the study period, the troop included between 39 and 44 individuals (7- 8 adult females, 2 subadult females, 7 - 11 adult males, 3 subadult males, 2 juvenile females, 13 juvenile males, 4 infant females and 1 infant male; For age classes, see Table 2). Kinship between the individuals is not known.

2.1.6 Data analyses

Multimodel inference

We used an information theoretic approach called multimodel inference (Burnham & Anderson, 2002; Burnham, Anderson, & Huyvaert, 2011), as a statistical tool for much of the data analysed in this thesis. Traditionally, researchers use null hypothesis testing, where the research hypothesis is tested against a null hypothesis. If the null hypothesis is rejected, it is assumed that there is some support for the research hypothesis but only by default, as the null hypothesis has little meaning in a biological sense and as the original science hypothesis is never tested. Rejection occurs when a test statistic generated from observed data goes below an arbitrary probability threshold, usually $p < 0.05$. The multimodel approach does not seek to reject the null hypothesis but compares and ranks several different, biologically informed models in term of their relative explanatory power of the response variable (Burnham et al., 2011).

A first step consists in translating biological hypotheses into mathematical equations (i.e. models). Biological variables, such as age, sex, or rank are combined so that they reflect biological hypotheses. This part is where strong reasoning is needed in order to choose the variables or combination of them that reflect biological hypotheses. Then, these models are weighted and ranked relative to each other in order to obtain “a quantitative measure of relative support for each competing hypotheses” (Grueber, Nakagawa, Laws, & Jamieson, 2011, p.699). We used Akaike’s information criterion (AICc, corrected for small sample sizes) to rank the models. AIC is defined as “an estimate of the expected Kullback-Leibler information lost by using a model to approximate the process that generated observed data (full reality)” (Johnson & Omland, 2004, p.102). The Kullback-Leibler information represents the information lost and can be seen as the distance between a given model and full reality (Burnham et al., 2011).

For inference, we used model weight (w_i), which represents the relative likelihood of the model given the data. A model that obtains a weight close to one is best supported by the data. Models with more or less equal weights have a similar level of support in the data (Johnson & Omland, 2004).

An important point is that if more variables are added into a model (i.e. the model is more complex), then the model will be penalized in comparison with a model with fewer variables (less complex). Therefore, this model will rank higher (i.e. it will obtain a larger AICc) and will be less likely. Another important point is that there will always be a ”best” model in the candidate set, as model ranking is relative (Anderson, 2008). However, there may be other models that have not been included in the set, which could still perform better. Also, additional meaningful biological variables may not have been included either because it was not possible to record them or because of other reasons. Similarly, interaction terms between variables may or may not be included depending on how meaningful they are judged in biological terms. In other words, the multi-model inference approach is subject to several researcher-biases, which makes the method less objective than traditional hypothesis testing.

3 Research questions

In a first empirical study (chapter **4**), we investigated the function of copulation calls in wild olive baboons. Copulation calls are well studied in primates and several hypotheses have been proposed (Maestripieri & Roney, 2005; Pradhan et al., 2006) but their function remains unclear. We focused on three hypotheses for the occurrence of copulation calls in olive baboons, namely sperm competition, female choice and male-male competition, which all fit with olive baboons sexual behaviour (i.e. multi-male, multi-female troops, multiple mates during the females oestrous cycles and consortship formation). The sperm competition hypothesis states that females have to mate with as many males as possible independently of their rank to obtain the "best" sperm, which will enable their sons to inherit competitive sperm (Keller & Reeve, 1995; O'Connell & Cowlishaw, 1994). Under the female choice hypothesis, females call to encourage mate guarding by preferred male partners (Maestripieri, Leoni, Roney, & Whitham, 2004; Maestripieri & Roney, 2005). Male-male hypothesis states that females call to attract non-consorting males from the audience to displace the current consorting male and to increase females' probability to mate with another more competitive male (i.e. friend or dominant) (Hamilton & Arrowood, 1978).

We built different models according to these hypotheses by adding combination of different variables (e.g. presence of friends or high ranking males in the audience, habitat visibility, relationship between the consort partners). As a statistical tool, we used multi-model inference which allows to compare and to rank models according to their likelihood to fit the data (Burnham & Anderson, 2002; Burnham et al., 2011).

In the second empirical study (chapter **5**), we aimed to further our understanding of the function of copulation calls by investigating their temporal acoustic structure. Several studies demonstrated that females change the acoustic parameters of their calls according to the strategy they use (Maestripieri et al., 2005; Pfefferle, Brauch, et al., 2008). Using information-theoretic approach, we built different models representing functional hypotheses of copulation calls (i.e. sperm competition, female choice and male-male competition) and investigated the variation in temporal acoustic parameters of these vocalizations in two separate analyses. In the first part, we replicated the models used in (Bouquet et al., 2018) which are a combination of female and male characteristics, audience composition and environmental variables. In the second part, we designed different models combining audience composition variable with variables describing how many times the consort female changes mating partners during a given day (i.e. male index) and how many times the consort female copulates with the same consort male in a row (i.e. copulation index).

In the third empirical study (chapter **6**), the focus was on the causes and consequences of the female olive baboons' social grunt. Baboons produce grunts in different contexts, including when two individuals come in close proximity, i.e. social grunts (Ransom, 1981). Several mechanisms have been proposed for the utterance of this vocalization, such as dominance (Goodall, 1986) or social bonds (Schel, Machanda, Townsend, Zuberbühler, & Slocombe, 2013; Slocombe et al., 2010). Grunts seem to serve different functions, such as facilitating subsequent friendly interactions (Cheney et al., 1995b; Masataka, 1989; Palombit, Cheney, & Seyfarth, 1999) or allowing infant handling (Bauers, 1993; Silk, Rendall, et al., 2003). To examine which are the mechanisms and the function of female olive baboons grunt, we use multimodel inference. We separated our data set in two as there are acoustic differences between grunts produced towards females with dependent infants (i.e. infant grunt) and grunts directed towards females without dependent infants (i.e. social grunts) (Meise et al., 2011). In the first part, we tested different combinations of variables (i.e. relative rank and social bonds) to examine the causes of grunt utterance. In the second part, we built different models to investigate if grunting during an approach facilitated friendly interactions or infant handling.

4 Comparing functions of copulation calls in wild olive baboons (*Papio anubis*) using multi-model inference

Manuscript published in 2018 in Animal Behaviour, Volume 135, p. 187 – 197

https://doi.org/10.1016/j.anbehav.2017.11.019

Yaëlle Bouquet [a], Claudia Stephan [a], Caley A. Johnson [b, c, d], Jessica M. Rothman [b, c, d],
Christof Neumann [a]*, Klaus Zuberbühler[a]*

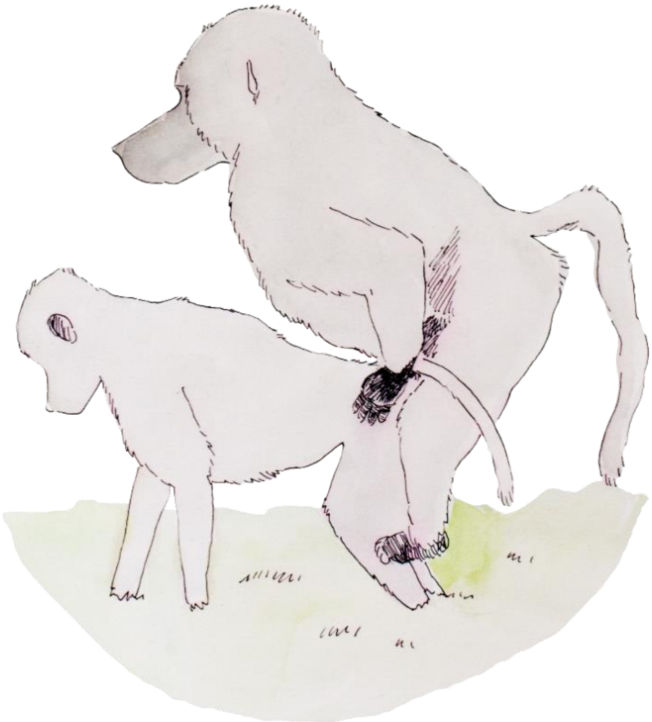
[a] *Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland*

[b] *Department of Anthropology, Hunter College of the City University of New York, USA*

[c] *New York Consortium in Evolutionary Primatology, New York, USA*

[d] *Department of Anthropology, The Graduate Center of the City University of New York, USA*

*: Shared senior author



4.1 Abstract

Female copulation calls are species-specific, distinct vocal signals sometimes given during or shortly after mating. Despite being common in primates and despite much empirical work, their function remains largely unclear for most species. Here, we used an information-theoretic approach to examine simultaneously three main competing hypotheses for the evolution of copulation calls. Two of the three hypotheses predict that female copulation calls function to incite competition between males, either directly (the male-male competition hypothesis) or indirectly (the sperm competition hypothesis), while the third one predicts that females use calls to choose mating partners (the female choice hypothesis). We collected data on copulations of wild female olive baboons, *Papio anubis*, in Kibale National Park, Uganda, to compare the relative support for these hypotheses by modelling whether or not females produced copulation calls after mounts. Our analytical approach enabled us to objectively rank models corresponding to the three hypotheses according to how well our data fit the models. Our data favoured the sperm competition hypothesis over the female choice hypothesis although much variation in calling remained unexplained. The male-male competition hypothesis seems unlikely given our data. We also discuss the possibility that copulation calls have no function, functions not included in our analysis, or that they are multifunctional, a reflection of the species social evolution history.

4.2 Introduction

Copulation calls are loud, rhythmic vocalizations given before, during or just after mating. They occur in a wide range of species from African elephants, *Loxodonta africana*, (Poole et al., 1988) to peacocks, *Pavo cristatus* (Yorzinski & Anoop, 2013). In some species, only one sex calls during mating (males: Hauser, 1993; Hsu et al., 2002; Manno et al., 2007); (females: Semple, 1998; Semple et al., 2002) while in others both sexes vocalize (Higham et al., 2012).

In primates, copulation calls are mostly found in females where they tend to co-occur with visual signals, i.e., exaggerated ano-genital swellings (Nunn, 1999). They are common in species that form multi-male, multi-female groups where females mate promiscuously (Maestripieri & Roney, 2005). Despite much interest and empirical work, e.g. (Engelhardt et al., 2012; Pfefferle, Brauch, et al., 2008) reviewed in (Maestripieri & Roney, 2005; Pradhan et al., 2006), the function of female copulation calls still remains debated. Several hypotheses have been proposed, from orgasm synchronization to strengthening the bonds between mating partners (Hamilton & Arrowood, 1978; Pradhan et al., 2006). Despite their function not yet being fully clarified, there is general agreement that copulation calls are vocalizations that allow the mating and surrounding males to gain information about the receptivity of the mating female, which increases her inclusive fitness (Cox & Leboeuf, 1977; Hauser, 1990; Pradhan et al., 2006), for example by inciting competition between males either directly or indirectly.

Below, we describe three major hypotheses that have been put forward in the current literature to explain female copulation calling. Our goal is to test these hypotheses with our study species, olive baboons, *Papio anubis*, using a multi-model inference framework. In contrast to traditional null hypothesis testing, the multi-model inference approach does not seek to reject null hypotheses, but compares and ranks different, biologically informed models in terms of their relative explanatory power of the dependent variable, in our case whether or not females produce calls after copulations. Given the complexity of evolutionary processes and the long evolutionary history of primate social systems, the multi-model inference approach is likely to generate more meaningful findings than traditional statistical methods (Burnham et al., 2011).

4.2.1 The male-male competition hypothesis

A first main hypothesis states that copulation calling induces direct male-male competition, by attracting non-consorting males (for consortship definition see Table 1) to physically interrupt or displace the consorting male, which will then increase the probability of the female mating with another, competitively stronger male (i.e., high-ranking or friendly male) (Hamilton & Arrowood, 1978). One prediction of this hypothesis is that female calling behaviour directed toward surrounding, non-consorting males should vary with the rank or age of the mating partner, factors that most likely impact on male competitiveness.

Some evidence for the male-male competition hypothesis is found in Japanese macaques, *Macaca fuscata*, where males regularly interrupt copulations if the female has vocalized (Oda & Masataka, 1995). The male-male competition hypothesis is also indirectly supported by evidence that the acoustic structure of copulation calls can provide relatively rich information to other group members. For example, in yellow baboons, *Papio cynocephalus*, copulation calls convey information about the calling female's swelling size (and thus temporal proximity of ovulation), her identity and the rank of the male partner, allowing the surrounding males to make decisions about whether or not to approach and interrupt the ongoing mating event (Semple et al., 2002). At the opposite, males long-tailed macaques, *Macaca fascicularis*, do not interrupt the mating when females utter copulation calls (Nikitopoulos, Arnhem, van Hooff, & Sterck, 2004). One well documented exception in non-primates is elephant seals, *Mirounga angustirostris*, where calling females are more often interrupted by high-ranking males if they are mounted by low-ranking males (Cox & Leboeuf, 1977). However, copulations in elephant seals can last for more than 60 seconds (Cox & Leboeuf, 1977), which gives ample opportunity for rival males to interrupt copulations. In contrast, primate copulations typically are of much shorter duration (olive baboons: 5s, YB personal observation; several primates species: <1min Dixson, 1987) thereby reducing the possibility of successful interruptions unless the interrupting male is in the direct vicinity of the mating pair.

4.2.2 The sperm competition hypothesis

A second main hypothesis is that females use copulation calls to induce indirect competition between males because they are primarily interested in obtaining the best sperm, which will enable their sons to inherit competitive sperm (Keller & Reeve, 1995). Females should therefore mate with all available males, including subadult males, whose phenotypic potential is not yet fully displayed. Here, females call to attract and mate with as many males as possible to obtain the best or most compatible sperm for their own genotype. To select the “best” sperm, females across different species have evolved several mechanisms, including mechanically complex genitalia, chemical and physical barriers or ova that are difficult to penetrate (Keller & Reeve, 1995). In cuis, *Galea musteloides*, females that mated with several males had higher offspring survival than those that mated with a single male (Keil & Sachser, 1998), suggesting direct reproductive consequences of sperm competition. For primates, we are not aware of strong evidence that females gain fitness benefits through sperm competition. However, a number of morphological features in both sexes suggest that sperm competition plays a role (e.g. male testis size / body weight ratio and long vaginal tracts in females, Dixson & Mundy, 1994).

The sperm competition hypothesis has been examined in chacma baboons, *Papio ursinus*, albeit with no clear conclusion. In one study, copulation call duration was longer if females mated with adult males than with subadults or juveniles and, importantly, if adult males ejaculated (O'Connell & Cowlishaw, 1994). However, in other populations (Henzi & Lycett, 1995; Ron, Henzi, & Motro, 1996; Smith, 1986) the majority of matings were with high-ranking males, which were not contested by other males despite female calls, suggesting that inciting sperm competition is not the main function of copulation calls in this species (Henzi, 1996). Instead, Henzi (1996) proposed three alternative hypotheses for the evolution of copulation calls: (1) no functional significance, (2) inciting sperm competition in ancestral populations but currently no longer evolutionarily relevant, and (3) encouraging consort behaviour in high-ranking males to increase their paternity certainty (i.e. female choice hypothesis, see below). However, sperm competition may only play a role in large multi-male groups, and some of the studies above featured an atypically low number of males (< 5), where male take-overs are difficult (Cowlishaw & O'Connell, 1996). One other complexity with the sperm competition hypothesis is that primate sperm is viable over several days, so that male mating success should be analysed over consecutive days, including the pre-oestrous period (Bercovitch, 1989). In Barbary macaques, *Macaca sylvanus*, females appear to influence male ejaculations by adjusting call onset and amplitude or suppressing calling behaviour all together, suggesting a role for sperm competition (Pfefferle, Brauch, et al., 2008).

4.2.3 The female choice hypothesis

Another set of studies (Maestripieri et al., 2005; Todt et al., 1995) have argued that, in some primates, females have an element of choice in whom they mate with such that (1) females should adjust calling decisions depending on whether mounted by a preferred male or not and (2) calling should induce mate guarding by this preferred partner. This way, a female can increase the paternity certainty in one single male, who might consequently be more likely to provide paternal care for her offspring or at least be tolerant of them (Buchan et al., 2003). Here, the call is primarily directed at the male consort partner and the female presumably provides information about her fertility (Maestripieri & Roney, 2005) but the fact that non-consorting males could also hear the call forces the consort male into mate guarding. Under this hypothesis, females have some control over whose genes their offspring will inherit (Maestripieri & Roney, 2005; Todt et al., 1995). In Guinea baboons, *Papio papio*, females that copulated with the most successful males were also most active in giving copulation calls (Maestripieri et al., 2005). In Eastern chimpanzees, *Pan troglodytes schweinfurthii*, females called significantly more with high-ranking than other males, possibly because being found copulating with a low-ranking male could expose the female to male aggression (Townsend et al., 2008).

In this study, we address these three hypotheses in olive baboons, *Papio anubis*, a species living in multi-male, multi-female troops with linear dominance hierarchies among females and males. Group size of olive baboons can range from 30 to more than 90 individuals, with between 5 and 16 males and 7 to 30 females (Ransom, 1981; Rowell, 1966; Strum & Western, 1982). Olive baboons are non-seasonal breeders and female oestrous cycles last between 30 and 40 days and they are fertile for 5 days (Higham, Heistermann, et al., 2008; Higham, MacLarnon, et al., 2008; Swedell, 2011). The females develop large swellings and, around the time of ovulation, males seek consortships with them, by shadowing them from a few hours to several days and by aggressively repulsing mating attempts by other non-consorting males (Bercovitch, 1988). Non-consorting males follow different strategies to take over the consortship, such as (1) following and (2) harassing the consort couple or (3) forming coalitions with other non-consorting males (Danish & Palombit, 2014). Previous studies have shown that females produce copulation calls between 10-62% of matings (Hall, 1965), (Bercovitch F., personal communication in Pradhan et al., 2006). Typically, females mate multiple times with different males across their cycle, generating a high consort turnover in this species (Ransom, 1981; Strum, 1982).

In olive baboons, females and males form long-lasting, durable social bonds, so-called ‘friendships’ (Smuts, 1985), which are manifested by high rates of grooming, close proximity and travelling together. Male friends also protect their females’ infants against predator or harassment from other baboons, even if they are not necessarily the infants’ fathers. Male infanticide rates are lower in olive than chacma baboons (Palombit, 2003).

Considering the on-going debate on the function of primate copulation calls, we revisit the direct vs. indirect competition and the female choice hypotheses. We analyse variables related to female and male characteristics, audience and environment. We use multi-model inference (Burnham & Anderson, 2002) with distinct models that represent the three hypotheses (direct competition, indirect competition, female choice) by investigating whether or not a female uttered a copulation call. Our approach allows us to quantify the relative support for each of the three functions we consider. The three hypotheses are biologically relevant for olive baboons in at least two major ways. First, olive baboons form consortships between males and oestrous females, a behaviour that is directly relevant for the female choice hypothesis. Second, they live in multi-female, multi-male groups, with multiple males having direct access to an oestrous female (Smuts, 1985), a behaviour directly relevant to induce both indirect sperm and direct male-male competition.

4.3 Material and Method

4.3.1 Study site and subjects

We studied the Kabasinguzi troop (Johnson et al., 2012) at the Kanyawara study site, Kibale National Park, Uganda (0.13 0.41°N; 30.19–30.32°E) from May until December 2015. The troop is fully habituated to human presence and all individuals (adults and juveniles) were individually identified. During the study period, the group included between 39 and 44 individuals (7- 8 adult females, 2 subadult females, 7 - 11 adult males, 3 subadult males, 2 juvenile females, 13 juvenile males, 4 infant females and 1 infant male).

4.3.2 Data collection

During each day of the study, we collected focal animal samples and 15min scan samples (Altmann, 1974). We recorded the nearest neighbour of the focal animal, as well as all the individuals' identities in a 10m diameter around the focal. We also recorded the identity of all the focal individual's grooming partners. We recorded these parameters because grooming and proximity are standard behavioural variables to calculate friendship indices (Silk, 2002; Silk, Alberts, et al., 2003).

We began consecutive daily follows from 7am until 4pm of females when they displayed perineal swelling signaling oestrus and when an adult male started consortship with them (see definition Table 1), ending daily follows when female baboons displayed detumescence (Smuts & Nicolson, 1989) and when adult males showed no more interest in them and ended the consortship. Mounts were recorded as all-occurrence samples during daily follows of tumescent individual females (Altmann, 1974). When a mount occurred, we recorded the adult male's identity, whether the female was parous or nulliparous, whether the female gave a copulation call, the audience around the consorting pair, the female's swelling state and the habitat visibility (for definitions, see Table 1). Genetic relatedness among troop members was unknown at the time of the study. It was not possible to determine with sufficient accuracy whether ejaculations occurred.

Table 1: Definitions of key terms

Term	**Definition**
Adult male	Individual that displays fully develop secondary sexual characteristics, such as large canines and long neck hair (Altmann, Altmann, Hausfater, & McCuskey, 1977)
Consortship	Adult male "… shows continual attention and awareness of the swelling female, and when one or both animals move so as to maintain close proximity with each other" (Hausfater, 1975, p.18). The adult male copulates with the female, grooms her frequently and aggressively repulses the takeover attempts of the other non-consorting males (Ransom, 1981)
Mount	Adult male "…grasps the pelvis of the female, elevates his forequarters over the hind end of the female and clasps the female's ankles with his feet" (Hausfater, 1975, p.14). The male makes an intromission with pelvic thrusting. It can occur with or without ejaculation.
Female parity	Parous: Females that have given birth to an infant (Smuts & Nicolson, 1989); Nulliparous: Subadult female reaching menarche that have not yet given birth but have full swellings (Smuts & Nicolson, 1989)
Full swelling	Top, middle and sides of the rumps are swollen around the day of ovulation (Higham, MacLarnon, et al., 2008)
Audience	Identities of the all the individuals within 10m radius circle around the focal
Friendship	Relationship between two individuals characterized by high rate of grooming, close proximity, low rate of aggression, and tolerance at food resources (Silk, 2002; Silk, Cheney, & Seyfarth, 2013)
Habitat visibility	Low: 50-100% tree cover High: 0-50% tree cover

4.3.3 Behavioural analyses

We calculated dominance status of females and males separately, using decided aggressive interactions (i.e. when the agonistic interactions outcome was clear, with a winner and a loser. For definitions, see below), displacements and uni-directional fear barks (given by subordinates to dominants only, Ransom, 1981). To assign dominance status, we calculated Elo-ratings (Albers & De Vries, 2001; Neumann et al., 2011), which is based on the following logic: For any observed agonistic interaction between two individuals, the Elo-rating increases by a certain amount for the winner (i.e. individual who displaces or chases another one) and decreases for the loser (i.e. individual who gives fear bark, gets displaced or chased). If the same two individuals have another agonistic interaction, then expected outcomes (i.e. the former winner wins again) add smaller changes in ratings than unexpected outcomes (i.e. the former winner loses). This method is useful in species with unstable dominance relations and male migration, such olive baboons (Ransom, 1981; Smuts, 1985), due to its dynamic properties (Neumann et al., 2011). We did not include Elo-ratings for the adult females in the analyses because one female accounted for about a third of all interaction data. For ease of interpretation, we refer to an individual's Elo-rating as its dominance rank.

To quantify friendships (for definition, see Table 1), we used the dyadic sociality index (DSI), which assesses the strength of affiliative relationships (Silk, Alberts, & Altmann, 2006; Silk et al., 2013). In order to obtain the DSI for all adult dyads, we considered grooming between the focal and other adult individuals, the focal individual's nearest neighbour and all adult individuals within 10m. Then, for each female, we determined the top three male friends, defined as the three males with which a female had the largest DSI. These three males were considered as 'friends', and all remaining males as 'non-friends'. In all analyses we used this dichotomized categorical variable (e.g. Silk, Alberts, et al., 2006; Young, Majolo, Schülke, & Ostner, 2014).

4.3.4 Model formulation and statistical analysis

To address our questions, we used multi-model inference (Burnham & Anderson, 2002; Burnham et al., 2011), which is based on the principle that models (corresponding to hypotheses) can be ranked and weighted relative to each other in order to obtain "…a quantitative measure of relative support for each competing hypothesis" (Grueber et al., 2011, p.699). We used Akaike's Information Criterion (AICc, corrected for small sample sizes) to rank our three models. One important aspect of this approach is that it represents a trade-off between model complexity and model fit. For example, if two models have the same fit (quantified with R^2, for example, see below), the one with fewer parameters (less complex) will have a smaller AICc and larger weight (see below) than the model with more parameters. Another important point is that any ranking of models is relative, such that there will be always a relative 'best' model, and evaluating fit of all candidate models should be used in conjunction with model ranking to assess whether the (best) model(s) are good in an absolute sense (Anderson, 2008; Dochtermann & Jenkins, 2011).

For inference, we used model weights, which represented normalized ratios of the difference of AICc between the target model and the best model in the candidate set. These model weights can be interpreted as probabilities that a given model is the best model in our set of models (Anderson, 2008).

It is important to note here that our goal was to compare relative support for the three functional hypotheses (i.e. three models, table 2). As such, we were not primarily interested in estimates of specific model parameters for which we could have used techniques, such as model averaging, to account for model selection uncertainty (Grueber et al., 2011; Johnson & Omland, 2004).

Table 2: Predictor variables used in the three functional models

Predictor variable	**Hypothesis/Model**			
	Male-male competition	Sperm competition	Female choice	Null
Habitat visibility	+	+		
Male Elo-rating	+		+	
At least one other swollen female in troop	+	+	+	
Focal female fully swollen	+	+	+	
Mating partner is friend			+	
Female parity	+			
N of males in the audience	+	+	+	
At least one high ranking male in audience	+			

+: Factor included in the model

We fitted generalized linear mixed models with binomial error structure and logit-link (Bolker et al., 2009). In all models, we entered whether or not the focal female uttered a copulation call as the response variable and the focal female identity and the copulating male identity as random intercepts (crossed design as any female could have mated with any male). We log transformed the number of males in the audience to achieve a more symmetric distribution (Schielzeth, 2010). We calculated the coefficient of determination for the three models (Nakagawa & Schielzeth, 2013), which represents the variance explained by the fixed effects (R^2_m) and the variance explained by fixed and random effects (R^2_c). In addition to the relative ranking of models via AICc, these measures allowed us to quantify the absolute explanatory value of our models.

In the following, we describe how we designed each model such that it reflected the corresponding hypothesis to be tested (Table 2), by considering different combinations of variables. Since our study questions are concerned with the function of copulation calls and not with the underpinning mechanisms, we refrained from making predictions about the direction of the effect, i.e., increased or decreased calling probabilities (Maestripieri et al., 2005; Semple et al., 2002).

Male-male competition

This hypothesis states that female calling behaviour induces competition between males over consortship. We thus expected consorting male’s rank to affect the female’s calling behaviour, for example, to encourage bystanders to displace the consort male (Bercovitch, 1991). Similarly, since male olive baboons sometimes form coalitions to displace consorting males, females should adjust their calling activity according to the number of male bystanders and/or the presence of high-ranking bystanders. We also included female parity because young/nulliparous females are less likely to raise offspring successfully than older females (Anderson, 1986), which may affect male motivation to compete for younger females. We further expected female swelling stage, an indicator of ovulation, to play a role, since this is likely to affect male motivation to challenge a consortship (Higham, Heistermann, et al., 2008). We also added whether at least one additional female in the troop was fully swollen since this is likely to influence the level of male-male competition (Muller & Wrangham, 2004). Finally, we included habitat visibility as this is likely to influence how easily mating events can be detected by other males.

Sperm competition

Under the sperm competition hypothesis, we expected females to modify their calling behaviour in order to facilitate their mating with as many males as possible. First, habitat visibility is likely to affect calling behaviour since it is more challenging for non-consorting males to locate the mating pair in closed habitat. As in the previous model, the presence of additional receptive females is likely to affect competition, so we included whether or not there was at least one more swollen female in the troop. We expected that female calling behaviour may change depending on whether the focal female was fully swollen, which could for instance lead to higher calling probability if the female wants to advertise her receptive/fertile state. Finally, we expected that females should adjust their calling behaviour depending on the number of bystanders. For example, females may adjust their vocal behaviour with larger male audiences in order to attract and to copulate with as many males as possible.

Female choice

Under this hypothesis, females should adjust their vocal behaviour to express preferences for specific males and encourage their mate guarding. Contrary to male-male competition and sperm competition, this hypothesis assumes that copulation calls are directed primarily towards the male mating partner. Hence, we expected calling to be influenced by male rank and friendship status (Henzi, 1996), either because they provide “good genes” or offer protection (Buchan et al., 2003). We added whether at least one additional fully swollen female was in the troop, as this is likely to affect intra-sexual competition for preferred males. We included female swelling stage, as calling may be affected with changing receptivity. Finally, since females may additionally communicate to non-consorting males to encourage the mating male’s mate guarding, we included the number of males in the audience in our model.

In addition to random intercepts for female ID and male ID, we included random slopes to account for variation between individuals in how predictors affected the response variable, i.e. whether a copulation call occurred or not (see Barr, Levy, Scheepers, & Tily, 2013; Bates, Kliegl, Vasishth, & Baayen, 2015). Since the focus of our study was to explain female copulation calling and in order to avoid overfitting, we only included uncorrelated random slopes for female ID (Table A1). Furthermore, we did not fit female parity as random slope because during our study period none of the females changed her parity status.

Finally, we included a null model in our analysis. It comprised a fixed intercept and all random slopes for female ID of the three other models and a random intercept for male ID. The null model can be conceptualised as none of the three functional models explaining copulation calling. For example, if the null model had a large weight (relative to the three functional models), the conclusion was that none of functional models is very likely to explain copulation calling. In contrast, if the null model had a small weight the conclusion was that the functional models had explanatory power for copulation calling. Also important is that, regardless of the null model's position in the ranking, there is always the possibility that some other model not included here might perform better.

We conducted all analyses in R (v.3.4.0, R Core Team, 2017), using the following packages for R: lme4 (v 1.1-12, Bates, Machler, Bolker, & Walker, 2015); MuMIn (v.1.16.6, Barton, 2016), EloRating (v. 0.43, Neumann & Kulik, 2014) and socialindices (v. 0.46-08, Neumann, unpublished). Raw data used in this study are available online at figshare (https://figshare.com/s/d7b998a4901999764582, 10.6084/m9.figshare.5383633)

4.4 Results

We observed N= 203 copulation events from five females mating with eight different males. Overall, the average percentage of copulation events with calls was 60.8% (N= 5 females; Table 3). For a presentation of the raw data for all variables and for all females separately, see Figure A1.

Table 3: Descriptive statistics of all consort females

Female ID	Elo-rating	Observed in consortship (h)	Observed in non-oestrus (h)	N cycles	N adult partners	N males/ cycle (mean, range)	N mounts	Percent calling
Ema	1157	47.75	24.5	2	8	6.50 (6-7)	131	24.8
Msa	835	21.25	27.25	4	3	1.75 (1-3)	33	72.7
Spe	665	12.25	24.75	3	5	2.00 (1-4)	23	56.5
Mga	*547*	*2.25*	*38.75*	*5*	*4*	*1.20 (1-2)*	*8*	*62.5*
Ria	342	3.5	22.5	2	2	1.50 (1-2)	8	87.5

Italics: nulliparous female

4.4.1 Multi model inference

Among our models, the model representing the sperm competition hypothesis had the highest weight (w_i = 0.55) and therefore the highest probability of being the best model in our set. The three models representing female choice, the null model and male-male competition had lower weights (0.31, 0.11 and 0.04, respectively; Table 4). Variance explained by our functional models ranged between 6% and 15% for the fixed effects and 54% and 62% for the combined random and fixed effects (R^2_m and R^2_c, respectively, Table 4). Detailed results of all models are in Table 5 and the random effect estimates are presented in Table A1.

Table 4: Results from the multi model inference

Model	**K**	**AICc**	**ΔAICc**	w_i	**ER**	R^2_m	R^2_c
Sperm competition	11	219.6	0	0.55	-	0.06	0.54
Female choice	13	220.8	1.2	0.31	1.8	0.15	0.55
Null	10	222.8	3.22	0.11	5	0	0.62
Male-male competition	16	225.1	5.5	0.04	15.7	0.11	0.57

K: number of variables included; AICc: Akaike's information criterion corrected for small samples; ΔAICc: Difference between the model with the lowest AICc and another model; w_i: Akaike weight: Model probabilities; ER: Evidence ratio: Weight of the model with the lowest AICc divided by the weight of another model; R^2_m: variance explained by fixed effects; R^2_c: variance explained by fixed and random effects combined

Table 5: Parameter estimates ± standard error for all three functional and the null models

Predictor variable	**Hypothesis/Model**			
	Male-male competition	Sperm competition	Female choice	Null
Intercept	-2.52±1.93	-1.65±0.83	-2.09±0.86	-0.82±0.76
Habitat visibility	0.65±0.44	0.59±0.42		
Male Elo-rating	-0.52±0.47		-0.40±0.46	
At least one other swollen female in troop	0.39±0.88	0.03±0.84	0.48±0.85	
Focal female fully swollen	1.51±1.00	1.67±0.89	1.31±0.94	
Mating partner is friend			1.38±0.64	
Female parity	0.54±1.74			
N of males in the audience	0.62±0.73	-0.20±0.60	-0.21±0.51	
At least one high ranking male in audience	-1.32±0.58			

4.5 Discussion

We investigated three major hypotheses for the occurrence of copulation calls in female olive baboons. In doing so, we followed an information theoretic approach, which enabled us to simultaneously evaluate relative support for three competing hypotheses that dominate the current literature on female copulation calling; the male-male competition, sperm competition and female choice hypotheses. Our results show two things. First, although no single hypothesis clearly outcompeted the others, inciting sperm competition is the best explanation for copulation calling in this study on olive baboons, at least amongst the alternatives we considered. The female choice hypothesis still received some support, while the male-male competition hypothesis received the least support and therefore seems very unlikely. The null model, i.e. the possibility that none of the three tested functional hypotheses explained copulation calling, also received some support and as such cannot be ruled out. Second, none of the models explained large amounts of variation in our data, which raises the possibility that females might apply different or conditional tactics with which they utter copulation calls or that they serve a different or no function altogether. In the following, we will discuss methodological considerations and evolutionary interpretations that seem plausible to explain our results.

To the best of our knowledge, this is the first empirical study that directly compared different functional hypotheses for the evolution of copulation calls to evaluate their relative explanatory value. Our approach, using information-theory based model ranking, illustrates some important conceptual advances with direct implications for other areas of research. Our goal was to provide a gradual interpretation of evidence, in light of a set of different functional hypotheses of copulation calling (Pradhan et al., 2006), and we suspect that this approach is likely to be useful for the study of signal evolution more generally. For instance, studies on copulation calls typically investigate and interpret individual factors that are hypothesised to reflect a functional hypothesis. However, it is crucial to realize that many, if not most, such factors are important in the context of several hypotheses (O'Connell & Cowlishaw, 1994). For example, Townsend et al (2008) tested the effect of male rank on calling probability in female chimpanzees. They found that females were more likely to call if they mated with a high-ranking male than with a low-ranking one. As this result was counter to their predictions, the authors concluded that their study "…lent no support to the 'male-male competition' hypothesis" (p. 3). However, the study did not address other potential functions of female copulation calls for which male rank is important, for example female choice, suggesting that the conclusion was premature (because the male-male competition hypothesis may still be a better explanation than, say, female choice). In our study, out of the eight variables that were present across the three models, we considered five variables as relevant in more than one model. This highlights the benefits of using multi-model inference based on integrated models over traditional interpretation of individual factors in studies where different (functional) hypotheses compete with each other. More generally, we believe that this approach also better addresses the complexity of biological systems that often allow for several plausible explanations on the basis of evolutionary principles.

Several aspects of olive baboon sexual behaviour also support our best model that copulation calling functions to incite sperm competition. Females are expected to copulate and obtain sperm from as many males as possible in a short period of time and female baboons typically gave copulation calls at the end of a mount, supposedly after ejaculation has taken place. By calling at the end of the mount, females allow the male to deposit his sperm before attracting other males subsequently. Furthermore, in olive baboons, females are typically consorted by several males in succession and simultaneously during their fertile period (Bercovitch, 1991; Danish & Palombit, 2014), which allows females to receive sperm from multiple males. Specifically, in our studied troop, females mated between 1.2 and 6.5 males per cycle (see Table 3), which suggests that females observed here have received sperm from on average three different males. Another relevant observation is that, at the end of the mount, females often run away from their consorting partners, up to a hundred metres (Smuts, 1985), which facilitates access by non-consorting males. Male olive baboons also have large testes relative to their body size, which enable them to deposit more sperm per ejaculation, in line with the sperm competition hypothesis (Bercovitch, 1989; Harcourt, Harvey, Larson, & Short, 1981).

Although the sperm competition model ranked first in our analysis, we also found some support for the female choice model. In olive baboons, there might be potential for female choice as mate guarding is relatively inefficient, especially around the time of ovulation when consort turnover rates are high (Ransom, 1981). Furthermore, some females try to escape after mating by running towards other males or by trying to split from a consorting male with constant movement (Saayman, 1970; Smuts, 1985). Whether females are able to exert such choice of potential mates in species where females are much more strictly monopolized by males during their fertile phase, and hence the potential for female choice seems much more limited, remains to be studied (e.g. Bulger, 1993).

The male-male competition model ranked last beneath the null model and thus seems a very unlikely explanation for copulation calling in our study animals. Although harassment and aggression toward consorting males have been reported in olive baboons (Niemeyer & Anderson, 1983; Rowell, 1966), we never witnessed non-consorting males (single or in coalition) interrupting an ongoing mating nor harassing the couple. This might be mainly due to very short mating durations (average: 5s, YB, unpublished data), which renders it unlikely for a non-consorting male to be able to disrupt copulations.

Interestingly, our results raise the possibility that copulations calls might actually serve multiple functions that vary with short-term changes in the ecological factors or social structure that individual females are exposed to. For instance, the degree of stability of the male dominance hierarchy has been shown to affect hormonal levels in non-human primates (e.g. Engh, Beehner, et al., 2006; Gesquiere et al., 2011). In such a scenario, if the male dominance hierarchy is unstable and females are not yet able to reliably infer male ranks, females should adopt a strategy that incites sperm competition. In contrast, if the hierarchy is more stable and females are able to associate ranks to individual males more easily, this scenario may select for females to apply strategies like male-male competition or female choice. In contrast to a general instability of social structure, which may have similar effects on all group members, individual attributes such as the ability to reliably keep track of social hierarchies might alternatively vary with a female's experience (e.g., age). Our results suggest a strong influence of individual identity on the preferred strategy, mainly because the variance attributable to female and male identities (R^2_c) is substantially higher than the variance explained by the fixed effects (R^2_m, Table 4). Consequently, the personal histories of females with the different males may impact on the likelihood of them producing copulation calls. Similarly, individual dietary variation might influence female reproductive behaviour when plant components have direct impact on the endocrine system (for a review on primates, see Wasserman, Milton, & Chapman, 2013). For instance, in red colobus, *Procolobus rufomitratus*, estrogenic plant components increased aggression and copulation rates and reduced affiliative interactions (Wasserman et al., 2012). Similar results come from wild baboons, where progestogen-like compounds in a plum species led to the prevention of sexual swellings and thus decreased male consortship and rates of copulation (Higham et al., 2007). To investigate whether behavioural changes in reproductive context due to dietary intake indeed result in switching behavioural strategies and impact on calling behaviour, it would be necessary to incorporate physiological data, especially hormone levels. In primates, female copulation calls are known to vary with oestrus cycles, suggesting that they are under hormonal control, e.g. (Engelhardt et al., 2012; Semple & McComb, 2000) but see (Townsend et al., 2008).

In sum, individual variation in female copulation calling might be due to short-term physiological differences or long-term differences in personality traits or ontogenetic experiences. As such, copulation calls could indeed serve different functions across females, which could account for the variation observed in the present results.

Another way to interpret the current findings is to investigate whether calling itself is not functional but remaining silent is (Townsend et al., 2008). If copulation calls can be reliably used to infer mating events, it might be beneficial to conceal some ongoing copulations to prevent potential post-copulatory aggression and punishment (le Roux, Snyder-Mackler, Roberts, Beehner, & Bergman, 2013).

This point has also been applied to the visual audience awareness (Gygax, 1995), including third-party inferences on bystander rank (Overduin-de Vries, Olesen, de Vries, Spruijt, & Sterck, 2013). In our data, females called in 60% of copulation events, which opens up the possibility that they tactically suppressed their vocal behaviour in the remaining cases. Predictor variable candidates for a model addressing the "tactical deception" hypothesis are whether the mating male is the normally associated male, his consorting distance, the local visibility of the habitat, the receptive state of the female and her location relative to the other males.

Yet another potential function for copulation calls that has been suggested is paternity confusion (O'Connell & Cowlishaw, 1994; Pradhan et al., 2006). However, it is difficult to disentangle paternity confusion from sperm competition because with both strategies females are expected to mate with as many male as possible, although for different purposes: Either to obtain the best genes with the former strategy or to induce paternity confusion with the latter. Raising offspring can be costly for females living in multi-male societies due to male infanticidal tendencies (Engh, Beehner, et al., 2006; Palombit et al., 2000) and one way to reduce such a motivation in males is to ensure that the probability of paternity for each male is larger than zero. Promising objectives for future studies would be to take the female's visual perspective into account (i.e. by studying first what is a female baboon visual range), to distinguish between sperm competition and paternity confusion. In particular, sperm competition predicts that females mate promiscuously in full view of other males whereas paternity confusion predicts the opposite. Another relevant issue to address in this context is whether females "keep track" of males they have mated with and allocate their copulation efforts accordingly.

It is also possible that copulation calls no longer have a biological function but are evolutionary remnants of an earlier socio-ecological environment. This somewhat counter-intuitive possibility is in line with evolutionary principles, provided call production is currently not costly for callers but had been adaptive in the previous evolutionary history of the species. This 'behavioural fossil' hypothesis has been proposed by Henzi (1996). However, we consider it unlikely that copulation calls are mere remnants of past evolutionary states, mainly because copulation calling can hardly be cost-free, but increases the risk of attracting predators and hostile conspecifics.

We also want to address some more points related to the methodological and conceptual approach we chose for this study. First, it is important to reiterate that the validity of any conclusions we derive from model ranking depends on the correct specification of the models we use to translate biological hypotheses into statistical models. It is possible that other researchers would add or remove specific variables or add interactions between variables. For example, one such variable might be female reproductive hormone levels, which are likely to play a role in signalling related to reproduction (e.g. Engelhardt et al., 2012; Semple & McComb, 2000). Whether their inclusion in the analysis would change the model order or the model weights is unknown at this point.

Second, our models explain small to intermediate amounts of variation, at least concerning the fixed effects, according to Cohen (Cohen, 1988): small effect: R^2=0.01, intermediate effect: R^2 = 0.09) However, our values are well within the usual range of observational studies in ecology and evolution (mean R^2: 5.4%; median R^2: 2.2% (Møller & Jennions, 2002), p. 495).

Finally, it is noteworthy to consider that copulation calls potentially carry information on two interrelated levels. First, in species like olive baboons, where a substantial proportion of copulations are silent (Aujard, Heistermann, Thierry, & Hodges, 1998; Fallon, Neumann, Byrne, & Zuberbühler, 2016; Oda & Masataka, 1992) the function may be inherent in the female decision to call or to remain silent. Second, the function may be conveyed by the acoustic structure in species in which virtually all copulations are accompanied by vocalizations (Engelhardt et al., 2012; O'Connell & Cowlishaw, 1994; Oi, 1996; Semple, 2001; Semple et al., 2002). An interesting perspective for future studies across a broader range of species is to investigate whether the acoustic structure (given a call is produced) relates to the same function as the calling/remaining silent distinction, or whether it carries different information.

To conclude, in our study we compared the relative merit of three main hypotheses regarding the function of copulation calls in female olive baboons. Our results do not clearly support one exclusive function, although sperm competition seems to be a more potent evolutionary force than female choice that promotes the utterance of copulation calls in this species, while male-male competition does not to appear to play any role. Another interpretation of our results suggests that copulation calls might actually be multifunctional with individual females applying different behavioural tactics to maximise their benefits from calling on the basis of their respective social experiences or situation. This would be in line with the usual complexity of biological systems and further highlights the flexibility with which communicative signals might be applied, taking contextual information into account and adjusting individual calling behaviour accordingly. We also raised the possibility that copulation calls could have lost their function over evolutionary time, or have a function different from the ones tested in this study. We further highlight the advantages of using model ranking to present relative evidence on a gradual scale. Future research is encouraged to build on our model set, and adapt or amend the model set to gain further insights into the function of copulation in olive baboons and other species.

4.6 Acknowledgements

We thank Cecily Pulver, Moses Araali Kugonza, Godfrey Adyeri and Edward Akiiki for their precious help and friendship in the field. We also thank Pawel Fedurek for comments on an early draft and Roger Mundry for discussions about multi-model inference. We are grateful to the Ugandan Wildlife Authority and the Uganda Council for Science and Technology for giving us the permission to conduct this research. The research has been funded by the Swiss National Science Foundation (310030_143359) and the European Research Council (PRILANG GA283871).

4.7 Appendix

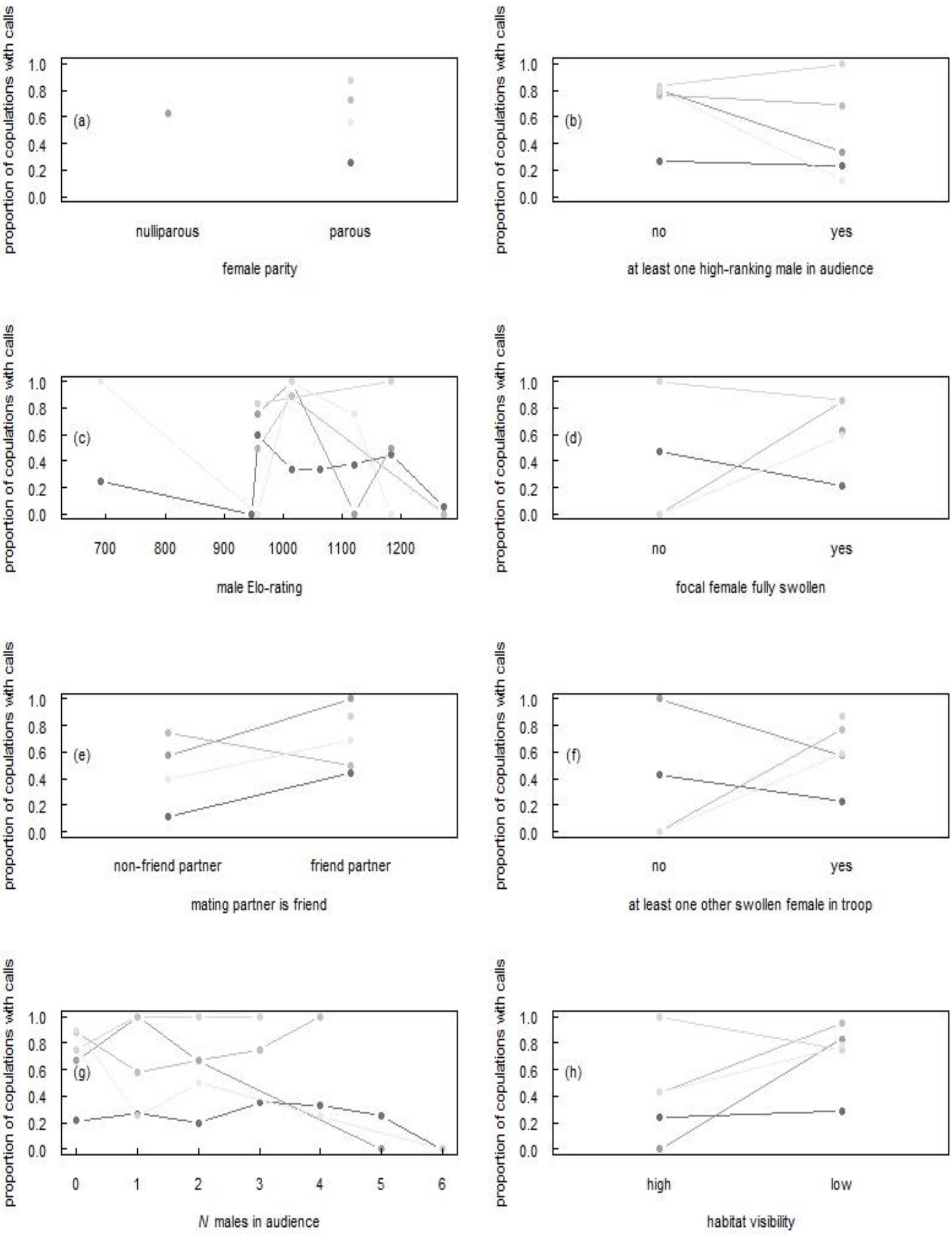


Figure A1: Proportion of copulations with calls for each predictor, separated by female. Predictors are (a) female parity, (b) if there was at least one high-ranking male in the audience, (c) male Elo-rating, (d) if the focal female was fully swollen, (e) if the mating partner is a friend, (f) if there was at least one other swollen female in the troop, (g) the number of males in the audience and (h) habitat visibility.

Table A1: Random effects of the four functional models. Values in the table reflect standard deviations

Random term	Hypothesis/Model			
	Male-male competition	Sperm competition	Female choice	Null
Male ID				
Intercept	1.23	1.38	1.22	1.32
Female ID				
Intercept	0	0	0	0
Habitat visibility	0	0		0
Male Elo-rating	0		0	0
At least one other swollen female in troop	0	0	0	0
Focal female fully swollen	1.19	1.02	1.16	1.7
Mating partner is friend			0	0
Female parity				
N of males in the audience	0.96	0.86	0.62	0.62
At least one high ranking male in audience	0			1.55

5 Wild female olive baboon, *Papio anubis*, modify the acoustic structure of copulation calls to maximise reproductive success

Yaëlle Bouquet [a], Caley A. Johnson [b, c, d], Jessica M. Rothman [b, c, d],
Eloïse Déaux [a]*, Klaus Zuberbühler[a]*

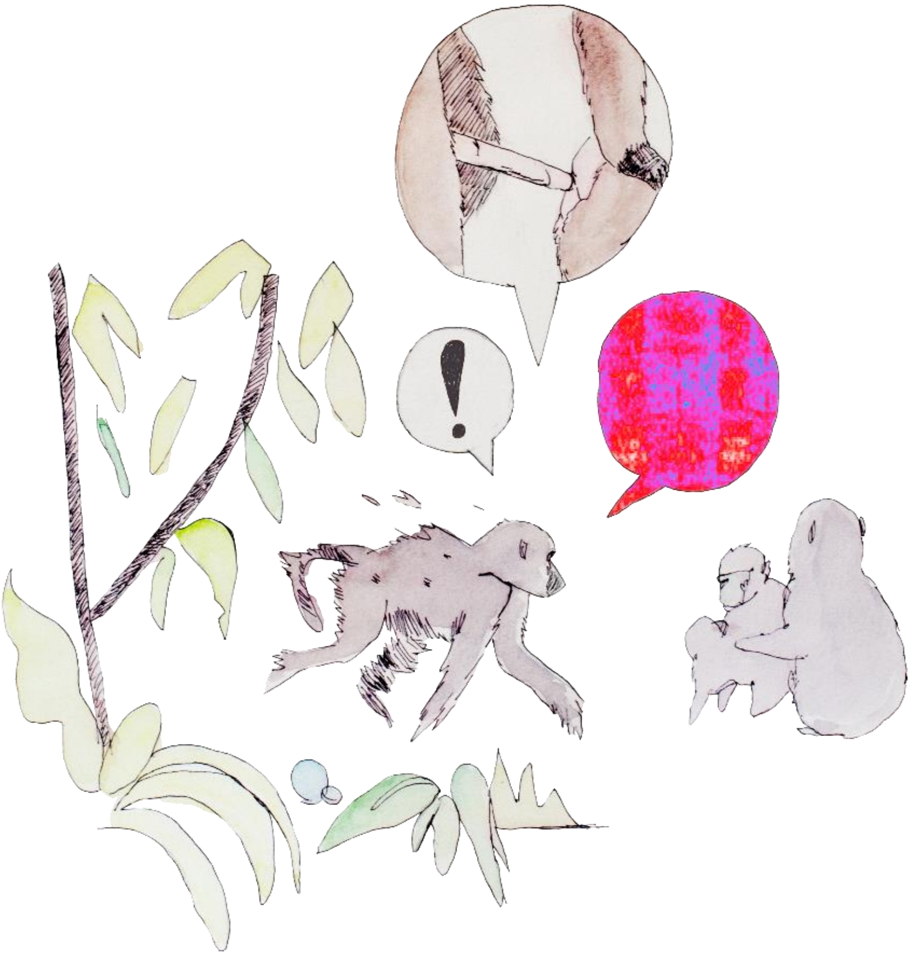
[a] *Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland*

[b] *Department of Anthropology, Hunter College of the City University of New York, USA*

[c] *New York Consortium in Evolutionary Primatology, New York, USA*

[d] *Department of Anthropology, The Graduate Center of the City University of New York, USA*

*: Shared senior author



5.1 Abstract

Some female primates utter copulation calls during or after sexual mounts but the function of these signal is still debated. In some species, the acoustic structure of copulation calls varies with specific external events (e.g. following ejaculation or depending on partner identity), which has functional implications. Using an information-theoretic approach, we tested various models representing the main functional hypotheses of copulation calls (i.e. sperm competition, female choice and male-male competition) by examining the acoustic variation of wild female olive baboon copulation calls. In a first analysis we designed a set of models that described the female's socio-ecological environment, containing individual, audience and environmental predictors. In a second analysis, we refined the models by taking behavioural measures into account, which amounted to descriptions of the different females' mating histories. For the first analysis, we found solid support for 'sperm competition' in how females devoted their calling efforts and some support for 'female choice' in how females structured their call sequences. In the second analysis, we found that when adding factors relating to the copulation history to the models, several hypotheses stood out for the different acoustic parameters, suggesting that females may use different strategies adaptively.

5.2 Introduction

Some primate species give acoustically distinct, rhythmic copulation calls before, during or just after mounts. Depending on the species, only males (Rhesus macaques, Macaca mulatta: Hauser, 1993; Formosan macaques, Macaca cyclopis: Hsu et al., 2002), only females (Yellow baboons, Papio cynocephalus: Semple, 1998; Semple et al., 2002) or both sexes (Crested macaques, Macaca nigra: Higham et al., 2012) produce such signals.

In females, copulation calls tend to occur in species that have co-evolved visual cues to advertise their oestrous, namely swellings and colour changes of their perineal skin (Nunn, 1999; Rowell, 1972). Copulation calls are prevalent in species that form multi-male, multi-female groups where females mate promiscuously (Maestripieri & Roney, 2005). Generally, copulation calls are thought to function to increase a female's inclusive fitness by advertising receptivity (Aich et al., 1990) and allowing potential mating partners and bystanders to extract information concerning her sexual behaviour. However, why it could be advantageous for a female to advertise her sexual activity to other group members is still debated. Three major hypotheses have been put forward, directly derived from sexual selection theory; sperm competition, female choice and male-male competition, but it has been difficult to propose a unified theory valid across the primate order (Bouquet et al., 2018).

5.2.1 The sperm competition hypothesis

This hypothesis states that females call to advertise their receptivity and attract as many males as possible, independently of their rank and other phenotypic features. Instead, the females seek to collect the sperm of multiple males in order to increase the probability of being fertilized by the 'best' sperm (O'Connell & Cowlishaw, 1994) and, as a consequence, conceiving sons that have inherited the 'best' sperm, a variant of the 'sexy-son hypothesis' (Keller & Reeve, 1995). A good example of sperm competition has been reported in Barbary macaques, *Macaca sylvanus*, where mating females adjust the onset and amplitude of their copulation calls to influence male ejaculation (Pfefferle, Brauch, et al., 2008), which gives them some control over whose sperm they collect. Also in Barbary macaques, Semple (1998) showed that broadcasting female copulation calls significantly decreased the time interval between copulations, hence increasing the amount of sperm a female will receive, a finding also interpreted in terms of sperm competition. Similarly, O'Connell et al. (O'Connell & Cowlishaw, 1994) demonstrated that copulation call duration in chacma baboons was longer when females mated with adult males and when ejaculation occurred compared to when mating with juveniles or if there was no ejaculation, suggesting that sperm collection rather than partner quality was a primary driver of call characteristics in this species.

5.2.2 The female choice hypothesis

The female choice hypothesis states that females have individual mating preferences for a specific male (e.g., high ranking or 'friend'). One prediction here is that copulation calls are directed at the preferred male in order to elicit his consort behaviour and mate guarding (Maestripieri & Roney, 2005). Females should engage in such behaviour particularly if the risk of infanticide is high, for example due to high rates of male immigration. In such cases, females benefit from biasing paternity towards one single male in order to secure his protection once the infant is born (Buchan et al., 2003). Another prediction is that females compete with each other over desired males, suggesting that some females may have to settle for lower quality males, as long as they provide sufficient protection from potentially infanticidal males (Palombit, Cheney, & Seyfarth, 2001). For instance, in Guinea baboons, *Papio papio*, high-ranking males are most successful in securing matings, and females are more likely to call when mating with a male who has been successful before with other females (Maestripieri et al., 2005). Although we are not aware of any more direct evidence, these results suggest that female choice is reflected in these calling patterns.

5.2.3 The male-male competition hypothesis

A third hypothesis states that female calls attract the most dominant (i.e. high quality) male to mate with him. Under this hypothesis, females do not have individual preferences for specific males but all prefer the top ranking male and use copulation calls to secure mating with him, that is, by letting him physically displace lower-ranking or otherwise undesired consort males (Hamilton & Arrowood, 1978). A study on Japanese macaques, *Macaca fuscata*, provided some evidence for this hypothesis as males were more likely to interrupt on-going matings if the females called (Oda & Masataka, 1995). In chimpanzees, *Pan troglodytes*, red colobus, *Procolobus badius*, and other multi-male living primates, however, males are astonishingly tolerant towards each other's mating behaviour, suggesting that it may be difficult for females to incite male-male competition. However, female primates are sexually active over considerable proportions of their ovarian cycles, while conception is usually only possible during a few days, suggesting that many mating events have no reproductive consequences. In some species, there is evidence that females actively try to conceal their fertile phase (Townsend et al., 2011), whereas in others females use copulation calls to advertise it, in line with predictions of the male-male competition hypothesis. For example, in yellow baboons, *Papio cynocephalus*, the acoustic characteristics of copulation calls were influenced by female identity, male rank and swelling state while ejaculation success was not (Semple, 2001; Semple et al., 2002). If females produce information about their fertility state and the rank of the mating partner, then bystander males could make informed decisions about whether interference with an ongoing consortship is worthwhile. Outside primates, there is some support for the male-male competition hypothesis in elephant seals, *Mirounga augustirotris*, with low ranking males being more likely interrupted by dominant individuals if females vocalized than if they remained silent (Cox & Leboeuf, 1977).

5.2.4 Copulation calling in olive baboon females

Olive baboons live in multi-female, multi-male troops with an unstable male dominance hierarchy (Smuts, 1985). They are non-seasonal breeders and female cycles last between 30 and 40 days with a fertile period of around five days (Higham, Heistermann, et al., 2008; Higham, MacLarnon, et al., 2008; Swedell, 2011). Around the time of ovulation, females develop large swellings and males seek consortships with them. A consorting male shadows the swollen female, copulates with her and aggressively repulses other, non-consort males' attempts to mate with her (Bercovitch, 1988). Non-consort males can follow a number of different strategies to take over a female, including following and harassing the mating couple or forming male coalitions to displace the consort male (Danish & Palombit, 2014). Males and females can form long-lasting bonds, or 'friendships' (Smuts, 1985), defined in terms of two animals staying in close proximity, showing high levels of mutual grooming and travelling together. In baboons, male friends protect a female's infant against harassment from other group members or predators, even if they are not the infant's father (Palombit, Seyfarth, & Cheney, 1997). Infanticide is rare in olive baboons, which is in stark contrast to chacma baboons (Palombit, 2003).

Female olive baboons, *Papio anubis*, produce copulation calls during or after mounts, yet the functional significance of this behaviour remains largely unexplored. Indeed, given the species' social organisation, all three aforementioned functional hypotheses could explain the patterns of call production. Also relevant is that, although sexually receptive females are usually guarded by one male, females nevertheless manage to mate with multiple males, sometimes at high rates (Ransom, 1981; Strum, 1982).

In a previous study, we investigated the three functional hypotheses outlined before to understand the probability of female call production during sex (Bouquet et al., 2018). We regarded all three hypotheses as biologically plausible for olive baboons since (a) females mate with several males during their cycling period (sperm competition hypothesis), (b) males form coalitions to displace the mating male (male-male competition hypothesis) and (c) the swelling female is mate-guarded by one male (female choice hypothesis). Using multi-model inference theory (Burnham & Anderson, 2002), we found that the sperm competition hypothesis was the most likely explanation for the utterance of olive baboon female copulation calls during matings, with some additional support for the female choice hypothesis but no support for the male-male competition hypothesis.

In this study, we follow up on this line of research, by investigating whether and to what extent sperm competition, female choice and male-male competition explained variation in the acoustic structure of female olive baboon copulation calls. This is because previous work on female long-tailed macaques, *Macaca fascicularis*, has shown that copulations calls contain acoustic information about the mating male's rank, whether or not the female was mate guarded and whether ejaculation occurred (Engelhardt et al., 2012). Information concerning ejaculation would lend support for the 'sperm competition hypothesis', while information concerning mate guarding and male rank would lend support to the 'male-male competition hypothesis'.

In a first analysis, we redeployed the models developed in our previous study (Bouquet et al., 2018) but this time focussing on the acoustic structure of copulation calls as the dependent variable. The previous models contained variables that described the socio-ecological, static environment of the females during their sexually active period. In a second analysis, we expanded the models by additionally taking into account the females' behaviour and prior copulation history. This way, we added proximate factors linked more directly to the females' behavioural decisions to test whether calling females actively sought to alter the outcome of their sexual encounters.

In some species, sexually selected vocal signals are structurally fixed whereas in others the structure can vary over the breeding cycle (Déaux, O'Neil, Charrier, & Iwaniuk, Submitted). For instance, red deer stags, *Cervus elaphus*, produce roars at higher rates during the night, probably as visibility decreases (Bocci, Telford, & Laiolo, 2013). In fallow bucks, *Dama dama*, both the rate of calling and call characteristics change throughout the breeding cycle, suggesting that physiological and psychological factors influence call structure (Vannoni & McElligott, 2009). Similarly, male chacma baboons produce loud calls, the 'wahoos', whose acoustic structure is correlated with male competitive ability. As males get older and fall in rank, the fundamental frequency of their vocalizations declines and formant dispersion decreases (Fischer et al., 2004). Thus, by taking into account such fine-scale changes, we may get a better understanding of the costs and benefits of female call copulation production.

5.3 Materials and method

5.3.1 Study site and subjects

We studied the Kabasinguzi troop (Johnson et al., 2012) at the Kanyawara study site, Kibale National Park, Uganda (0.13 0.41°N; 30.19–30.32°E) from May to December 2015. The troop is fully habituated to human presence and all adults and juveniles are individually identified. During the study period, the group consisted of between 39 and 44 individuals (7- 8 adult females, 2 subadult females, 7 - 11 adult males, 3 subadult males, 2 juvenile females, 13 juvenile males, 4 infant females and 1 infant male). At the time of the study, kinship between individuals was unknown.

5.3.2 Data collection

We conducted focal animal samples and 15 min scan samples (Altmann, 1974). We changed focal animals every hour, except when a female had a swelling. During the scans, we recorded a focal animal's nearest neighbour as well as the identities of all individuals in a 10m circle radius around the focal. We also recorded all occurrences of grooming between the focal and other individuals. Grooming and proximity are standard measures to calculate friendship indices (Silk, 2002; Silk, Alberts, et al., 2003).

We followed subjects daily from 0700 to 1600 hours, when we observed the presence of a perineal swelling (an indication of ovulation status) and when a male attempted a consortship with her. A male and a female are considered in consort as soon as the male starts to shadow the female by maintaining close proximity with her, copulates with her, grooms her frequently and aggressively repulses the takeover attempts of non-consorting males (Hausfater, 1975; Ransom, 1981). We ended the daily follows when the female displayed detumescence and when her last consorting male showed no more interest in her. In addition to scan data, we collected all occurrences data on adult (displays fully develop secondary sexual characteristics, such as large canines and long neck hair (Altmann et al., 1977), subadult (male that has not yet reached adult size but begins to spend time away from the troop (Lowe, 2014; Ransom, 1981) and juvenile (fully weaned individual that does not associate with its mother for lengthy periods (Lowe, 2014; Ransom, 1981) male mounts and associated female copulation calls. When a copulation call occurred, we recorded the identities of the calling female and mounting male, her parity (parous or nulliparous) and swelling stage (full or not), his age-class (adult, subadult or juvenile), the identities of all the individuals in the audience (10m radius) and the habitat visibility (low: 50-100% tree cover, high: 0-50% tree cover).

5.3.3 Dominance hierarchy

We calculated female and male hierarchies separately using decided agonistic encounters (i.e. when the outcome of the fight was clear, with a winner and a loser), as well as displacements and unidirectional fear-barks (i.e. vocalizations given only by dominants towards subordinates (Ransom, 1981)). To calculate an individual's rank, we used the Elo-rating method (Albers & De Vries, 2001; Neumann et al., 2011). When two individuals were involved in an agonistic interaction, the winner (i.e. individual who chases or displaces another one) increased his or her Elo-rating by a certain amount while the loser (i.e. individual who was chased or displaced) decreased his or her Elo-rating. If the two same individuals had a subsequent fight and if the former winner won again, the Elo-rating increased by a relatively smaller amount. Conversely, if the former loser won, his or her Elo-rating increased by a relatively larger amount (for an example, see Fig S1). This method is useful as it takes into account male migration and resulting unstable hierarchies, which is typical for olive baboons (Ransom, 1981; Smuts, 1985). We did not collect data on juvenile agonistic interactions and were thus unable to calculate their Elo-rating. However, as we included mounts by juveniles in our analyses, we created a categorical rank variable. Specifically, we defined the following categories: 1 = high ranking (top three males with the highest Elo scores), 2 = middle ranking (males with Elo scores between 1062 and 947), 3 = low ranking (males with Elo scores between 796 and 691), 4 = subadult and 5 = juvenile. Given their small size and limited competitive abilities, juveniles are always lower-ranking than adults (Holekamp & Smale, 1991).

5.3.4 Friendship

To calculate friendship, we used the dyadic social index (DSI), which assesses the strength of affiliative relationships (Silk, Altmann, & Alberts, 2006; Silk et al., 2013). Friendly relationships between two individuals, indexed by high DSI scores, are characterized by high rates of grooming, close proximity, low rates of aggression, and tolerance at food resources (Silk, 2002; Silk et al., 2013). We used the grooming and proximity data to determine the DSI score of each adult female-male dyad. For the statistical analyses, we considered the three males with which the female had the largest DSI as “friends” while the other males (N = 3) were coded as “non-friends”. All juveniles and subadult males were coded as non-friends as they do not typically form friendships with adult females (Smuts, 1985). In the analyses, we removed the category 3 as there was only one data point.

5.3.5 Sexual interactions

On a given day, we considered the chronological order of consecutive copulations occurring in the same female-male dyad and attributed an index to each observed copulation event (labelled “Copulation index”). For instance, a copulation was given an index of 3 if it was the third time that the consort female was observed to copulate with the same male in a row on a given day (See Table S2). Furthermore, we scored the daily order of consecutive mating partners for each female (labelled “male index”). For example, a male was given an index of 2, if he was the second male with whom the consort female was observed to copulate on that day (See Table S2). These data were collected from daily scan follows (as continuous monitoring was mandatory), such that copulations recorded during opportunistic, all occurrence samplings were not included in the analyses. We built daily copulation and male indices (rather than over the full cycle) because of our lack of information on interactions happening after the end of a daily follow and before the start of the next day follow, and because previous research suggests that copulations and take overs can happen during the night (Smuts, 1985).

5.3.6 Acoustic analyses

We recorded all vocalizations using a Sennheiser ME66 directional microphone and a Marantz PMD 660 recorder. All files were saved in WAV format. Before analysis, we used a high pass filter (100 Hz and 36 dB) to remove low-frequency background noise, which improved visual inspection of the oscillograms. Spectrograms (FFT window: 512 points, overlap= 50%) were visually inspected and calls with low temporal resolution were discarded from the analysis. Baboon copulation calls are typically composed of low-frequency, chaotic vocal elements, such that we could not reliably extract frequency parameters. Instead, we focused on temporal parameters and, using oscillograms, we recorded the following acoustic features (Fig 1): (a) call duration (s), (b) number of vocal elements, (c) mean duration of vocal elements and (d) mean duration of inter elements intervals. We conducted the analyses in Audacity version 2.2.2.

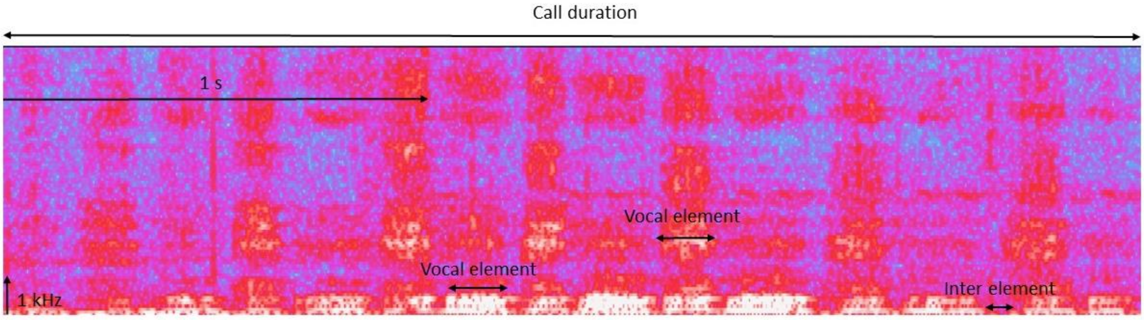


Figure 1: Time-frequency spectrogram of a female baboon copulation call illustrating how call duration, number and duration of vocal elements and duration inter elements intervals were measured.

5.3.7 Models and statistical analyses

To address our questions, we used multi-model inference theory (Burnham & Anderson, 2002; Burnham et al., 2011), which is based on the principle that biologically plausible models (corresponding to hypotheses) can be ranked and weighted relative to each other in order to obtain "…a quantitative measure of relative support for each competing hypothesis" (Grueber et al., 2011, p.699). We used Akaike's Information Criterion (AICc, corrected for small sample sizes) to rank our models. For inference, we used model weights, which represent normalized ratios of the difference of AICc between the target model and the best model in the candidate set. Model weights can be interpreted as probabilities that a given model is the best model in a set of models (Anderson, 2008).

We built mixed effect models with each of the four acoustic parameters entered as the response variables. We used linear models for call duration, the number of vocal elements, the mean duration of vocal elements and the mean duration of inter elements intervals. We used generalized models for the variable 'number of vocal elements' with a Poisson distribution and a log link function. Finally, we built a null model for all our analyses. It included a fixed intercept and a random intercept for female identity. The null model can be conceptualized as none of the models explaining the variation in the acoustic parameters.

Table 1: Predictor variables of the three basic functional models, following (Bouquet et al., 2018)

Predictor variable	**Hypothesis/Model**			
	Sperm competition	Female choice	Male-male competition	Null
Habitat visibility	+		+	
Male rank category		+	+	
Focal female fully swollen	+	+	+	
Mating partner is friend		+		
Female parity			+	
N of males in the audience	+	+	+	
At least one high ranking male in audience			+	

+: Factor included in the model

Table 2: Predictor variables used in the three extended functional models taking female behaviour into account

Predictor variable	**Hypothesis/Model**			
	Sperm competition	Female choice	Male-male competition	Null
Habitat visibility	+			
Male rank category		$+^{2}$	$+^{2}$	
Mating partner is friend		$+^{1}$	$+^{1}$	
N of males in the audience	+	+		
At least one high ranking male in audience			+	
Male index	+			
Copulation index		$+^{1,2}$	$+^{1,2}$	

+: Factor included in the model; Bold: factors added to the basic models; 1 and 2: Interactions

Table 1 shows which variables were combined to build the three models corresponding to the three hypotheses for copulation calls in the first analysis. For the explanations of the addition of a variable into a model, see (Bouquet et al., 2018). We removed the fixed effect “At least one other swollen female in the troop” from the analyses as we expected this variable to have no effect on the acoustic structure. We also included female and male identity as random effects but did not include random slopes, as the models did not converge. The dataset included all copulation events recorded during scan and opportunistic, all occurrence sampling, resulting in N=103.

For the extended analysis, we additionally included information on the females’ previous copulation history (See Table 2). The dataset was different and smaller for this analysis, as it was only possible to use data from the scan samples. The resulting sample size (N=60) was smaller, precluding us from building the full models. Therefore, we based our decisions to include or exclude a predictor variable on a combination of statistical and biological considerations. Furthermore, while we included female identity as a random effect, we did not include male identity, as the models would not converge otherwise. Below, we described how we designed each model corresponding to a functional hypothesis each.

Sperm competition

Under this hypothesis, the consorted female is expected to counteract mate guarding and try to mate with as many males as possible, within a short time period, such that she can be fertilised by the 'best' sperm. We thus added 'male index' to the model, as consorted females should benefit from a large number of mate switches in their attempts to collect different sperm. We also included the number of male bystanders, as females should advertise their receptivity to attract as many males as possible. We incorporated habitat visibility as vocalizations are more degraded in closed than in open habitats (Wiley & Douglas, 1982), suggesting that females should compensate call structure accordingly. We did not include the variable "focal female fully swollen" as we only had three instances of females not being fully swollen in the current dataset (N=60).

Female choice

This hypothesis states that a consort female calls to increase mate guarding by the consort male. Unlike sperm competition and male-male competition, the female's calls target the mating male rather than the audience. First, we expected acoustic parameters to be influenced by the male's friendship status and rank category (Clay & Zuberbühler, 2011; Semple et al., 2002) as females can benefit from protection or "good genes" from the consort male. In this dataset we only had high-ranking adults and juveniles, so we recoded the variable as a binary (high/low rank) predictor. We included the copulation index and its interaction with male rank or friendship as the consort female should change her calling efforts according to whom she was in consort with and how many times in a row she copulated with the same individual. Although copulation calls are directed towards the consort male, male bystanders can still extract information about the on-going mating while the mating female increases the consort male mate guarding. Consequently, we included the number of males in the audience in our models.

Male-male competition

Under the male-male competition hypothesis, we expected a female to call when she was in consort with a lower ranking and/or a non-friend to attract more dominant males from the audience to displace the current male. Thus, we included male rank (binary high/low predictor) and the presence of a higher-ranking male in the models. We added an interaction term between copulation index and male rank or friendship as acoustic parameters should be influenced by how many times the consort female copulated with the same consort male and his dominance or friendship status. However, we could not include female parity, habitat visibility and the number of males in the audience because of the small sample size.

We conducted all analyses in R (v.3.4.0, R Core Team, 2017), using the following packages for R: lme4 (v 1.1-12, Bates, Machler, et al., 2015); MuMIn (v.1.16.6, Barton, 2016), EloRating (v. 0.43, Neumann

& Kulik, 2014) and socialindices (v. 0.46-08, Neumann, unpublished). Raw data will be made available on figshare (www.figshare.com) upon acceptance of the manuscript.

5.4 Results

5.4.1 Analysis 1: Basic functional models

Data for the first analysis were based on N=103 matings from six different females copulating with six adult and nine juvenile males, observed either as focal female scan follows or opportunistically from nearby females (Basic models: Bouquet et al., 2018).

As in our previous study, the sperm competition model ranked first (w_i = 0.97), but only for number of vocal elements as the response variable (See Tables 3 and S4). The ΔAICc between the sperm competition and the other models was large (> 7.66), meaning that the other models were relatively unimportant.

The female choice model was the more likely explanation for the variation of the inter elements intervals duration (w_i = 0.76), followed by the male-male competition model (w_i = 0.24; ΔAICc = 2.26). The other models received almost no support (Tables 3 and S6). Variation in call duration and mean duration of the vocal element was not better explained by any of our models than by the null model, which had the highest relative weight (Call duration, w_i = 0.43; Mean duration of vocal elements, w_i = 0.92) (See Tables 3, S3 and S5).

Table 3: Summary of Akaike weights (w_i) of the three functional hypotheses (basic analysis)

	Sperm competition	Female choice	Male-male competition	Null
Call duration	0.12	0.34	0.09	0.43
Number of vocal elements	**0.97**	0	0.02	0.01
Mean duration of vocal elements	0.07	0.01	0	**0.92**
Mean duration inter-element intervals	0	**0.76**	0.24	0

Bold: 2 ≥ **Δ**AICc between the model with the lowest AICc and the second model with the lowest AICc

5.4.2 Analysis 2: Extended models

For the second analysis, we used a different and smaller data set consisting of N=60 matings with copulation calls recorded during daily scan follows from six different females mating with five adult and eight juvenile males.

We extended the models by adding information about the females' copulation behaviours and found that, as with the basic models, none of them explained call duration (null model ranked first (w_i = 0.88; see Tables 4 and S7). When the number of vocal elements was the response variable, the male-male competition ranked first (w_i = 0.42), closely followed by the female choice model (w_i = 0.42; ΔAICc = 0.40). The sperm competition model ranked below the null model and was therefore unlikely (See

Tables 4 and S8). The sperm competition model ranked first when the mean duration of vocal elements was the response variable (w_i = 0.54), closely followed by the null model (w_i = 0.46; ΔAICc = 0.36). The models that ranked below the null model are unlikely (See Tables 4 and S9). The female choice model was the more likely explanation for the variation in the duration of the inter elements intervals (w_i = 0.66). The male-male competition received some support (w_i = 0.34; ΔAICc = 1.35). The other models obtained considerably lower weights and were therefore unlikely (See Tables 4 and S10).

Table 4: Summary of the Akaike weight (w_i) for every functional hypotheses (extended analysis)

	Sperm competition	Female choice	Male-male competition	Null
Call duration	0.05	0.02	0.04	**0.88**
Number of vocal elements	0.1	0.35	0.42	0.14
Mean duration of vocal elements	0.54	0	0	0.46
Mean duration of inter elements intervals	0	0.66	0.34	0.01

Bold: 2 ≥ **Δ**AICc between the model with the lowest AICc and the second model with the lowest AICc

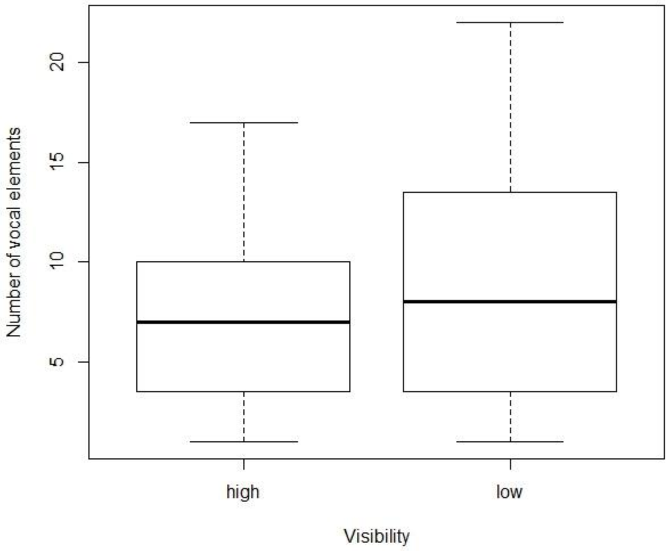


Figure 1: Number of vocal elements uttered by consort female baboons when the habitat visibility is high (on the left) or low (on the right) (N= 103)

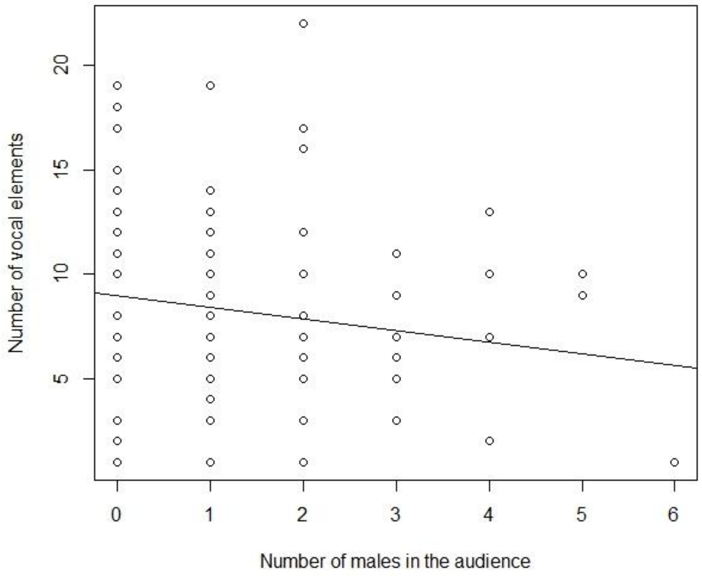


Figure 2: Number of vocal elements uttered by consort female baboons depending on the numbers of males in the audience (N = 103)

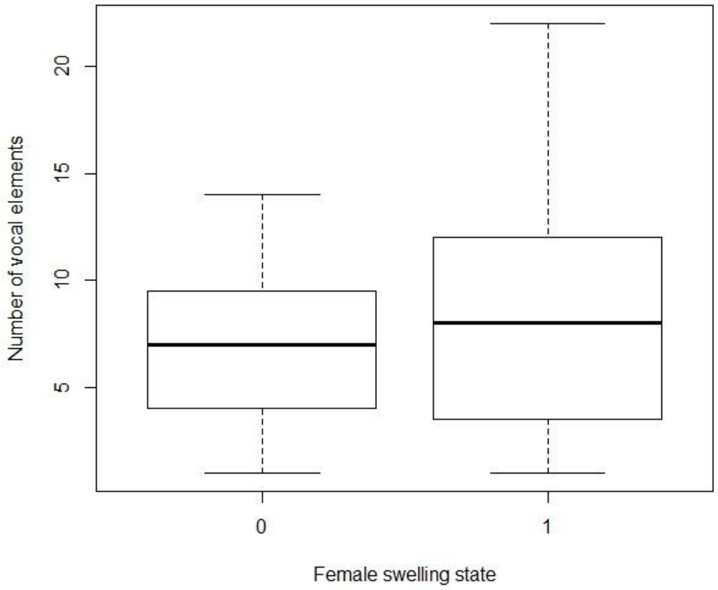


Figure 3: Number of vocal elements uttered by consort female baboons depending on the consort females swelling state (0 = Not fully swollen, 1 = Fully swollen) (N = 103)

5.5 Discussion

We investigated how different combination of variables, representing the main functional hypotheses for primate copulation calls, influenced the acoustic structure of female olive baboon copulation calls. Olive baboon copulation calls are acoustically simple (Fig 1), consisting of sequences of noisy, chaotic pulsed elements, which prevented us from describing the calls in terms of frequency parameters. Instead, we opted for a description of the temporal, pulsed structure of these calls.

Vocalizations with such structures are especially well suited to elicit listener attention (Owren & Rendall, 2001), allowing females to inform nearby males of their availability for mating. Moreover, noisy, chaotic vocalizations are more conspicuous than tonal signals, as such structure generally prevents habituation in recipients (Fitch, Neubauer, & Herzel, 2002). To address the question of whether the acoustic structure of female copulation calls has been under selection pressure, we used two sets of models. In a first basic analysis, we replicated the models used in an earlier study (Bouquet et al., 2018), which are based on a static description of the females' socio-ecological environment during their oestrous. We found that, as in the previous study, sperm competition had the strongest explanatory power, as it influenced the number of vocal elements produced by the females along the predictions made by the sperm competition hypothesis. We also found some support for the female choice hypothesis, in terms of the inter-element interval duration, a structural feature that is highly conspicuous to listeners.

We then extended the basic models, by adding two proximate factors that related to actual female behaviour during the oestrous period, that is, how many different times she copulated with the same male in a row (i.e. copulation index) and how many times she changed her mating partners on a given day (i.e. male index). Here, we were forced to work with a much smaller dataset, which correspondingly reduced the power of the analysis All three functional hypotheses received mixed support depending on the acoustic parameter considered. In other words, no clear pattern emerged, suggesting that consort females may switch strategies and that copulation calls could be multifunctional.

5.5.1 Sperm competition as an evolutionary driver of primate vocal behaviour

In the following section, we discuss parameter estimates, without model averaging, as recommended by (Johnson & Omland, 2004). In a first basic model set, which excluded female mating behaviour, we replicated the finding of our previous study, which was that sperm competition was the best model in explaining calling effort. In the previous study, we found that sperm competition explained whether or not females produced copulation calls whereas in this study we found that, in cases in which she called, sperm competition explained her calling effort. We found that the number of vocal elements in a copulation call increased when visibility was low and when the number of males present in the audience decreased (Table S11, Fig 1 and 2), suggesting that females are trying to advertise their sexual receptivity. The calling behaviour is thus flexibly deployed in terms of maximising obtaining attention and attracting distant males.

In forest habitats, where the studied troop lives, vocal signals are easily degraded, suggesting that signal repetitions allow for better detectability and localization of the signaler (Wiley & Douglas, 1982). This has been shown, for instance, for Carolina wrens, *Thryothorus ludovicianus*, which tend to repeat the same song pattern several times, especially over long distances, to improve signaler localization (Brown & Lemon, 1979; Simpson, 1984). Forest monkeys, such as blue monkeys, *Cercopithecus mitis*, and mona monkeys, *Cercopithecus mona*, also utter long distance vocalizations that contain repetitive call bouts that allow for better detection by conspecifics (Waser & Waser, 1977). Furthermore, Ey et al. (Ey et al., 2009) demonstrated that female olive baboons utter social grunts, a close range vocalization, at higher rates in forest than in open habitats.

Similarly, we found that higher numbers of vocal elements were included when few males were visible, suggesting that females invested more effort into calling when third-party males would be unable to gain information concerning her reproductive status and/or location.

The results also demonstrate that the swollen females utter copulation calls with more vocal elements than non-swollen females (Table S11, Fig 3). Swellings in primates are an indicator of fertility (Nunn, 1999). Thus, males may be able to assess female receptivity from the structure of her copulation calls, although playback experiments will be needed to confirm it.

In chacma baboons, (O'Connell & Cowlishaw, 1994) also suggested that sperm competition was the primary driver of call production because of the finding that call duration was related to the occurrence of ejaculations (O'Connell & Cowlishaw, 1994, see above). This is quite surprising as infanticide rate is high in this species (Palombit, 2003), such that we would expect females to concentrate their mating efforts in dominant individuals to gain protection for their future offspring (i.e. female choice hypothesis). A possible explanation is that females are not trying to maximise sperm competition but paternity confusion. Indeed, both functions make similar predictions, i.e. to mate with as many males as possible, although for different purposes. For sperm competition, females try to obtain good genes whereas for infanticide avoidance they to induce paternity uncertainty. Raising offspring is generally costly for mammalian females, such that infanticidal males are a major selection factor in the evolution of female reproductive behaviour (Engh, Beehner, et al., 2006; Palombit et al., 2000). One way to counteract infanticidal tendencies in males is for females to dilute paternity across as many males as possible and therefore decrease the males' aggressive motivation towards future infants, provided they remember which females they have mated with.

A second strategy to prevent infanticide, followed by chacma baboons, is to build social bonds with specific males, with the more general goal of obtaining their commitments to protect them and their infants against other infanticidal males (Palombit et al., 1997). If females follow this strategy, then the female choice model should have some explanatory power, which is what we observed in this (Table S6) and a previous study (Bouquet et al., 2018). According to this scenario, females follow the predictions made by sperm competition but, in addition, seek to minimise the costs of infanticide by socially affiliating themselves to one protector male.

In yellow baboons, Semple et al. (Semple, 2001; Semple et al., 2002) suggested that male-male competition was the primary driver of call production. Indeed, they found that females encoded their identity, the mating male rank and their swelling state in their copulation calls, which could allow the surrounding males to decide whether to take over the consortship. In this species, however, infanticide is rare (Palombit, 2003) and male hierarchy is stable (Hausfater, 1975). Therefore, concentrating mating efforts into higher-ranking males becomes a viable strategy, mainly because females can rely on the fact that high-ranking males are likely to keep their social position in the future after their infants are born. Following a male-male competition strategy, in other words, only makes sense in species (or populations) where male hierarchy is stable, allowing females to make predictions about individual males' social position for the following years when they have vulnerable offspring.

Why did sperm competition receive the strongest support in olive baboons? Several socio-ecological factors may be relevant to understand this pattern. First, during the study period, one male emigrated and four left the troop thus resulting in unstable male hierarchies (See Fig S1). Therefore, females derived no benefit from mating exclusively with the dominant male (as predicted by the female choice hypothesis), as he was unlikely to keep his position by the time the infant was born. Second, male infanticide is low in olive baboons (Palombit, 2003), such that there may be limited selective advantages for females in securing male protection for their infants.

5.5.2 Copulation calls multifunctional

Sperm competition, in contrast, is often thought of as an evolutionary old strategy that is prevalent in many animal species (Pradhan et al., 2006). It does not require complex behavioural decisions, but simply requires females to evolve mechanisms that expose them to as many males as possible. In this view, maximising sperm competition will always provide benefits for females, suggesting that selection will act to preserve this mechanism. However, this does not necessarily imply that females should rely solely on sperm competition to maximise their reproductive behaviour. Indeed, it may be advantageous for females to use a combination of strategies. In both our studies, we found some support for the female choice hypothesis when considering calling vs. not calling (Bouquet et al 2018) and when looking at structure of the calling sequences (i.e. the mean duration of inter element intervals; Table S6).

Furthermore, preliminary evidence for the possible multi-layered strategies employed by females comes from the results of the extended analyses. We found equivalent support for male-male competition and female choice hypotheses for the variation of the number of elements. While we found weak support for the sperm competition hypothesis (as the null hypothesis ranked closely) for the variation in mean element duration. Finally, there was support for the female choice and the male-male competition hypotheses for the variation in mean element interval. In other words, when factors relating to the copulation history of females are taken into account, there is no functional hypothesis that stands out, suggesting that females may adaptively switch between strategies, depending on their relative needs at the time of the event. Such flexible behaviours have also been proposed for chimpanzees, *Pan troglodytes spp*. Fallon et al. (Fallon et al., 2016) demonstrated that parous and nulliparous females used copulation calls strategically, depending on their own sexual attractiveness to increase male-male competition. Taï forest chimpanzee females strategically adjust their level of selectiveness depending on the timing of the copulation relative to their conception period and this female choice influences male mating success (Stumpf & Boesch, 2005, 2006). Townsend et al. (Townsend et al., 2008) found that females uttered more calls when they mated with high ranking males, which provides support for the female choice hypothesis. The same authors demonstrated that females did not encode in their calls their fertile state. They suggested that females conceal their ovulation period to prevent monopolization from dominants and thereby increasing paternity confusion (Townsend et al., 2011). In summary, these studies on chimpanzees demonstrated that females use different strategies in the use and acoustic structures of copulation calls. Female baboons might behave similarly.

Surprisingly, despite call duration being highly correlated with the number of vocal elements in a call (For the basic analyses: R^2=0.83; For the extended analyses: R^2=0.79), we found that none of the three functional hypotheses explained its variability. A possible explanation is that the overall variation in call duration was too low to detect any effect of the parameters investigated (Table S1). Alternatively, it may be because while this acoustic feature may not be influenced by parameters such as male characteristics or audience composition, it may be affected by other important factors, such as female reproductive hormones levels or the presence of an ejaculation. For instance, copulation call duration is positively affected by the occurrence of ejaculation in chacma baboons and long-tailed macaques, *Macaca fascicularis* (Engelhardt et al., 2012; O'Connell & Cowlishaw, 1994). It may thus be that female olive baboons similarly adjust the temporal characteristics of their calling behaviours depending on the outcome of the copulation and/or their physiological status rather than on male or audience characteristics. An alternative explanation may be that these calls' acoustic structure could still reflect their evolutionary function, but that we failed to analyse the adequate parameters. Indeed, we focused our analyses on temporal parameters because we could not reliably extract frequency-related features. However there is evidence in Barbary macaques, *Macaca sylvanus*, that peak frequency is linked to the occurrence of ejaculation, which is a valuable information to convey in the context of sperm competition (Pfefferle, Brauch, et al., 2008). Future research on the relationships between olive baboons copulation calls acoustic features and their functional significance should thus aim to include analyses on their frequency parameters as well as additional physiological and contextual factors.

5.5.3 Conclusions

We designed and compared different combinations of variables representing functional hypotheses to examine the temporal variation of copulation calls in two separate analyses. In the first analysis, sperm competition received the highest support, when considering the number of vocal elements, in agreement with a previous study that showed that sperm competition hypothesis influenced the probability of call production (Bouquet et al., 2018). We propose that in olive baboons, the limited benefits in concentrating paternity into a high-ranking male (due to migration-related instability of hierarchy) and low rates of infanticide provides little selection pressure for females to evolve mating strategies beyond securing high quality sperm. Nevertheless, we found support for the female choice hypothesis when considering the mean duration of inter elements, also in agreement with our earlier research (Bouquet et al., 2018). Interestingly, however, when including the females' previous copulation history, all three functional hypotheses received some support. We thus conclude that female olive baboons employ a combination of reproductive strategies, depending on their relative benefits at the time of copulation. How much these effects are born out of ontogenetic or species-specific phylogenetic flexibility, however, will have to be addressed by future research.

5.6 Supplementary material

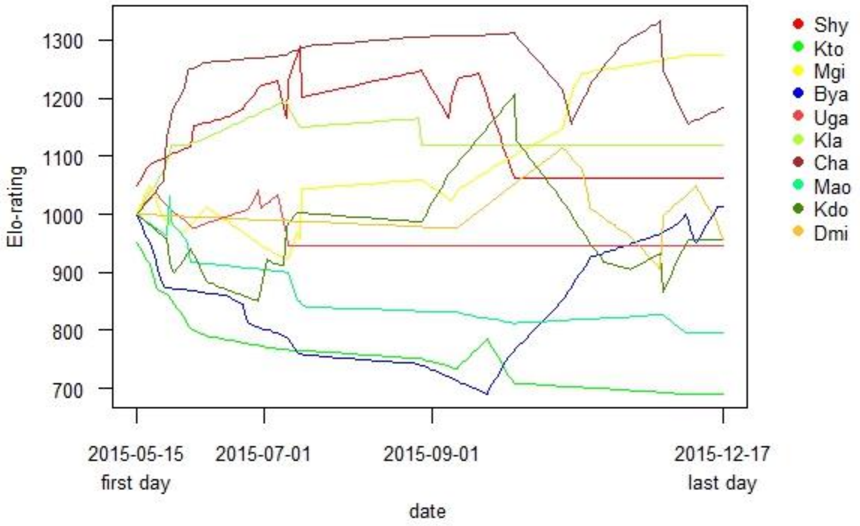


Fig S1: Elo-rating scores for the Kabasinguzi males during the study period. The three letters names of the males are on the right

Table S1: Description of the copulation calls for each female (Mean acoustic parameters ± SD)

Female ID	**Mean call duration**	**Mean number of vocal element**	**Mean duration of vocal elements**	**Mean duration of inter element intervals**
Els	1±0.66	5.33±2.67	0.07±0.02	0.14±0.10
Ema	1.25±0.47	11.22±4.58	0.06±0.03	0.07±0.07
Mga	0.74±0.36	6.65±4.31	0.06±0.05	0.10±0.05
Msa	1±0.65	8.94±6.72	0.08±0.04	0.08±0.07
Ria	0.82±0.59	7.14±5.08	0.08±0.02	0.05±0.03
Spe	0.92±0.52	7.75±4.25	0.07±0.03	0.05±0.03

Table S2: Examples on how “Male index” and “Copulation index” indexes were built

Day	Female ID	Male ID	Male index	Copulation index
1	A	A	1	1
1	A	A	1	2
1	A	A	1	3
1	A	B	2	1
1	A	C	3	1
1	A	C	3	2
2	A	C	1	1
2	A	A	2	1
2	A	B	3	1

Table S3: Multi-model inference results with call duration as the response variable (basic analysis)

Model	K	AICc	ΔAICc	w_i	ER
Null	4	170.6	0	0.43	-
Female choice	10	171.2	0.59	0.34	1.35
Sperm competition	7	173.2	2.6	0.12	3.68
Male-male competition	12	173.8	3.25	0.09	5.08

K: number of variables included; AICc: Akaike’s information criterion corrected for small samples; ΔAICc: difference between the model with the lowest AICc and another model; w_i (Akaike weight): model probabilities; ER (evidence ratio): weight of the model with lowest AICc divided by the weight of another model

Table S4: Multi-model inference results with the number of vocal elements as response variable (basic analysis)

Model	K	AICc	ΔAICc	w_i	ER
Sperm competition	6	683.6	0	0.97	-
Male-male competition	11	691.3	7.66	0.02	45.99
Null	3	694.1	10.5	0.01	190.95
Female choice	9	699.4	15.73	0	2599.66

K: number of variables included; AICc: Akaike’s information criterion corrected for small samples; ΔAICc: difference between the model with the lowest AICc and another model; w_i (Akaike weight): model probabilities; ER (evidence ratio): weight of the model with lowest AICc divided by the weight of another model

Table S5: Multi-model inference results with mean duration of vocal elements as the response variable (basic analysis)

Model	K	AICc	ΔAICc	w_i	ER
Null	4	-423.2	0	0.92	-
Sperm competition	7	-418	5.22	0.07	13.6
Female choice	10	-413	10.21	0.01	165
Male-male competition	12	-411.5	11.78	0	361.58

K: number of variables included; AICc: Akaike's information criterion corrected for small samples; ΔAICc: difference between the model with the lowest AICc and another model; w_i (Akaike weight): model probabilities; ER (evidence ratio): weight of the model with lowest AICc divided by the weight of another model

Table S6: Multimodel inference results with the mean duration of inter elements intervals as the response variable (basic analysis)

Model	K	AICc	ΔAICc	w_i	ER
Female choice	10	-224.3	0	0.76	-
Male-male competition	12	-222	2.26	0.24	3.1
Null	4	-203.2	21.11	0	38388.73
Sperm competition	7	-197.2	27.1	0	768647.81

K: number of variables included; AICc: Akaike's information criterion corrected for small samples; ΔAICc: difference between the model with the lowest AICc and another model; w_i (Akaike weight): model probabilities; ER (evidence ratio): weight of the model with lowest AICc divided by the weight of another model

Table S7: Multi-model inference results with call duration as the response variable (extended analysis)

Model	K	AICc	ΔAICc	w_i	ER
Null	3	73.5	0	0.88	-
Sperm competition	6	79.1	5.6	0.05	16.41
Male-male competition	9	79.6	6.1	0.04	21.15
Female choice	9	80.7	7.2	0.02	36.63

K: number of variables included; AICc: Akaike's information criterion corrected for small samples; ΔAICc: difference between the model with the lowest AICc and another model; w_i (Akaike weight): model probabilities; ER (evidence ratio): weight of the model with lowest AICc divided by the weight of another model

Table S8: Multimodel inference results with the number of vocal elements as the response variable (extended analysis)

Model	K	AICc	ΔAICc	w_i	ER
Male-male competition	8	363.9	0	0.42	-
Female choice	8	2364.3	0.4	0.35	1.24
Null	2	366.2	2.29	0.14	3.14
Sperm competition	5	366.9	3	0.1	4.48

K: number of variables included; AICc: Akaike's information criterion corrected for small samples; ΔAICc: difference between the model with the lowest AICc and another model; w_i (Akaike weight): model probabilities; ER (evidence ratio): weight of the model with lowest AICc divided by the weight of another model

Table S9: Multimodel inference results with the mean duration of vocal elements as the response variable (extended analysis)

Model	K	AICc	ΔAICc	w_i	ER
Sperm competition	6	-343.4	0	0.54	-
Null	3	-343	0.36	0.46	1.2
Male-male competition	9	-331.8	11.59	0	328.18
Female choice	9	-330.1	13.21	0	739.8

K: number of variables included; AICc: Akaike's information criterion corrected for small samples; ΔAICc: difference between the model with the lowest AICc and another model; w_i (Akaike weight): model probabilities; ER (evidence ratio): weight of the model with lowest AICc divided by the weight of another model

Table S10: Multimodel inference results with the mean duration of inter elements intervals as the response variable (extended analysis)

Model	K	AICc	ΔAICc	w_i	ER
Female choice	9	-167.5	0	0.66	-
Male-male competition	9	-166.2	1.35	0.34	1.96
Null	3	-157.6	9.89	0.01	140.66
Sperm competition	6	-152.8	14.71	0	1560.57

K: number of variables included; AICc: Akaike's information criterion corrected for small samples; ΔAICc: difference between the model with the lowest AICc and another model; w_i (Akaike weight): model probabilities; ER (evidence ratio): weight of the model with lowest AICc divided by the weight of another model

Table S11: Parameters estimates ± SD when the call duration is the response variable (basic analysis)

Predictor variable	**Hypothesis/Model**			
	Null	Sperm competition	Female choice	Male-male competition
Intercept	0.97±0.08	0.73±0.21	1.11±0.22	0.65±0.29
Habitat visibility		0.12±0.11		0.16±0.11
Male rank category 2			-0.24±0.19	-0.22±0.18
Male rank category 4			1.05±0.55	1.35±0.55
Male rank category 5			-0.38±0.22	-0.13±0.22
Focal female fully swollen		0.25±0.17	0.25±0.17	0.29±0.18
Mating partner is friend			-0.15±0.17	
Female parity				0.22±0.21
N of males in the audience		-0.09±0.09	-0.11±0.17	-0.03±0.12
At least one high ranking male in audience				-0.10±0.13

Table S12: Parameters estimates ± SD when the number of vocal elements is the response variable (basic analysis)

Predictor variable	**Hypothesis/Model**			
	Null	Sperm competition	Female choice	Male-male competition
Intercept	2.04±0.13	1.55±0.22	2.17±0.22	1.37±0.29
Habitat visibility		0.31±0.08		0.31±0.08
Male rank category 2			-0.20±0.23	-0.15±0.23
Male rank category 4			-0.61±0.55	-0.16±0.56
Male rank category 5			-0.39±0.22	-0.04±0.22
Focal female fully swollen		0.37±0.16	0.29±0.16	0.36±0.17
Mating partner is friend			-0.30±0.15	
Female parity				0.04±0.22
N of males in the audience		-0.01±0.07	-0.08±0.07	0.06±0.09
At least one high ranking male in audience				-0.12±0.10

Table S13: Parameters estimates ± SD when the mean duration of vocal elements is the response variable (basic analysis)

Predictor variable	Hypothesis/Model			
	Null	Sperm competition	Female choice	Male-male competition
Intercept	0.07±0.003	0.07±0.01	0.07±0.01	0.08±0.02
Habitat visibility		-0.004 ±0.006		-0.007 ±0.006
Male rank category 2			0.004± 0.01	0.005±0.01
Male rank category 4			-0.03±0.03	-0.03±0.03
Male rank category 5			-0.005±0.01	-0.006±0.01
Focal female fully swollen		0.001±0.01	0.001±0.01	-0.00004 ±0.1
Mating partner is friend			-0.003±0.008	
Female parity				-0.002±0.01
N of males in the audience		-0.006±0.005	-0.004±0.005	-0.01± 0.007
At least one high ranking male in audience				0.01±0.008

Table S14: Parameters estimates ± SD when the mean duration of inter elements intervals is the response variable (basic analysis)

Predictor variable	**Hypothesis/Model**			
	Null	Sperm competition	Female choice	Male-male competition
Intercept	0.08±0.01	0.06±0.03	0.05±0.03	0.08±0.04
Habitat visibility		0.002±0.02		0.006±0.02
Male rank category 2			0.02±0.03	0.02±0.02
Male rank category 4			0.48±0.08	0.44±0.08
Male rank category 5			0.04±0.03	0.006±0.03
Focal female fully swollen		0.02±0.03	0.005±0.02	0.005±0.02
Mating partner is friend			0.003±0.02	
Female parity				-0.04±0.02
N of males in the audience		0.01±0.02	0.001±0.01	0.004±0.02
At least one high ranking male in audience				-0.003±0.02

Table S15: Parameters estimates ± SD when the call duration is the response variable (extended analysis)

Predictor variable	**Hypothesis/Model**			
	Null	Sperm competition	Female choice	Male-male competition
Intercept	1.08±0.06	1.08±0.09	1.13±0.11	1.18±0.11
Habitat visibility		-0.008±0.12		
Male rank category			-0.46±0.23	-0.40±0.22
Mating partner is friend			0.09±0.14	0.10±0.14
Female parity				
N of males in the audience		-0.07±0.06	-0.08±0.05	
At least one high ranking male in audience				-0.21±0.11
Male index		-0.03±0.06		
Copulation index			0.02±0.10	0.08±0.10
Copulation index * Male rank category			-0.57±0.36	-0.56±0.36
Copulation index * Male partner is a friend			0.005±0.12	-0.06±0.13

*: Interaction

Table S16: Parameters estimates ± SD when the number of vocal elements is the response variable (extended analysis)

Predictor variable	**Hypothesis/Model**			
	Null	Sperm competition	Female choice	Male-male competition
Intercept	2.20±0.09	2.17±0.11	2.35±0.13	2.37±0.14
Habitat visibility		0.02±0.09		
Male rank category			-0.74±0.27	-0.56±0.30
Mating partner is friend			-0.08±0.14	-0.05±0.14
Female parity				
N of males in the audience		-0.11±0.05	-0.12±0.04	
At least one high ranking male in audience				-0.28±0.10
Male index		-0.02±0.04		
Copulation index			0.02±0.07	0.08±0.08
Copulation index * Male rank category			-0.80±0.40	-0.74±0.40
Copulation index * Male partner is a friend			-0.11±0.10	-0.20±0.10

*: Interaction

Table S17: Parameters estimates ± SD when the mean duration of the vocal elements is the response variable (extended analysis)

Predictor variable	**Hypothesis/Model**			
	Null	Sperm competition	Female choice	Male-male competition
Intercept	0.06±0.002	0.07±0.002	0.06±0.003	0.06±0.004
Habitat visibility		-0.004±0.003		
Male rank category			-0.002±0.007	-0.0004±0.007
Mating partner is friend			0.001±0.005	0.001±0.005
Female parity				
N of males in the audience		-0.004±0.002	-0.002±0.002	
At least one high ranking male in audience				-0.003±0.004
Male index		-0.004±0.002		
Copulation index			0.0004±0.003	0.0009±0.003
Copulation index * Male rank category			-0.0002±0.01	0.0006±0.01
Copulation index * Male partner is a friend			0.002±0.004	0.001±0.004

*: Interaction

Table S18: Parameters estimates ± SD when the mean duration of the inter elements intervals is the response variable (extended analysis)

Predictor variable	**Hypothesis/Model**			
	Null	Sperm competition	Female choice	Male-male competition
Intercept	0.08±0.008	0.07±0.01	0.07±0.02	0.07±0.02
Habitat visibility		0.02±0.02		
Male rank category			0.05±0.03	0.04±0.03
Mating partner is friend			0.006±0.02	0.006±0.02
Female parity				
N of males in the audience		0.007±0.009	0.008±0.007	
At least one high ranking male in audience				0.007±0.01
Male index		-0.002±0.008		
Copulation index			-0.004±0.01	-0.005±0.01
Copulation index * Male rank category			0.07±0.04	0.07±0.05
Copulation index * Male partner is a friend			0.05±0.01	0.05±0.02

*: Interaction

6 Causes and consequences of wild female olive baboons, *Papio anubis*, grunting calls

Yaëlle Bouquet [a], Christof Neumann [a], Caley A. Johnson [b, c, d], Jessica M. Rothman [b, c, d],
Reinhard Neier [e], Klaus Zuberbühler[a]

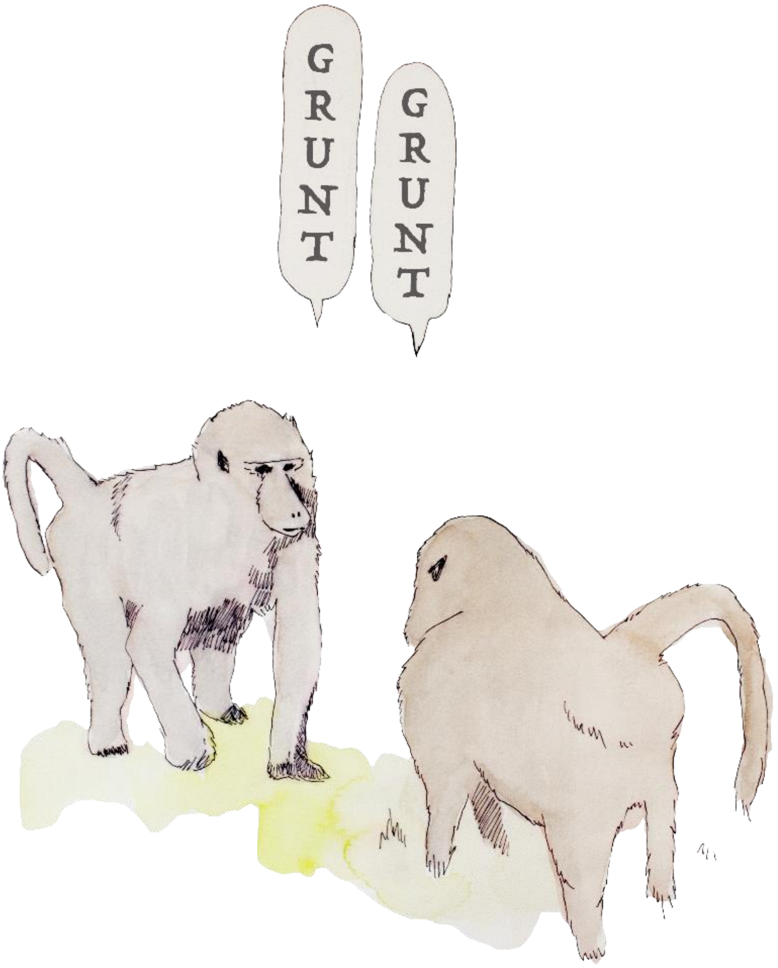
[a] *Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland*

[b] *Department of Anthropology, Hunter College of the City University of New York, USA*

[c] *New York Consortium in Evolutionary Primatology, New York, USA*

[d] *Department of Anthropology, The Graduate Center of the City University of New York, USA*

[e] *Institute of Chemistry, University of Neuchâtel, Neuchâtel, Switzerland*



6.1 Abstract

Many social species produce dedicated signals during close approaches, but there is no unified theory about the function and meaning of this behaviour. We collected data on grunting behaviour during approaches between wild female olive baboons, *Papio anubis*, in Kibale National Park, Uganda. Using an information-theory approach, we found that none of the tested social models convincingly explained grunt production, but that the presence or absence of young infants changed their relative rankings. In particular, when subjects interacted with mothers the ‘friendship’ model ranked highest, whereas when they interacted with other females, the ‘dominance’ model ranked highest, suggesting that motherhood changes the pertinent features of a female-female relationship. We further demonstrated that grunting by itself did not predict the outcome of subsequent social interactions, regardless of the presence of infants, suggesting that callers vocalised only when a desired outcome was indeterminate. We discuss these findings in relation to the dominance-controlled use of grunts in female chacma baboons, *Papio ursinus*, highlighting how primates use morphologically inflexible signals in socially flexible ways.

6.2 Introduction

Primates use acoustically distinct vocalizations in a wide range of contexts, such as during feeding (Gros-Louis, 2004; Kalan, Mundry, & Boesch, 2015; Schel et al., 2013) or predator encounters (Arnold & Zuberbühler, 2006; Evans, Evans, & Marler, 1993; Price et al., 2015). Many of the calls used in these contexts have relatively rigid, species-specific acoustic morphologies, which is often cited as evidence for a hard-wired and cognitively inflexible nature of primate vocal communication (e.g. Tomasello, 2014). The fact that primates have species-specific vocal repertoires that are structurally inflexible is not disputed, but it is less clear how flexible primates are in how they deploy these signals during social interactions and in response to external events in the world. For example, cross-site comparisons have revealed a considerable habitat influence in how Diana monkeys, *Cercopithecus diana*, use alarm calls to predators and other disturbances (Stephan & Zuberbühler, 2008, 2014, 2016).

Many primates produce acoustic signals during close-range interactions, such as when approaching another group member, and these calls appear to be very flexible in both form and function (Bouchet, Koda, Masataka, & Lemasson, 2016). A particularly interesting type is the 'grunt', a low amplitude, tonal signal, produced in a variety of contexts by many primate species, including humans, great apes, baboons, macaques and other Old World monkeys. For instance, vervet monkeys, *Chlorocebus pygerythrus*, produce grunts during intragroup encounters, when interacting with infants, but also during group movement (Cheney & Seyfarth, 1982; Seyfarth & Cheney, 1986a; Seyfarth & Cheney, 1984, 1986b; Struhsaker, 1967). One recently discovered function of this vocalization in vervet monkeys is to recruit valuable partners in risky situations (Mercier et al., 2017). Grunting behaviour has also been well studied in baboons. For example, in chacma baboons, *Papio ursinus*, grunts are socially directed at other group members (Engh, Hoffmeier, et al., 2006; Ey et al., 2009; Ransom, 1981), similar to how great apes use gestures to interact with each other (Tomasello, 2007). Furthermore, grunts are individually distinct, allowing listeners to recognize who is approaching, even without visual contact (Engh, Hoffmeier, et al., 2006; Owren et al., 1997). Here again, a range of different functions and mechanisms have been proposed, such as reconciling opponents after fights (Cheney & Seyfarth, 1997; Cheney et al., 1995b), initiating group movement (Owren et al., 1997; Rendall et al., 1999), or coordinating spatial proximity while searching for food (Meise et al., 2011).

A particularly important function of baboon grunting is the facilitation of friendly social interactions, such as grooming, embracing or sitting in contact. In chacma baboons, dominant females are less likely to supplant subordinates and more likely to engage in a friendly interaction if they utter grunts during approach (Cheney et al., 1995b). Similarly, adult males that grunt towards females appear to signal a desire for increased proximity and affiliative interactions (Palombit et al., 1999). A similar finding has been shown in female Japanese macaques, *Macaca fuscata*, that produce grunt-like 'girney' vocalizations that are often produced prior to grooming, suggesting that they facilitate friendly interactions (Masataka, 1989).

Grunting also occurs in the context of infant handling. In chacma baboons, when a female approaches and grunts towards a female with dependant offspring, she is more likely to have access to that infant compared to when she approaches without grunting (Silk, Rendall, et al., 2003). This is true especially if the approached females are low-ranking, suggesting that callers are keen to express their benign intent (Silk et al., 2016). Grunts given in this context are acoustically distinct from grunts given in other contexts, such as prior to move, suggesting they carry meaning for listeners (Meise et al., 2011). Similar findings have been reported for the grunts of stump-tailed macaques, *Macaca arctoides* (Bauers, 1993).

Given their flexibility and social nature, a natural question to ask is whether there are any underlying cognitive universals that govern grunting behaviour in primates. Perceptions of social dominance and friendships are promising candidates (Silk, 2002; Silk et al., 2013), as several studies have already underlined the importance of dominance relationships in grunt production. In chimpanzees, *Pan troglodytes*, for instance, subordinates produce unidirectional 'pant grunts' when approaching dominant individuals (Goodall, 1986) and rank equally determines vocal interactions in olive baboons, *Papio anubis* (Ransom, 1981).

More recent work has also highlighted the importance of social bonds ('friendship') as drivers of grunt production. For instance, chimpanzees are more likely to produce 'rough grunts' (i.e. indicating the discovery of a valuable food source) when arriving at a food tree with 'friends' than with other group members (Slocombe et al., 2010). Similarly, chimpanzees are more likely to utter 'rough grunts' to an experimentally simulated arrival of a friend than a non-friend (Schel et al., 2013). Overall, these and many other studies highlight a more general pattern in primate call production, that is, that grunts are characterised by considerable amounts of flexibility in how they are used, with dominance and friendship being main drivers of call production. Additional drivers can be the presence of different audiences or the caller's own rank or personality. For instance, female chimpanzees refrain from uttering pant-grunts (see above) towards a male if higher-ranking males are in the audience (Laporte & Zuberbühler, 2010).

In the present study, we used multi-model inference theory to investigate the role of multiple variables on grunting behaviour in female olive baboons, *Papio anubis*. We thus refrained from traditional null hypothesis testing, which is based on rejecting a reality that has no biological structure using a probability threshold. Instead, we sought to compare different biologically informed models in term of their relative explanatory power of the response variable (Burnham et al., 2011), the production of grunts (analysis 1) and the outcome of an approach (analysis 2).

Olive baboons live in multi-female, multi-male troops with a strict dominance hierarchy (Smuts, 1985). Females are philopatric and form strong social bonds (Silk, Altmann, et al., 2006) whereas males leave the troop when they reach sexual maturity (Smuts, 1985). Like chacma baboons, olive baboons produce grunts when one individual approaches another (Ransom, 1981) but, to our knowledge, the mechanisms of call production have not been studied systematically. One previous study has found that grunts uttered in the forest were longer than in open habitat, suggesting some amount of control in call structure (Ey et al., 2009), but little is known about whether baboons use grunts in flexible ways, to obtain a desired interaction or social outcome.

To address this, we collected data on females approaching other females and recorded all vocal and behavioural interactions, with and without the presence of dependent infants. In a first analysis, we were interested in how dominance and friendship affected call production. In a second analysis, we were interested in how grunts facilitated subsequent interactions, that is, how rank difference, friendship, and vocal production influenced subsequent social behaviours.

6.3 Materials and method

6.3.1 Study site and subjects

We studied the Kabasinguzi troop (Johnson et al., 2012) at the Kanyawara study site of Kibale National Park, Uganda (0.13 0.41°N; 30.19–30.32°E) from May until December 2015 (Bouquet et al., 2018). The troop is fully habituated to human presence and all adults and juveniles were individually identified. During the study period, the group consisted of between 39 and 44 individuals (7- 8 adult females, 2 subadult females, 7 - 11 adult males, 3 subadult males, 2 juvenile females, 13 juvenile males, 4 infant females and 1 infant male). At the time of the study, kinship between individuals was unknown.

6.3.2 Data collection

Data collection consisted of 1-hour focal animal sampling (Altmann, 1974). Grooming interactions were recorded continuously and, every 15 minutes, we collected instantaneous samples with the nearest neighbour of the focal animal and the identities of all adult females within a 10 m radius of the focal animal. We recorded these parameters because grooming and proximity are standard behavioural variables to calculate friendship indices (Silk, 2002; Silk, Alberts, et al., 2003). We recorded female-female dyadic approaches. We recorded 1-hour focal animal sampling and, every 10 min, we collected instantaneous samples of approaches. Approaches were defined as the focal animal crossing a 5 m radius around the perimeter of the partner individual. As soon as this happened, we recorded the behaviour of the focal and the partner and whether the focal uttered a grunt during the approach. Once an approach was recorded, we imposed a minimum of 10 min waiting time to consider the next interaction as a separate approach to avoid interdependency. We collected approaches data for 10 different females (total observation time: 30.6 hours).

6.3.3 Behavioural analyses

We calculated female dominance status using displacements, unidirectional fear barks by subordinates (Ransom, 1981) and aggressive interactions with clear a winner or loser (for definitions, see below). We designated individual dominance status using Elo-rating (Albers & De Vries, 2001; Neumann et al., 2011), based on the following logic. If two individuals interacted aggressively, the winner (i.e. the individual who chased or displaced another one) increased her Elo score, while the loser (i.e. the individual who got chased, displaced or who gave fear barks towards another one) decreased hers. If the two same individuals had another agonistic interaction and if the former winner won again, her Elo-score slightly increased. Conversely, if the former winner lost, the winner Elo-score decreased considerably.

To quantify social relationships, we used the dyadic social index (DSI), which assesses the affiliative relationship strength between two individuals relative to all other dyads in a group (Silk, Alberts, et al., 2006; Silk et al., 2013). To calculate this index, we collected data on the focal grooming partners, the focal nearest neighbours and the focal audience (i.e. all the adults in a 10 m radius circle around the focal). Grooming and proximity are standard variables to calculate friendship indices (Silk, 2002; Silk, Alberts, et al., 2003). Rather than categorising social relationships into strong and weak bonds (or friend vs. non-friend), we treated social relationship strength as a continuous variable (e.g. Duboscq et al., 2017). However, for ease of writing, we refer to ‘friends’ and ‘non-friends’, where ‘friend’ is shorthand for females with which the focal female had relatively large DSI values and ‘non-friend’ indicates low DSI values.

The behaviours of interest after approaches were affiliative behaviours and infant handling. We considered grooming, embracing and sitting in contact as affiliative behaviours. We defined infant handling when the focal female touched or muzzled another female's infant after an approach.

Previous research suggested that there are subtle acoustic differences between grunts directed at females with dependent infants and grunts directed at other individuals (Meise et al., 2011). We therefore separated the dataset, depending on whether the approached female had a dependent offspring (≤ 3 months; Silk, Rendall, et al., 2003).

6.3.4 Models and statistical analyses

To address our questions, we used multi-model inference (Burnham & Anderson, 2002; Burnham et al., 2011), which is based on the principle that models are ranked and weighted relatively to each other in order to obtain "…a quantitative measure of relative support for each competing models" (Grueber et al., 2011, p.699). We used Akaike's information criterion (AICc, corrected for small sample sizes) to rank the models. An important point here is that model rankings are relative, meaning that there will be always a relative "best" model, and evaluating fit of all candidate models should be used in conjunction with model ranking to assess whether the (best) model(s) are good in an absolute sense (Anderson, 2008; Dochtermann & Jenkins, 2011).

For inference, we used model weights, which represented normalised ratios of the difference of AICc between the target model and the best model in our candidate set. These model weights can be interpreted as probabilities that a given model is the best model in a set of models (Anderson, 2008). We fitted generalized linear mixed models with linear error structure and logit-link (Bolker et al., 2009). We reported evidence ratios which provide a measure of how much more likely the best model (i.e. with the highest weight) is than any of the remaining models in the model set (Burnham & Anderson, 2002; Symonds & Moussalli, 2011).

6.3.5 Analysis overview

In a first analysis, we were interested in how females produced grunts during approaches, whereas in a second analysis, we investigated if grunting increased the probability of affiliative behaviours or infant handling after an approach. Because we considered two contexts (infant present or not), we ran different analyses in each set (Fig A1 and Table 1). When an infant was present (i.e. when the partner had a dependant infant), we conducted one analysis for grunt occurrence and two analyses for interaction outcome (i.e. affiliative behaviours and infant handling). When there was no infant (i.e. the partner had no infant), we ran one analysis for grunt occurrence and one analysis for the affiliative behaviours outcome. We did not run analysis for the infant handling outcome, as infants had to be present to conduct this part.

Table 1: Overview of the different analyses carried out

	Causes ? → grunt		**Consequences** Grunt → ?		
Context	Without infant	With infant	Without infant	With infant	
Response	Grunt	Grunt	Affiliative behaviours	Affiliative behaviours	Infant handling
Observations	117	67	117	67	67
Number of models	6	6	16	16	14

6.3.6 Causes of grunt production

Frist, we were interested in whether relationship features predicted whether or not the focal female uttered a grunt while approaching another female. The response variable was grunt production of the focal (0/1), while focal female identity was the random intercept. We included combinations of the variables rank difference (i.e. Elo-rating difference) and friendship (i.e. DSI) as fixed effects and the focal's own rank (i.e. Elo-rating) as the control factor (i.e. it occurred in all models but the intercept-only model), including two-way interactions between rank difference and friendship strength, leading to total of six models (Table 2).

Table 2: Predictor variables used in the models when the approached female had or not a dependent infant and where grunting behaviour was the response variables

Model	DSI	Elo-rating difference	Elo-rating
'Friendship'	+		+
'Relative dominance'		+	+
Full	+	+	+
Interaction friendship X dominance	+*	+*	+
Null 1			
Null 2 ('Rank')			+

+: Variable included into the model;*: Interaction between two variables; Null 1: Intercept only model; Null 2: Informed null model

6.3.7 Consequences of grunt production

Second, we were interested in whether grunting influenced affiliative interactions and infant handling. We conducted two separated analyses, one with infant handling as the response variable (0/1) (Table 4) and another with affiliative behaviours as the response variable (0/1) (Table 3). For the latter, we separated the dataset into cases where partners were females with dependent offspring or females without dependent offspring (see above). We included grunting from the focal, relative dominance (i.e. Elo-rating difference) and friendship (i.e. DSI) as fixed effects, rank (i.e. Elo-rating) as control factor and built models with different combination of variables including two-way interactions (Tables 3 and 4). We then compared model with grunt variable with the same model without grunt variable to see if grunting added some weight to a given model (Table 7, 8 and 9). For example, when affiliative behaviours were the response variable and the partner infant was present, we compared the model with Elo-rating (Table A2, Model 1) with the model including the same variable plus the grunt variable (Table A2, Model 3) and inspected whether the model that included the grunt variable had higher weight or not, or in other words, whether the evidence ratio was in favour of the model with the grunt variable.

Table 3: Predictor variables used in the models when the approached female had or not a dependent infant and when *affiliative behaviour* was the response variables

Model	**DSI**	**Elo-rating difference**	**Elo-rating**	**Grunt**
1			+*	+*
2	+		+	
3			+	+
4	+*		+	+*
5		+	+	
6	+		+	+
7	+	+	+	
8		+	+	+
9	+*	+	+	+*
10		+*	+	+*
11	+*	+*	+	
12	+	+*	+	+*
13	+	+	+	+
14	+*	+*	+	+
Null				
Null 2			+	

+: Variable included into the model;*: Interaction between two variables; Null 1: Intercept only model; Null 2: Informed null model

Table 4: Predictor variables used in the models when the approached female had or not a dependent infant and when *infant handling* was the response variables

Model	**DSI**	**Elo-rating difference**	**Elo-rating**	**Grunt**
1			+*	+*
2	+		+	
3			+	+
4	+*		+	+*
5		+	+	
6	+		+	+
7	+	+	+	
8		+	+	+
9	+*	+	+	+*
10		+*	+	+*
11	+*	+*	+	
12	+	+*	+	+*
Null 1				
Null 2			+	

+: Variable included into the model;*: Interaction between two variables; Null 1: Intercept only model; Null 2: Informed null model

For the models designed to explore whether grunting predicted a social outcome, we included whether or not the focal or the partner received or gave affiliative behaviours as response variable and focal female identity as random intercept. We ran the analyses separately for approaches between females with and without infants. We obtained a total of sixteen different models for each context (Tables 3). We obtained these models by combining different variables and including two-way interactions for those variables for which it seemed most appropriate to us. For example, for model 3 in Table A3, we included the vocalization of the focal (production of grunts, yes or no) as studies have shown that grunting may facilitate subsequent friendly behaviours (Cheney et al., 1995b). We added the focal individual rank (i.e. Elo-rating) as high-ranking individuals tend to receive more affiliative behaviours, such as grooming, than subordinates (e.g. Schino, 2001).

For the models concerning whether grunt facilitated access to an infant, we included whether or not the focal handled the infant (response variable) and focal female identity as the random intercept. We obtained fourteen different models (Table 4). For instance, for model 2 in Table A4, we added friendship strength as a variable as we hypothesized that friends are more likely to handle infants as friends have better relationship. We included the individual rank (i.e. Elo-rating) as another variable as dominant mothers have greater access to infants than subordinates (Silk, Rendall, et al., 2003). Two of the 14 models did not properly converge and hence could not be included in the model ranking (see Table A4).

In all models, we included random slopes, in addition to random intercepts for female ID, to account for variation between individuals in how predictors affected the response variables, i.e. whether or not a grunt, an affiliative behaviour or handling an infant occurred (See Barr et al., 2013; Bates, Kliegl, et al., 2015). Since the focus of our study was grunting of the approaching female and how grunts affected outcomes of approaches, we only included uncorrelated random slopes for those variables that varied within focal female ID.

For both analyses, we also included a null model in our analyses. It comprised a fixed intercept and all random slopes for female ID of all the different models. The null model can be interpreted as none of the models explaining the occurrence of grunting, affiliative behaviour or infant handling. If the null model obtains a large weight (relative to the other models), then all models with a lower rank are highly unlikely to explain the data patterns. Conversely, if the null model obtains a small relative weight, other models have more explanatory power.

We added the individual rank (i.e. Elo-rating) as control factor as a variable in all models as individual rank could affect call rates and behaviours (Cheney & Seyfarth, 1985; Kitchen, Cheney, & Seyfarth, 2003; Schino, 2001; Silk, Rendall, et al., 2003).

We conducted all analyses in R (v. 3.4.0, R Core Team, 2017), using the following packages for R: lme4 (v. 1.1e12, Bates, Machler, et al., 2015), MuMIn (v. 1.16.6, Barton, 2016), EloRating (v. 0.43, Neumann & Kulik, 2014) and socialindices (v. 0.46e08, Neumann, 2016). Raw data used in this study will be made available on figshare (https://figshare.com)

6.4 Results

We observed a total of N=184 approaches between two females (Tables 1 and A1). N= 67 of these occurred between a focal female and another female with an infant and N=117 between the focal female and a female without infant. The overall mean call proportion was 25.1% (range 0.0 - 54.6%, N = 10 females; Table A1).

6.4.1 Causes of grunt production

When the approached female had an infant, the model with the highest weight contained the predictors DSI and Elo-rating, followed by the model with only Elo-rating as predictor (Table 5, "friendship": $w_i = 0.50$ vs. "Null 2": $w_i = 0.29$; ΔAICc = 1.06), meaning that the 'friendship' model was not substantially better than the 'rank' model, which served as our informed null model. All remaining models ranked lower than that null informed model.

Table 5: Causes of grunt production when the approached female had a dependent infant. Left column: predictor variables used in the models. Right column: results from multi-model inference

Variables				***Multi-model inference***				
Model	**DSI**	**Elo-rating difference**	**Elo-rating**	**K**	**AICc**	**ΔAICc**	w_i	**ER**
"Friendship"	+		+	6	84.9	0	0.5	-
Null 2 ("Rank")			+	4	85.9	1.06	0.29	1.7
"Relative dominance"		+	+	6	87.8	2.86	0.12	4.2
Full	+	+	+	8	89	4.1	0.06	8.3
Interaction friendship x dominance	+*	+*	+	9	91.4	6.54	0.02	25
Null 1				5	92.4	7.55	0.01	50

+: Variable included into the model;*: Interaction between two variables; Null 1: Intercept only model; Null 2: Informed null model; K: number of variables included; AICc: Akaike's information criterion corrected for small samples; ΔAICc: difference between the model with the lowest AICc and another model; w_i (Akaike weight): model probabilities; ER (evidence ratio): weight of the model with lowest AICc divided by the weight of another model

If females without infants were approached, the model with Elo-rating difference and Elo-rating ranked first (Table 6, 'relative dominance' model; $w_i = 0.39$), but it was almost indistinguishable from the 'rank' model (Table 6, Model Null 2; $w_i = 0.31$; ΔAICc = 0.47). The remaining models ranked below the informed null model.

Table 6: Causes of grunt production when the approached female had no dependent infants. Left column: predictor variables used in the models. Right column: results from multi-model inference

Variables				***Multi-model inference***				
Model	**DSI**	**Elo-rating difference**	**Elo-rating**	**K**	**AICc**	**ΔAICc**	w_i	**ER**
"Relative dominance"		+	+	6	84	0	0.39	-
Null 2			+	4	85.5	0.47	0.31	1.3
Null1				5	86.4	2.3	0.12	3.3
Full	+	+	+	9	86.7	2.68	0.1	3.9
Interaction friendship x dominance	+*	+*	+	8	88.5	4.46	0.04	9.8
"Friendship	+		+	6	88.9	4.87	0.03	13

+: Variable included into the model;*: Interaction between two variables; Null 1: Intercept only model; Null 2: Informed null model; K: number of variables included; AICc: Akaike's information criterion corrected for small samples; ΔAICc: difference between the model with the lowest AICc and another model; w_i (Akaike weight): model probabilities; ER (evidence ratio): weight of the model with lowest AICc divided by the weight of another model

6.4.2 Consequences of grunt production

In pairwise comparisons, models without grunting as the predictor variable were better (i.e. had higher weights) in explaining affiliative behaviour compared to models with grunting regardless of the presence or absence of infants (Tables 7 & 8). Similarly, if infant handling was the response variable models that contained grunting as a predictor did worse than those without grunting (Table 9). In other words, in all cases was the evidence ratio in favour of the model without grunting included.

Table 7: Pairwise comparisons of models with and without grunting (without infants): effects on affiliative behaviour

Model			***Better model***	***Model number (Table A3)***		***ER***
DSI	**Elo-rating difference**	**Elo-rating**		**Model with grunt**	**Model without grunt**	
		+	No grunt	1	Null 2	1.3
		+	No grunt	3	Null 2	3.6
+		+	No grunt	4	2	1.7
+		+	No grunt	6	2	3.6
	+	+	No grunt	8	5	2.6
+	+	+	No grunt	9	7	2.3
	+	+	No grunt	10	5	6.9
+	+	+	No grunt	12	7	2.9
+	+	+	No grunt	13	7	4.6
+	+	+	No grunt	14	7	11.8

ER (evidence ratio): weight of the model with higher AICc divided by the weight of the model with lower weight in a pair

Table 8: Pairwise comparisons of models with and without grunting (with infants): effects on affiliative behavior

Model			***Better model***	***Model number (Table A2)***		***ER***
DSI	**Elo-rating difference**	**Elo-rating**		**Model with grunt**	**Model without grunt**	
		+	No grunt	2	Null 2	10.6
		+	No grunt	4	Null 2	36.9
	+	+	No grunt	5	1	12
+		+	No grunt	8	3	12.5
	+	+	No grunt	9	1	40.2
+		+	No grunt	10	3	38.5
+	+	+	No grunt	11	6	14.7
+	+	+	No grunt	12	6	19
+	+	+	No grunt	13	6	48.4
+	+	+	No grunt	14	6	54.4

ER (evidence ratio): weight of the model with lower AICc divided by the weight of the model with higher AICc in a pair

Table 9: Pairwise comparisons of models with and without grunting (with infant): effects on infant handling

Model			***Better model***	***Model number (Table A4)***		***ER***
DSI	**Elo-rating difference**	**Elo-rating**		**Model with grunt**	**Model without grunt**	
		+	No grunt	2	Null 2	3.5
		+	No grunt	3	Null 2	8.3
+		+	No grunt	5	1	8.6
	+	+	No grunt	7	4	4.1
+		+	No grunt	9	1	73.7
+	+	+	No grunt	10	6	10.4
+	+	+	No grunt	11	6	25.5
+	+	+	No grunt	12	6	38.4

ER (evidence ratio): weight of the model with higher AICc divided by the weight of the model with lower weight in a pair

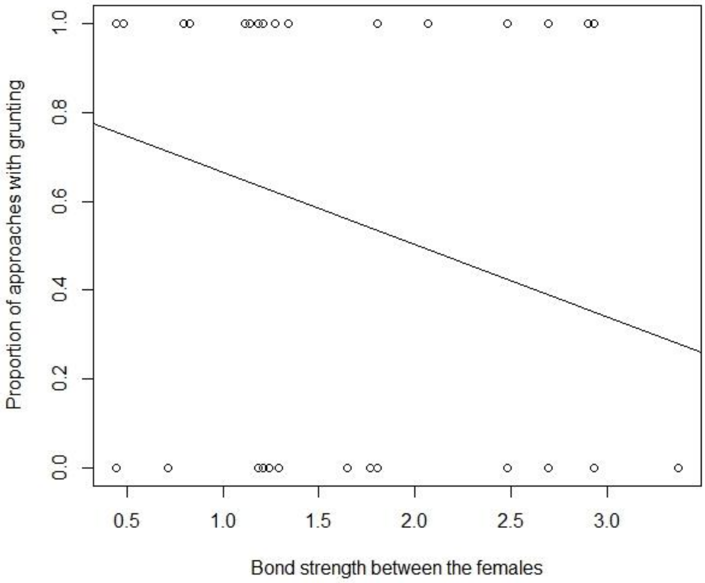


Figure 1: Proportion of approaches with grunting according to the bond strength between females when the partner has a dependent infant (N = 67; Basic analyses)

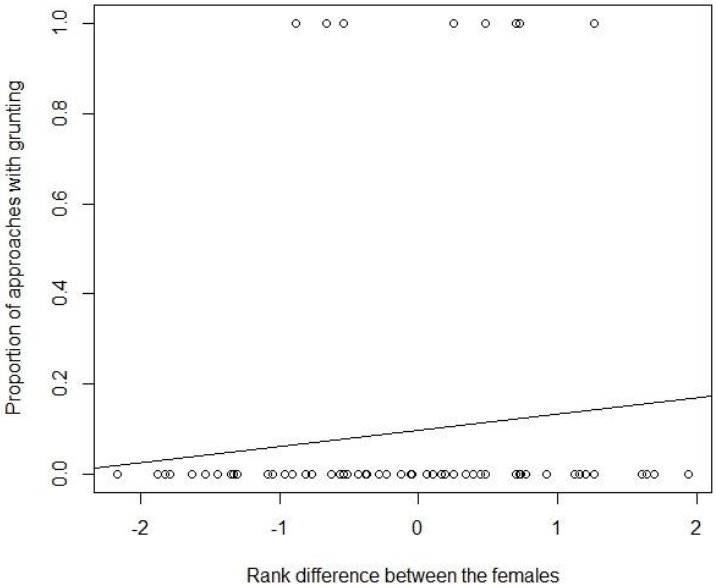


Figure 2: Proportion of approaches with grunting according to the rank difference between females when the partner does not have a dependent infant (N = 67; Basic analyses)

6.5 Discussion

In this study, we investigated the causes and consequences of grunt production in wild female olive baboons. In the first part, we analysed how bond strength and rank differences affected grunt utterance of females approaching mothers with dependent offspring or other females with no dependent infants. If infants were involved, the best model contained bond strength with grunting being more likely if bond strength was weak between the females (Fig 1). If no infants were involved, however, the best model contained rank differences with grunting being more likely if rank differences were large (Fig 2). Also relevant is that, with no infants involved, the friendship model became completely irrelevant, ranking last and much below the null model. However, in both cases the evidence for a role of dyadic features was weak at best because the model that only contained subjects' ranks (i.e. informed null model) also received substantial support.

Although our results did not conclusively explain the socio-cognitive factors driving female baboon grunting when approaching each other, one interesting finding was that the presence or absence of a dependent infant of the female partner changed the ranking of our models (Tables 5 and 6). When an infant is present, the model including the strength of social bonds and the focal rank as variables ranked first, whereas when an infant is absent, it is the model including the rank difference between the females and the focal rank as variables which ranked first. One possible reason for this change of strategy could have been that raising infants is energetically costly for female baboons (Altmann & Samuels, 1992; Bercovitch, 1987), even after weaning (Ross et al., 2011; Smuts, 1985). The presence of infants can also lead to severe strains in individuals relationships, exemplified by the fact that females sometimes kidnap each others' infants, which can last several days and can lead to infant dehydration or starvation (Brain, 1992; Hrdy, 1976; Shopland & Altmann, 1987). Moreover, adult males sometimes use infants as social buffers during agonistic interactions, which can be dangerous for infants (Smith & Whitten, 1988; Strum, 1983). Therefore, when an infant is present, the grunting behaviour of the focal female should change accordingly to these costs in order to be able to approach the female with a dependent offspring.

The effects we found, however, were not particularly strong and we can think of a number of possible explanations. One possible explanation is that we were unable to include kinship data in our models. Silk et al. (Silk et al., 2016) found that female chacma baboons were more likely to grunt towards sisters than towards mothers or daughters, a pattern that reflected the ambiguous relationship between sisters, as their level of aggression is higher than between mothers and daughters. Habitat could also be considered as an additional variable. Olive baboons in Budongo Forest, Uganda, utter grunts at higher rate in forest areas than in open habitat (Ey et al., 2009). The Kabasinguzi troop occupies mainly forest but crosses from time to time open areas, where their grunting behaviour could change.

6.5.1 Consequences of grunt production

In the second part of the study, we investigated whether grunting during approaches had an impact on subsequent social interactions. Our analysis strategy here was to run pairwise comparisons of models, each time with or without grunting as a predictor variable. Here, we found that, in all cases, the models without grunting explained the data better than the models with grunting, in contrast to previous findings in chacma baboons. Olive baboons thus draw a more nuanced picture of grunting behaviour than what has been reported in chacma baboons where grunting facilitates access to infants and predicts subsequent friendly behaviours (Cheney et al., 1995b; Silk, Rendall, et al., 2003).

One possible explanation is that, in most cases (75%), grunting was not needed in olive baboons because the interaction already developed in excepted ways, so that animals did not have an incentive to alter the outcome. If grunting occurred, then this probably was because the outcome was unclear, or the probability of conflict was high, although this was only in a minority of cases (25%).

Several other reasons could explain the surprising species differences with chacma baboons. First, different statistical methods were used. In the other studies, authors used null hypothesis testing, where one variable at the time is tested against the null hypothesis. They found significant results. However, other variables or combination of them could have play a role but were not tested. In our study, we used multi-model inference, where several variables and combination of them are tested and ranked against each other, which allows a broader view of grunting behaviour. Second, although the vocal structures of grunts are very similar in chacma and olive baboons (Ey et al., 2009; Owren et al., 1997) with grunt production rates also being very similar (chacma: 23-28% (Cheney et al., 1995b; Silk et al., 2016); olive: 25%), there may still be important differences in the underlying social perceptions. Most remarkably, there is an almost seven-fold difference in aggression rates between the two species (agonistic interactions per hour; chacma: 1.13 ± 0.12 (Ron et al., 1996); olive: 0.17±0.04 (Smuts & Nicolson, 1989)), and we suspect that this factor is mainly responsible for the interspecies differences. As aggression rates are high in chacma baboons, dominant females use grunts mainly to signal benign intent towards subordinates, in order to facilitate subsequent interactions with them (Cheney et al., 1995b). In olive baboons, however, this is less necessary, suggesting that animals do not need these signals to interact in a friendly way or with infants. One prediction is that grunting behaviour in Guinea baboons, *Papio papio*, a species living in socially tolerant social structures, with strong friendships between males, but less so between females (Patzelt et al., 2014; Patzelt et al., 2011), would be similar as olive baboons.

Our results raise an important question: Why then do olive baboons produce grunts at all? One interpretation is that animals seek to advertise their presence to other individuals and to attract attention to the caller (Hinde, 1981). There some evidences that baboons recognize each other’s voices (Cheney, Seyfarth, & Silk, 1995a), such that, by announcing their arrival, other individuals can anticipate who is approaching. Gorillas, *Gorilla gorilla*, produce “close-calls” that serve in this way, i.e. an exaggerated announcement of individual presence (Harcourt & Stewart, 1996). One prediction that directly follows from this hypothesis is that individuals who approach from behind should be more likely to grunt than individuals approaching face to face. In addition to this basic function, it is probably true that, even though aggression rates are low in olive baboons, females still benefit from advertising each other’s behavioural intentions. With low levels of aggression, social relationships other than dominance, such as friendships, are able to play a role, something that has not been reported in the highly aggressive chacma baboons.

6.5.2 Conclusions

We designed and compared models with different combinations of social variables (relative dominance and friendship) to examine the production of grunts, a relatively widespread vocalization in non-human primates, given during close range approaches. We then compared the relative strength of the models in their ability to explain observed patterns of grunts produced by wild female olive baboons and found that none of the combination of variables tested explained grunt utterance. However, the models ranking changed according to the presence or absence of young infants. When infants were present, the model including friendship received most support, whereas when infants were absent, the model including the relative dominance ranked first. In a second analysis, we found that models including grunt variable had little influence on certain subsequent outcomes, such as affiliative behaviours and infant handling. More studies are needed to understand the causes and consequences of grunt in olive baboons, such as including other more explanatory variables into models, testing other models or conducting playback experiments.

6.6 Appendix

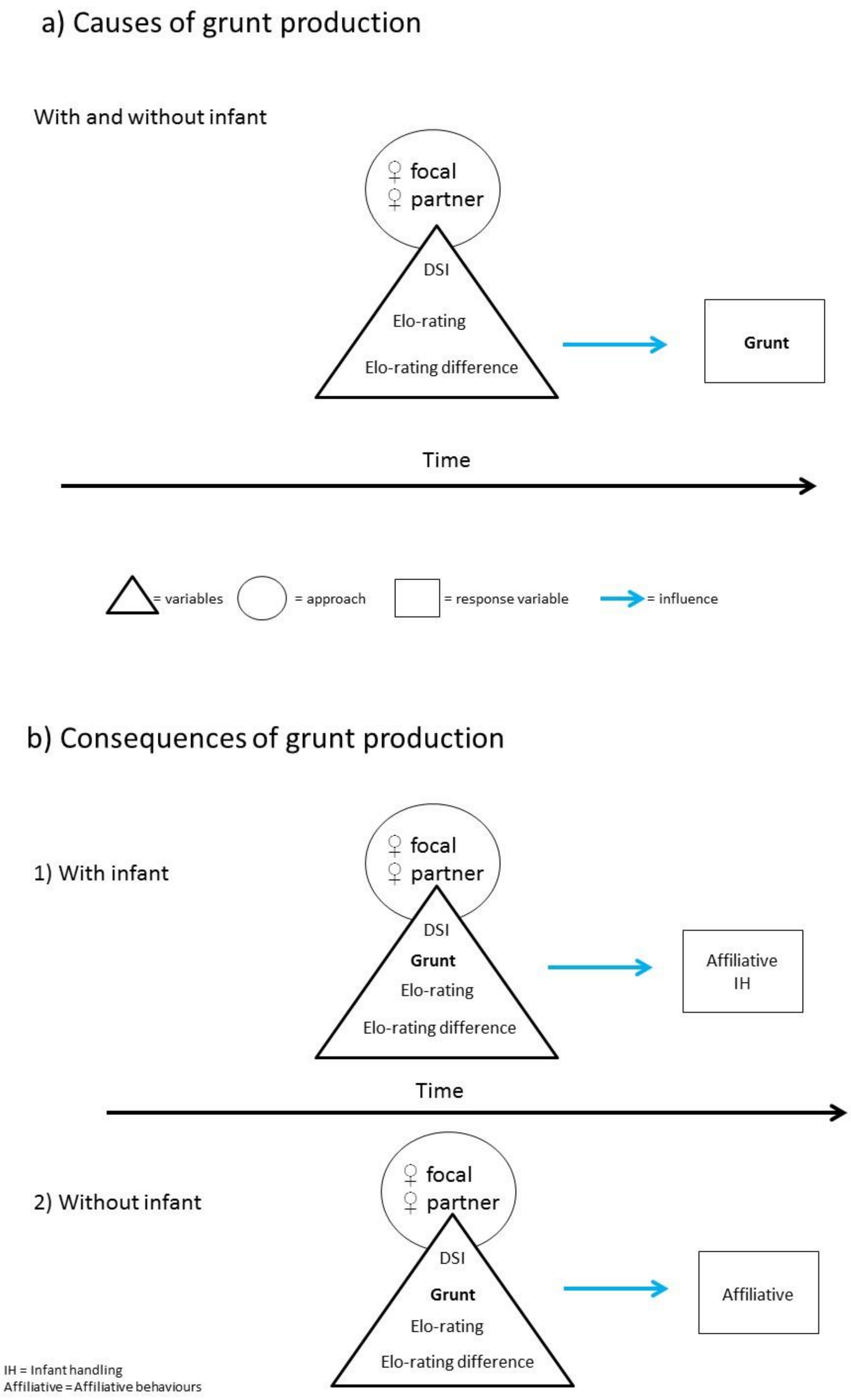


Figure A1: Graphic representation of the two analyses a) Grunt production with grunt as the response variable with and without the presence of dependent infants, b) Interaction outcomes analyses where b1) grunt is a fixed effect and affiliative behaviours or infant handling are the response variables when an infant was present, b2) grunt is a fixed effect and affiliative behaviours are the response variable when an infant was absent.

Table A1: Description of the focal females

ID female	**Female Elo-rating**	**N approaches**	**Percentage calling**
Hpy	1590	11	18.2
Els	*1565*	*15*	*0*
Sim	1413	8	12.5
Ema	1157	33	27.3
Nga	1070	12	16.7
Msa	835	20	35
Sce	816	9	44.4
Spe	665	17	17.6
Mga	*547*	*37*	*24.3*
Ria	342	22	54.6

Italic: Subadult female

Table A2: Multi-model inference results with affiliative behaviour as response variable when the approached female had a dependent infant. Left column: predictor variables used in the models. Right column: results from multi-model inference

Variables					***Multi-model inference***				
Model	**DSI**	**Elo-rating difference**	**Elo-rating**	**Grunt**	**K**	**AICc**	**ΔAICc**	w_i	**ER**
Null 2			+		4	72.5	0	0.71	-
1		+	+		6	76.7	4.25	0.09	8.4
2			+	+	6	77.2	4.72	0.07	10.6
3	+		+		6	77.2	4.75	0.07	10.8
Null 1					6	79.9	6.87	0.02	31
4			+*	+*	7	79.7	7.22	0.02	36.9
5		+	+	+	8	81.7	9.22	0.01	100.6
6	+	+	+		8	81.7	9.27	0.01	103
7	+*	+*	+		9	82.1	9.61	0.01	122.3
8	+		+	+	8	82.3	9.8	0.01	134.2
9		+*	+	+*	9	84.1	11.64	0	336.2
10	+*		+	+*	9	84.5	12.06	0	414.8
11	+	+	+	+	10	87.1	14.65	0	1515
12	+*	+*	+	+	11	87.6	15.16	0	1956.4
13	+*	+	+	+*	11	89.5	17.03	0	4988.1
14	+	+*	+	+*	11	89.7	17.26	0	5603

+: Variable included into the model;*: Interaction between two variables; Null 1: Intercept only model; Null 2: Informed null model; K: number of variables included; AICc: Akaike's information criterion corrected for small samples; ΔAICc: difference between the model with the lowest AICc and another model; w_i (Akaike weight): model probabilities; ER (evidence ratio): weight of the model with lowest AICc divided by the weight of another model

Table A3: Multi-model inference results with affiliative behaviour as response when the approached female had a no dependent infant. Left column: predictor variables used in the models. Right column: results from multi-model inference

Variables					***Multi-model inference***				
Model	**DSI**	**Elo-rating difference**	**Elo-rating**	**Grunt**	**K**	**AICc**	**ΔAICc**	w_i	**ER**
Null 2			+		4	130.1	0	0.3	-
1			+*	+*	7	130.6	0.5	0.23	1.3
2	+		+		6	131.8	1.75	0.12	2.4
3			+	+	6	132.6	2.54	0.08	3.6
4	+*		+	+*	9	132.9	2.8	0.07	4.1
Null 1					6	133.3	3.21	0.06	5
5		+	+		6	133.9	3.79	0.04	6.7
6	+		+	+	8	134.4	4.32	0.03	8.7
7	+	+	+		8	135.8	5.71	0.02	17.4
8		+	+	+	8	137	6.92	0.01	31.8
9	+*	+	+	+*	11	137.4	7.36	0.01	39.7
10		+*	+	+*	9	137.7	7.65	0.01	45.9
11	+*	+*	+		9	137.8	7.74	0.01	48
12	+	+*	+	+*	11	137.9	7.81	0.01	49.6
13	+	+	+	+	10	138.8	8.76	0	79.7
14	+*	+*	+	+	11	140.7	10.64	0	204.5

+: Variable included into the model;*: Interaction between two variables; Null 1: Intercept only model; Null 2: Informed null model; K: number of variables included; AICc: Akaike's information criterion corrected for small samples; ΔAICc: difference between the model with the lowest AICc and another model; w_i (Akaike weight): model probabilities; ER (evidence ratio): weight of the model with lowest AICc divided by the weight of another model

Table A4: Multi-model inference results with infant handling as response variable. Left column: predictor variables used in the models. Right column: results from multi-model inference

Variables					***Multi-model inference***				
Model	**DSI**	**Elo-rating difference**	**Elo-rating**	**Grunt**	**K**	**AICc**	**ΔAICc**	w_i	**ER**
Null 2			+		4	51.1	0	0.5	-
1	+		+		6	53.2	2.12	0.17	2.9
2			+	+	6	53.6	2.51	0.14	3.5
3			+*	+*	7	55.4	4.24	0.06	8.3
4		+	+		6	55.8	4.71	0.05	10.5
5	+		+	+	8	57.5	6.42	0.02	24.7
6	+	+	+		8	58	6.85	0.02	30.7
Null 1					6	58.3	7.14	0.01	35.5
7		+	+	+	8	58.7	7.56	0.01	43.9
8	+*	+*	+		9	60.3	9.14	0.01	96.4
9	+*		+	+*	10	61.8	10.72	0	212.7
10	+	+	+	+	10	62.7	11.53	0	319
11	+*	+	+	+*	11	64.4	13.32	0	782
12	+*	+*	+	+	11	65.3	14.14	0	1178.5
13**		+*	+	+*					
14**	+	+*	+	+*					

+: Variable included into the model;*: Interaction between two variables; Null 1: Intercept only model; Null 2: Informed null model; K: number of variables included; AICc: Akaike's information criterion corrected for small samples; ΔAICc: difference between the model with the lowest AICc and another model; w_i (Akaike weight): model probabilities; ER (evidence ratio): weight of the model with lowest AICc divided by the weight of another model

7 General discussion

7.1 Summary of findings

The main goal of this thesis was to examine how wild olive baboons minimize the costs of living in groups by using vocal communication in two specific contexts: Reproduction and close-range interactions. To address this topic, I carried out a pilot study with a group of olive baboons at Gashaka Gumti National Park in Nigeria and the main research project with another group of olive baboons at Kibale National Park, Uganda, which consisted of three different studies.

In the first study, I focused on the function of females' copulation calls in Kabasinguzi troop (chapter 4). Several functions for the utterance of copulation calls in primates have been proposed, but without a clear consensus. We tested three functional hypotheses that are in line with olive baboon sexual behaviour, i.e., sperm competition, female choice and male-male competition. I recorded 203 copulation events from five different females mating with eight different males. Overall, the females called in 60% of the cases. Using a multi-model inference approach, we then built different models, each corresponding to one of the different hypotheses, with combinations of variables related to environment, audience composition and male and female characteristics (i.e. dominance, social bonds). I then compared and ranked the different models and found that the sperm competition hypothesis was the most likely explanation for the utterance of copulation calls. There was some additional evidence for the female choice hypothesis but male-male competition seemed unlikely. Taken together, these results raise the possibility that copulation calls may be multifunctional. As females did not call in 40% of the mounts, I proposed that remaining silent could be functional. For instance, it might be beneficial for females to conceal copulations to avoid postcopulatory aggressions from certain males (le Roux et al., 2013). I also suggested that copulation calls could carry information on two levels: In the utterance, i.e. calling or not, and in the acoustic structure of the calls.

Following from the findings of the first study, I then examined the variation in the temporal acoustic parameters of copulation calls in wild olive baboons (chapter 5). Using information theory, I again designed different models representing different functional hypotheses (i.e. sperm competition, female choice and male-male competition). I conducted two separated analyses. First, I replicated the models used in chapter 4 (Bouquet et al., 2018). Second, I then built on these models by adding variables that took into account how many times the female switched mating partners in a given day (i.e. the 'male index') and how many times the consort female mated with the same male in a row (i.e. the 'copulation index'). As olive baboon copulation calls are composed of chaotic vocal elements, I did not manage to extract frequency parameters but it was possible to analyse the following temporal measures: call duration, number of vocal elements and mean duration of vocal and inter elements. In the first study, I recorded 103 mating events from six different females copulating with six adult and nine juvenile males during daily scan follows and opportunistic mating. In the second study, I observed 60 copulation calls from six different females mating with five adult and eight juvenile males. This data set did not comprise the same number of copulation calls as in the first analyse as I used only vocalizations that I recorded during daily scan follows. In the first analysis, I found that the sperm competition hypothesis was the best explanation for the variation of the number of elements, which was in agreement with our previous findings (Bouquet et al., 2018). I also found some partial support for the female choice hypothesis when considering the mean duration of inter elements, another finding reported in the previous chapter (Bouquet et al., 2018). In the second analysis, I demonstrated that, when the previous copulatory history of the calling female was added into the models, all three functional hypotheses received some support. Overall, I propose that, at the ultimate level, the social organisation of this species, particularly the low rate of infanticide and the unstable male dominance hierarchy (during the study period or in general for this species) may provide limited socio-contextual pressures that would favour the evolution of more advanced mating strategies than just obtaining high-quality sperm. However, at a more proximate level, I suggest that consort females adjust their behaviour flexibly and employ different strategies depending on their relative benefits following copulation.

In the third study, I investigated the causes and consequences of female social grunts, a vocalization given at close-range (chapter 6). It has been argued that grunt utterance is driven by several mechanisms, including dominance and friendship (Silk, 2002; Silk et al., 2013). Grunts seem also to facilitate friendly interactions (i.e., grooming) (Cheney et al., 1995b) and to facilitate the access to young infants (Silk, Rendall, et al., 2003).

Using multi-model inference, I conducted two separated analyses. In the first analysis, I was interested in the effects of dominance and friendship on grunt utterance. In the second analysis, I investigated whether grunts facilitate subsequent interactions, that is, how rank difference, friendship, and vocal production influenced subsequent social behaviours. As there are acoustic differences between grunts given towards mothers with dependent infants (i.e. infant grunts) and grunts given towards other females (i.e. social grunts), I separated each analysis into two different sets. I found that none of the tested variables combination explained grunt production. However, the presence or absence of young infants changed their relative rankings of the models, suggesting that motherhood changes the salient features of a relationship between two females. I demonstrated that grunting only had minor effects on subsequent social interactions, regardless of the presence of an infant, suggesting that females call when what they reach for is indeterminate. I further proposed that grunting might function to advertise the individual presence.

7.2 Sperm competition

Both studies on the utterance and acoustic structure of female olive baboon copulation calls highlight the importance of the sperm competition hypothesis. This hypothesis is in line with several aspects of olive baboon sexual behaviour. Females mate with several different males during their cycles (Bercovitch, 1991; Danish & Palombit, 2014). Furthermore, the females call at the end of the mount, supposedly just before the ejaculation takes place, allowing the consorting male to deposit his sperm and simultaneously attract non-consorting males from the audience. In addition, females usually run away, up to 100m, after a mount, allowing non-consorting males to take over the consortship (Smuts, 1985). Finally, male olive baboons have relative large testes in comparison to body size, enabling them to deposit a large amount of sperm per ejaculation (Bercovitch, 1989; Harcourt et al., 1981).

How did this mating strategy evolve in olive baboons? First, as infanticide rates are low in this species (Palombit, 2003), females do not have to seek out dominant males to obtain protection for their current and future offspring. In primate species where infanticide is high females should concentrate paternity to high-ranking individuals to gain their protection for their future offspring. Second, the stability of the male hierarchy may be another factor. During this study, it was particularly instable because one male immigrated whereas four emigrated. This was in contrast with what I observed during my almost one-year pilot study in Nigeria where only one new male immigrated. If male turnover is high females should not concentrate their mating efforts to dominant individuals as they might have been displaced by other males at the time their infants are born. A low rate of infanticide and an unstable male hierarchy might lead female primates to employ sperm competition as a mating strategy.

Another possible sperm competition species is Barbary macaques that have a promiscuous mating system, with low rates of male infanticide (Angst & Thommen, 1977) and unstable male hierarchies (Berghänel, Ostner, & Schülke, 2011). Several studies demonstrated that females of this species use sperm competition as a mating strategy (Pfefferle, Brauch, et al., 2008; Pfefferle, Heistermann, Hodges, & Fischer, 2008).

A possible explanation for why the females from the Kabasinguzi troop rely on sperm competition as a reproductive strategy may reside in the fact that this troop has an unusual sex ratio of 1:1 (usually 2:1 (Smuts, 1985)). This allows females to collect more sperm from different males compared to species with relatively fewer number of males also because there is less intra-sexual competition for mating partners. Another explanation could be the unstable male hierarchy during the study period as mentioned above. Finally, the forest environment of the study group could allow consort females to switch mating partners more easily. As consort females run away when the mount is over, partner switching may be easier than in less dense vegetation.

7.3 Flexibility

Although olive baboons seem to employ sperm competition as a mating strategy, I found some support for the female choice hypothesis, which suggests that copulation calls could be multifunctional. This may be because olive baboons exhibit flexibility in their calling behaviour, depending on the relative benefits at the time of copulation. Several factors could lead to changes in female strategy, such as the female's age or the composition of the audience. Fallon et al. (Fallon et al., 2016) found that nulliparous and parous female chimpanzees produce different copulation call rates, with nulliparous females being less attractive to males than parous females. Intra- and intersexual competition also played a role with females increasing their calling as a function of the number of other females in oestrous in the group (Fallon et al., 2016).

As mentioned above, my study group had an unusual sex ratio, with a relatively high number of males. I suspect that with fewer males, females would have switched from sperm competition to female choice. Here, it might have been more beneficial for females to "secure" a male by calling to increase his mate guarding. Females should run away shorter distances after the mount or should not run at all. Consequently, the other competing females would not have access to this particular male. I also found that the identity of the mating partner affected the rate of copulation calls, suggesting that the females' interaction histories with the different males affected copulation call rates. If females indeed keep track of who they mated with and adjust their signal output accordingly, this would suggests a surprising level of cognitive complexity.

In 40 % of mounts, females remained silent while copulating. This behaviour demonstrates flexibility and suggests that females might tactically supress their calls to conceal some matings, perhaps to avoid postcopulatory aggression (le Roux et al., 2013). Although anecdotal, I witnessed a nulliparous female copulating with a juvenile male not far from the adult consort male in dense forest. Strikingly she did not vocalize nor run after the mount, suggesting that she was aware of the consequences of her behaviour.

Female olive baboons exhibit flexibility not only in their copulation calls but also in their social grunts. Females utter grunts in only 25% of approaches. One interpretation here is that, in most cases (75%), the interaction between the two females already developed in expected ways, such that signalling was unnecessary. If grunting occurred, it was probably because the outcome was unclear or there was a danger of aggression.

An interesting finding in this study, further demonstrating flexibility in call production, was that the presence of young infants changed the relationship features that females used to determine grunt production. If infants were present, the friendship model received most support, whereas if infants were absent, the dominance model ranked first, which suggests that females assess each others' relationships at different levels. I am not aware of similar findings in the literature, apart from a study on vervet monkeys where the presence of infants altered adult vocal behaviour, such that females uttered more alarm calls in the presence of kin than non-related individuals (Cheney & Seyfarth, 1985).

7.4 Simple signals

The social complexity hypothesis states that social life acts as a selective pressure that favours the evolution of greater cognitive abilities (Byrne & Whiten, 1989; Humphrey, 1976; Jolly, 1966). This hypothesis has support by vocalisation studies, with evidence that species with complex social systems have more complex communicative systems than those with more simple social systems, possibly to regulate interactions and relations among group members (Freeberg, Dunbar, & Ord, 2012). Bouchet et al. (Bouchet, Blois-Heulin, & Lemasson, 2013), for example, examined the vocal variability of several primate species. They found that red-capped mangabeys, *Cerocebus torquatus*, had the most complex social structure and displayed the largest and most complex vocal repertoire, whereas De Brazza's monkeys, *Cercopithecus neglectus*, the species with the simplest social structure, displayed the smallest and simplest repertoire. Interestingly, the same effect is also seen within species. For instance, Carolina chickadees, *Poecile carolinensis*, utter calls with greater complexity (i.e. with more information) in larger groups than in smaller groups (Freeberg, 2006).

The number of individuals of the Kabasinguzi troop varied from 39 to 44 during my study, which represents already a complex group. Overall, however, I did not get a sense of a complex vocal system. Moreover, the two vocalizations that I studied are acoustically relatively simple: They are short atonal bursts of acoustic energy, with no involvement of the larynx, i.e. no visible fundamental frequencies or harmonics. Complexity was more in terms of how subjects deployed their signals in social interactions, but not in terms of acoustic structure. Low level of aggression and infanticide in this species (Palombit, 2003; Smuts & Nicolson, 1989), that is, relatively relaxed social conditions, may be at the source of this, suggesting that signal complexity does not emerge if there is no need to constantly interfere with other group members' behaviour.

In summary, the two vocalizations that I studied, copulation calls and grunts, are acoustically simple, have evolved under relaxed social pressure. However, I also found that both calls are flexible in how they were uttered, a possible sign of complex cognitive capacities.

7.5 Limitations and perspectives

7.5.1 Methodological considerations

The studies on this thesis are subject to various limitations that need to be highlighted. One limitation concerns a number of variables that I did not measure and, therefore, not include into the models. Male ejaculation, for example, is crucial for the sperm competition hypothesis where the females' main goal is to collect sperm from all males. For instance, in chacma baboons, female copulation calls were longer if the consort male ejaculated than if he did not (O'Connell & Cowlishaw, 1994). Determining the presence of ejaculation is difficult (Hausfater, 1975; Personal observations), although there are behavioural indicators, as males appear to stop thrusting for a few seconds just before ejaculating, the "ejaculatory pause" (Hausfater, 1975; Smuts, 1985), which is easily observable. I began to record this behaviour but unfortunately not in a systematic way.

Hormone levels, such as progesterone and oestrogen, are other variables that would have been relevant in some of the models to estimate the timing of ovulation. There is important variation in these hormone levels around the time of ovulation (Higham, Heistermann, et al., 2008), suggesting that females could either honestly advertise or tactically conceal the timing. Several studies demonstrated that, in different species, female primates did not encode information about ovulation in their copulation calls (Engelhardt et al., 2012; Pfefferle, Heistermann, Pirow, Hodges, & Fischer, 2011), so it would have been interesting to study the effects of these variable on model performance. Females produce sexual swelling around the time of ovulation, so I included whether or not the female was fully swollen in the analyses, although this was a very approximate way of estimating ovulation. For hormones levels, I would have expected females to hide their reproductive status under sperm competition, as they want to stay attractive to as many males as possible to collect their sperm. Conversely, under female choice and male-male competition they should provide honest information about their reproductive status in their vocal behaviour, either to concentrate paternity to one or several dominant males or to announce that they are close to ovulation and therefore incite male competition, respectively.

Regarding the social dynamics in the group, it would be interesting to conduct the same study during a period with more stability in the male hierarchy, i.e. with less male migration. It would be interesting to see if, under such conditions, females still employed sperm competition as their main reproductive strategy or if they switched their mating efforts towards the dominant males.

Finally, kinship would have been a useful variable to add to the models, especially for the social grunts study. For example, Silk et al. (Silk et al., 2016) found that female chacma baboons were more likely to grunt towards females with whom they had the most ambivalent relationships, suggesting that grunting could serve to reduce uncertainty about the likelihood of subsequent outcomes. Unfortunately, I was unable to determine the kinship relations between the individuals, as no genetic data were available at the time of the study for the Kabasinguzi troop.

7.5.2 Future research

Copulation calls

In line with the previous considerations, in future research it would be important to collect data on whether or not the consort male ejaculates during the mount (see above) and analyse whether ejaculation is encoded in the acoustic structure of vocalizations. Such data would help to further investigate if sperm competition is a common strategy used by female olive baboons. If this were the case, it would also be possible to use a design developed by Pfefferle et al. (Pfefferle, Heistermann, et al., 2008), i.e. playback of copulation calls recording with or without ejaculation, to investigate nonconsorting male responses. In Barbary macaques the calls given during ejaculatory matings elicited more rapid and stronger reactions from nonconsorting males than calls given during non-ejaculatory matings. Further, the authors found that non-consorting males spent more time in the vicinity of the call-providing female, after the playback. The sperm competition hypothesis predicts that consort females call to attract males' attention to their receptivity, suggesting that similar behaviour patterns would be expected from non-consorting male olive baboons. Another possibility to further test the sperm competition hypothesis is to analyse whether consort females "keep track" of the males they mated with. I should expect that females stop calling once they mate with every adult males of the troop.

As consort females remained silent in 40% of mounts, it may also be possible to build a model to test whether consort females conceal some of their matings. This model would contain the following variables: Whether the mating male is the normally associated male, his consorting distance, habitat visibility, the swelling state of the female and her location relative to the other males.

Regarding copulation call structure, future research may want to include the spectral features of calls, but this may require more complex procedures, such as automated feature extraction coupled with machine learning. This method allows extracting and analysing large numbers of acoustic features and it not limited to tonal (laryngeally produced) calls. For example, Fedurek et al. (Fedurek, Zuberbühler, & Dahl, 2016) demonstrated that the four phases of chimpanzees pant-hoots, a long and syntactically complex call utterance, contained different levels of social information, that is, the age of the caller (introduction and build-up phase), the rank (climax phase) and the general activity of the caller (let-down phase). Caller identity was apparent in all four phases. Whether or not spectral features would lead to different results regarding the function of copulation calls is unclear.

Social grunts

Regarding the social grunts, I proposed that these calls functioned to announce the presence of an arriving individual. To further test this hypothesis, the visual perspectives of interacting individuals should matter, such that, for example, grunts should be more common to individuals with their backs turned to the caller than other individuals. Moreover, in my analyses I only focussed on female-female dyads. Further studies could investigate female-male or male-male dyads to see whether the same models explain the interaction patterns as descried for the female-female dyads.

Social grunts play a role in infant handling and the subsequent friendly interactions, but it is unclear whether subjects use this call for other functions, such as reconciliation after agonistic interactions. Cheney et al. (Cheney et al., 1995b) used playback experiments to demonstrate that subordinates responded less strongly to threatening screams when dominants reconciled with grunts than when they did not interact with them again, a study that could be replicated with olive baboons.

Finally, several studies examined the mechanisms and functions of grunts in chacma baboons (Cheney et al., 1995b; Silk, Rendall, et al., 2003) but data were analysed with classic null hypothesis testing and not model inference theory. Therefore, it would be interesting to compare chacma and olive baboons grunting behaviour with the same statistical tools.

7.6 Conclusions

Overall, my research shows that female olive baboons seem to rely on sperm competition as a mating strategy. However, I find some support for the other functional hypotheses, suggesting that copulation calls could be multifunctional. For the social grunts, I find that the presence of a young infant alters how female olive baboons utter their grunts. As a general conclusion, these findings demonstrate that, although copulation call and social grunts are acoustically simple vocalizations, their production is most likely under cognitive control as calls are uttered in flexible ways to maximise the callers’ benefits in constantly changing socio-ecological environments.

8 General acknowledgments

I would like to thank Klaus Zuberbühler who gave me this amazing opportunity and privilege to work with wild primates, for his support, discussions and for all the hours that he spent correcting the present thesis.

I would like to thank Stuart Semple for his role as expert and his kindness. I would also like to thank Redouan Bshary who first sent me to Africa to study vervet monkeys and drink savannahs, for his kindness and his role as an expert.

Un énorme merci à Reinhard qui m'a beaucoup soutenue durant l'écriture de cette thèse et qui a passé de nombreuses heures à me relire.

I am more than grateful to Christof (R God), Eloïse (Dingo Lady) and Claudia for their patience with me, their kindness and twisted sense of humour, their precious advices and explanations. This thesis would simply not have been possible without them. They make me a better scientist.

My fieldwork would not have been possible without the precious help of Moses Araali Kugonza, Godfrey Adyeri, Edward Akiiki, Halidu Lliyasu (Dandy), Buba Hammaselbe, Ibrahim Usman, Maigari Ahmadu, Maikanti Hassan, Hammaunde Guruza. For their unbelievable talent to find the baboons and their way back to the camp, their help to recognize them, their kindness and generosity.

I would like to thank my incredible volunteers Lucretia Deplaces (Schätzeli) and Cecily Pulver (Slave) who were brave enough to follow me to run after baboons. For their help collecting the data, their unshakeable friendship, their motivation and hard work, their laughs and craziness, their love for the baboons and their moral support in the difficult times. I am also very grateful to Adriana Lowe (English Rose) who supported me during hard times. For her help in the field and drinking palm vine in front of silly TV movies.

I would like to thank Volker Sommer and Jessica Rothman who allowed me to work on their field sites and for their help for the administrative matters.

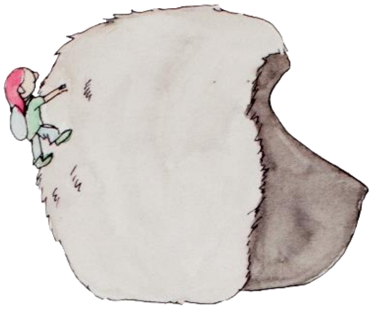
Many thanks to my incredible friends/colleagues Stéph', Coco, Emilie, Noémie, Mélissa (Pink Poney), Julie, Gladez and Alice. For their precious friendship, their amazing support, their laughs, their drunkenness, their hugs and their huge sense of humor.

Un énormissime merci à mes merveilleuses et incroyables amies Celia, N'Astrid et Chris. Pour leurs encouragements, leur aide, leur indéfectible soutien durant mes périodes sombres, leurs blagues idiotes, leur écoute attentive et leur folie.

Je tiens à remercier Guillaume (Lapin) pour ces illustrations grandioses. Pour avoir supporté ma mauvaise humeur et de m'avoir cuisiné de bons petits plats. Pour son rire communicatif et sa gentillesse, son soutien et sa culture.

Mille mercis à mes parents (Génitrice et Géniteur) et à mon frère (Le Nain) d'avoir pris soin de moi, de m'avoir offert un lieu de refuge et de m'avoir permis de leur présenter mes précieux poilus. Pour leurs discussions autours de bons repas, leurs rires et leur soutien moral, logistique et financier.

Last but not least a huge thank you to my precious and fluffy baboons from the Kwano and the Kabasinguzi troops. For tolerating my presence amongst them and showing me their incredible behaviours. To walk with them in the forest was pure happiness and one of the best time of my life.



9 Bibliography

Adanu, J., Sommer, V., & Fowler, A. (2011). Hunters, fire, cattle: Conservation challenges in Eastern Nigeria, with special reference to chimpanzees. In V. Sommer & C. Ross (Eds.), *Primate of Gashaka, Socioecology and conservation in Nigeria's biodiversity hotspot* (pp. 55-99): Springer.

Aich, H., Moos-Heilen, R., & Zimmermann, E. (1990). Vocalizations of adult gelada baboons (*Theropithecus gelada)*: Acoustic structure and behavioural context. *Folia Primatologica, 55*, 109-132.

Albers, P. C. H., & De Vries, H. (2001). Elo-rating as a tool in the sequential estimation of dominance strenghts. *Animal Behaviour, 61*, 489-495.

Alberts, S. C., & Altmann, J. (2001). Immigration and hybridization patterns of yellow and anubis baboons in and around Amboseli, Kenya. *American Journal of Primatology, 53*(4), 139-154. doi:doi:10.1002/ajp.1

Altmann, J. (1974). Observational study of behavior - sampling methods. *Behaviour, 49*(3-4), 227-267. doi:10.1163/156853974x00534

Altmann, J. (1980). *Baboon mothers and infants*: The University of Chicago Press.

Altmann, J., Altmann, S. A., Hausfater, G., & McCuskey, S. A. (1977). Life history of yellow baboons: physical development, reproductive parameters, and infant mortality. *Primates, 18*(2), 315-330.

Altmann, J., & Samuels, A. (1992). Costs of maternal care: infant-carrying in baboons. *Behavioral Ecology and Sociobiology, 29*(6), 391-398. doi:10.1007/bf00170168

Anderson, C. (1986). Female age, male preference and reproductive success in primates. *International Journal of Primatology, 7*(3), 305-326. doi:10.1007/bf02736394

Anderson, D. (2008). *Model based inference in the life science: a primer on evidence* (N. Y. Springer Ed.).

Andersson, M. (1994). *Sexual selection*. Princeton, New Jersey: Princeton University Press.

Angst, W., & Thommen, D. (1977). New data and a discussion on infant killing in Old world monkeys and apes. *Folia Primatologica*(27), 198-229.

Arnold, K., & Zuberbühler, K. (2006). The alarm-calling system of adult male putty-nosed monkeys, Cercopithecus nictitans martini. *Animal Behaviour, 72*, 643-653. doi:10.1016/j.anbehav.2005.11.017

Aujard, F., Heistermann, M., Thierry, B., & Hodges, J. K. (1998). Functional significance of behavioral, morphological, and endocrine correlates across the ovarian cycle in semifree ranging female Tonkean macaques. *American Journal of Primatology, 46*(4), 285-309.

Barclay, R. M. R., & Thomas, D. W. (1979). Copulation Call of Myotis lucifugus: A Discrete Situation-Specific Communication Signal. *Journal of Mammalogy, 60*(3), 632-634. doi:10.2307/1380109

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language, 68*(3), 255-278. doi:http://dx.doi.org/10.1016/j.jml.2012.11.001

Barton, K. (2016). MuMIn: Multi-Model Inference. R package version 1.15.6. https://CRAN.R-project.org/package=MuMIn.

Bates, D., Kliegl, R., Vasishth, S., & Baayen, H. (2015). Parsimonious mixed models. http://arxiv.org/abs/1506.04967.

Bates, D., Machler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1-48.

Bauers, K. A. (1993). A Functional Analysis of Staccato Grunt Vocalizations in the Stumptailed Macaque (Macaca arctoides). *Ethology, 94*(2), 147-161. doi:10.1111/j.1439-0310.1993.tb00555.x

Bercovitch, F. B. (1983). Time budgets and consortships in olive baboons (Papio anubis). *Folia Primatologica, 41*(3-4), 180-190. doi:10.1159/000156130

Bercovitch, F. B. (1987). Female weight and reproductive condition in a population of olive baboons (Papio anubis). *American Journal of Primatology, 12*(2), 189-195.

Bercovitch, F. B. (1988). Coalitions, cooperation and reproductive tactics among adult male baboons. *Animal Behaviour, 36*(4), 1198-1209. doi:http://dx.doi.org/10.1016/S0003-3472(88)80079-4

Bercovitch, F. B. (1989). Body size, sperm competition, and determinants of reproductive success in male savanna baboons. *Evolution, 43*(7), 1507-1521. doi:10.2307/2409465

Bercovitch, F. B. (1991). Mate selection, consortship formation, and reproductive tactics in adult females savanna baboons. *Primates, 32*(4), 437-452. doi:10.1007/bf02381935

Berghänel, A., Ostner, J., & Schülke, O. (2011). Coalitions destabilize dyadic dominance relationships in male Barbary macaques (). *Behaviour, 148*(11-13), 1256-1274. doi:doi:https://doi.org/10.1163/000579511X600628

Bocci, A., Telford, M., & Laiolo, P. (2013). Determinants of the acoustic behaviour of red deer during breeding in a wild alpine population, and implications for species survey. *Ethology Ecology & Evolution, 25*(1), 52-69. doi:10.1080/03949370.2012.705331

Boesch, C., Kohou, G., Néné, H., & Vigilant, L. (2006). Male competition and paternity in wild chimpanzees of the Taï forest. *American Journal of Physical Anthropology, 130*(1), 103-115. doi:doi:10.1002/ajpa.20341

Boinski, S., & Campbell, A. F. (1995). Use of Trill Vocalizations To Coordinate Troop Movement Among White-Faced Capuchins: a Second Field Test. *Behaviour, 132*(11), 875-901. doi:doi:https://doi.org/10.1163/156853995X00054

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution, 24*(3), 127-135. doi:10.1016/j.tree.2008.10.008

Bouchet, H., Blois-Heulin, C., & Lemasson, A. (2013). Social complexity parallels vocal complexity: a comparison of three non-human primate species. *Frontiers in Psychology, 4*(390). doi:10.3389/fpsyg.2013.00390

Bouchet, H., Koda, H., Masataka, N., & Lemasson, A. (2016). Vocal flexibility in nonhuman primates and the origins of human language. *Revue de primatologie*. doi:10.4000/primatologie.2637

Bouquet, Y., Stephan, C., Johnson, C. A., Rothman, J. M., Neumann, C., & Zuberbühler, K. (2018). Comparing functions of copulation calls in wild olive baboons, Papio anubis, using multimodel inference. *Animal Behaviour, 135*, 187-197. doi:https://doi.org/10.1016/j.anbehav.2017.11.019

Brain, C. (1992). Deaths in a desert baboon troop. *International Journal of Primatology, 13*(6), 593-599. doi:10.1007/bf02551255

Brown, R. N., & Lemon, R. (1979). Structure and evolution of song form in the wrens Thryothorus sinaloa and T. felix. *Behavioral Ecology and Sociobiology, 5*(2), 111-131.

Buchan, J. C., Alberts, S. C., Silk, J. B., & Altmann, J. (2003). True paternal care in a multi-male primate society. *Nature, 425*(6954), 179-181. doi:10.1038/nature01866

Bulger, J. B. (1993). Dominance rank and access to estrous females in male savanna baboons. *Behaviour, 127*(1), 67-103. doi:doi:https://doi.org/10.1163/156853993X00434

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and model inference: A practical information-theoric approach*: Springer.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology, 65*(1), 23-35. doi:10.1007/s00265-010-1029-6

Byrne, R., & Whiten, A. (1989). *Machiavellian Intelligence : Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans (Oxford Science Publications)*: {Oxford University Press, USA}.

Caine, N. G., Addington, R. L., & Windfelder, T. L. (1995). Factors affecting the rates of food calls given by red-bellied tamarins. *Animal Behaviour, 50*, 53-60. doi:10.1006/anbe.1995.0220

Chapman, C. A., Chapman, L. J., Wrangham, R., Isabirye-Basuta, G., & Ben-David, K. (1997). Spatial and temporal variability in the structure of a tropical forest. *African Journal of Ecology, 35*(4), 287-302. doi:doi:10.1111/j.1365-2028.1997.083-89083.x

Chapman, C. A., & Lefebvre, L. (1990). Manipulating foraging group size: spider monkey food calls at fruiting trees. *Animal Behaviour, 39*(5), 891-896.

Cheney, D. L., & Seyfarth, R. M. (1982). How vervet monkeys perceive their grunts: Field playback experiments. *Animal Behaviour, 30*(3), 739-751. doi:https://doi.org/10.1016/S0003-3472(82)80146-2

Cheney, D. L., & Seyfarth, R. M. (1985). Vervet monkey alarm calls - Manipulation through shared information. *Behaviour, 94*, 150-166. doi:10.1163/156853985x00316

Cheney, D. L., & Seyfarth, R. M. (1997). Reconciliatory grunts by dominant female baboons influence victims' behaviour. *Animal Behaviour, 54*, 409-418. doi:10.1006/anbe.1996.0438

Cheney, D. L., & Seyfarth, R. M. (2018). Flexible usage and social function in primate vocalizations. *Proceedings of the National Academy of Sciences*. doi:10.1073/pnas.1717572115

Cheney, D. L., Seyfarth, R. M., Fischer, J., Beehner, J., Bergman, T., Johnson, S., . . . Silk, J. B. (2004). Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *International Journal of Primatology, 25*(2), 401-428.

Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995a). The responses of female baboons (Papio cynocephalus ursinus) to anamalous social interactions - Evidence for causal reasoning. *Journal of Comparative Psychology, 109*(2), 134-141. doi:10.1037//0735-7036.109.2.134

Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995b). The role of grunt in reconciling opponents and facilitating interactions among adult female baboons. *Animal Behaviour, 50*, 249-257. doi:10.1006/anbe.1995.0237

Cheng, M.-F. (1992). For whom does the female dove coo? A case for the role of vocal self-stimulation. *Animal Behaviour, 43*(6), 1035-1044. doi:https://doi.org/10.1016/S0003-3472(06)80016-3

Clay, Z., & Zuberbühler, K. (2011). The Structure of Bonobo Copulation Calls During Reproductive and Non-Reproductive Sex. *Ethology, 117*(12), 1158-1169. doi:10.1111/j.1439-0310.2011.01975.x

Cohen, J. (1988). *Statistical power analysis for the behavioural sciences* (2nd ed.). Hoboken, NJ: Lawrence Erlbaum Associates.

Cowlishaw, G., & Dunbar, R. I. M. (1991). Dominance rank and mating success in male primates. *Animal Behaviour, 41*(6), 1045-1056. doi:http://dx.doi.org/10.1016/S0003-3472(05)80642-6

Cowlishaw, G., & O'Connell, S. M. (1996). Male-male competition, paternity certainty and copulation calls in female baboons. *Animal Behaviour, 51*, 235-238. doi:10.1006/anbe.1996.0022

Cox, C. R., & Leboeuf, B. J. (1977). Female incitation of male competition - mechanism in sexual selection. *American Naturalist, 111*(978), 317-335. doi:10.1086/283163

Crockford, C., Wittig, R. M., Whitten, P. L., Seyfarth, R. A., & Cheney, D. L. (2008). Social stressors and coping mechanisms in wild female baboons (Papio hamadryas ursinus). *Hormones and Behavior, 53*(1), 254-265. doi:10.1016/j.yhbeh.2007.10.007

Danish, L. M., & Palombit, R. A. (2014). "Following," an alternative mating strategy used by male olive baboons (*Papio hamadryas anubis*): Quantitative behavioral and functional description. *International Journal of Primatology, 35*(2), 394-410. doi:10.1007/s10764-013-9743-3

Déaux, E., C., O'Neil, N., P., Charrier, I., & Iwaniuk, A., N. (Submitted). Daily variation in ruffed grouse drumming displays: Evidence of a "warm-up" period for a non-vocal acoustic signal. *Behavioral Ecology and Sociobiology*.

Dias, P. A. D., Luna, E. R., & Espinosa, D. C. (2008). The functions of the "Greeting Ceremony" among male mantled howlers (Alouatta palliata) on Agaltepec Island, Mexico. *American Journal of Primatology, 70*(7), 621-628. doi:10.1002/ajp.20535

Dixson, A. F. (1987). Observations on the evolution of the genitalia and copulatory behaviour in male primates. *Journal of Zoology, 213*(3), 423-443. doi:10.1111/j.1469-7998.1987.tb03718.x

Dixson, A. F., & Mundy, N. I. (1994). Sexual behaviour, sexual swelling, and penile evolution in chimpanzees (*Pan troglodytes*). *Archives of Sexual Behavior, 23*(3), 267-280. doi:10.1007/bf01541563

Dochtermann, N. A., & Jenkins, S. H. (2011). Developing multiple hypotheses in behavioral ecology. *Behavioral Ecology and Sociobiology, 65*(1), 37-45.

Duboscq, J., Neumann, C., Agil, M., Perwitasari-Farajallah, D., Thierry, B., & Engelhardt, A. (2017). Degrees of freedom in social bonds of crested macaque females. *Animal Behaviour, 123*, 411-426. doi:https://doi.org/10.1016/j.anbehav.2016.11.010

Dunayer, Erica S., & Berman, Carol M. (2017). Infant handling enhances social bonds in free-ranging rhesus macaques (). *Behaviour, 154*(7-8), 875-907. doi:doi:https://doi.org/10.1163/1568539X-00003448

Dunn, A., & Ejebare, G. B. (1999). *Gashaka National Park, A guide book*.

Elgar, M. A. (1986). The establishment of foraging flocks in house sparrows: risk of predation and daily temperature. *Behavioral Ecology and Sociobiology, 19*(6), 433-438.

Engelhardt, A., Fischer, J., Neumann, C., Pfeifer, J.-B., & Heistermann, M. (2012). Information content of female copulation calls in wild long-tailed macaques (*Macaca fascicularis*). *Behavioral Ecology and Sociobiology, 66*(1), 121-134. doi:10.1007/s00265-011-1260-9

Engh, A. L., Beehner, J. C., Bergman, T. J., Whitten, P. L., Hoffmeier, R. R., Seyfarth, R. M., & Cheney, D. L. (2006). Female hierarchy instability, male immigration and infanticide increase glucocorticoid levels in female chacma baboons. *Animal Behaviour, 71*(5), 1227-1237. doi:https://doi.org/10.1016/j.anbehav.2005.11.009

Engh, A. L., Hoffmeier, R. R., Cheney, D. L., & Seyfarth, R. M. (2006). Who, me? Can baboons infer the target of vocalizations? *Animal Behaviour, 71*, 381-387. doi:10.1016/j.anbehav.2005.05.009

Evans, C. S., Evans, L., & Marler, P. (1993). On the meaning of alarm calls - Functional reference in an avian vocal system. *Animal Behaviour, 46*(1), 23-38. doi:10.1006/anbe.1993.1158

Ey, E., Rahn, C., Hammerschmidt, K., & Fischer, J. (2009). Wild Female Olive Baboons Adapt their Grunt Vocalizations to Environmental Conditions. *Ethology, 115*(5), 493-503. doi:10.1111/j.1439-0310.2009.01638.x

Fallon, B. L., Neumann, C., Byrne, R. W., & Zuberbühler, K. (2016). Female chimpanzees adjust copulation calls according to reproductive status and level of female competition. *Animal Behaviour, 113*, 87-92. doi:http://dx.doi.org/10.1016/j.anbehav.2015.12.028

Fedurek, P., Zuberbühler, K., & Dahl, C. D. (2016). Sequential information in a great ape utterance. *Scientific Reports, 6*, 38226. doi:10.1038/srep38226

Fischer, J., Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology, 56*(2), 140-148. doi:10.1007/s00265-003-0739-4

Fitch, W. T., Neubauer, J., & Herzel, H. (2002). Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour, 63*(3), 407-418.

Freeberg, T. M. (2006). Social Complexity Can Drive Vocal Complexity:Group Size Influences Vocal Information in Carolina Chickadees. *Psychological Science, 17*(7), 557-561. doi:10.1111/j.1467-9280.2006.01743.x

Freeberg, T. M., Dunbar, R. I. M., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1597), 1785-1801. doi:10.1098/rstb.2011.0213

Gesquiere, L. R., Learn, N. H., Simao, M. C. M., Onyango, P. O., Alberts, S. C., & Altmann, J. (2011). Life at the Top: Rank and Stress in Wild Male Baboons. *Science, 333*(6040), 357-360. doi:10.1126/science.1207120

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, Massachusetts: Harvard University Press.

Gouzoules, H., Gust, D., Donaghey, B., & St. Andre, E. (1998). Estrus vocalizations in two primate species (*Cercocebus torquatus* and *Macaca nemestrina*): Evidence for an effect of intrasexual competition. *Evolution of communication, 2*, 189-215.

Gros-Louis, J. (2004). The function of food-associated calls in white-faced capuchin monkeys, Cebus capucinus, from the perspective of the signaller. *Animal Behaviour, 67*(3), 431-440.

Groves, C. (2001). *Primate taxonomy* (E. D'Araujo Ed.): Smithonian.

Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology, 24*(4), 699-711. doi:10.1111/j.1420-9101.2010.02210.x

Gygax, L. (1995). Hiding Behaviour of Longtailed Macaques (*Macaca fascicularis*). I. Theoretical Background and Data on Mating. *Ethology, 101*(1), 10-24. doi:10.1111/j.1439-0310.1995.tb00340.x

Hall, K. R. L. (1965). *Primate behavior: field studies on monkeys and apes* (I. DeVore Ed.). New York: Holt, Rinehart, and Winston.

Hamilton, W. J., & Arrowood, P. C. (1978). Copulatory vocalizations of chacma baboons (*Papio ursinus*), gibbons (Hylobates hoolock), and humans. *Science, 200*(4348), 1405-1409. doi:10.1126/science.663622

Harcourt, A., & Stewart, K. (1996). Function and Meaning of Wild Gorilla'Close'Calls. *Behaviour, 133*(11), 827-845.

Harcourt, A. H., Harvey, P. H., Larson, S. G., & Short, R. V. (1981). Testis weight, body-weight and breeding system in primates. *Nature, 293*(5827), 55-57. doi:10.1038/293055a0

Hauser, M. D. (1990). Do chimpanzee copulatory calls incite male male competition. *Animal Behaviour, 39*, 596-597. doi:10.1016/s0003-3472(05)80427-0

Hauser, M. D. (1993). Rhesus-monkey copulation calls - Honest signals for female choice. *Proceedings of the Royal Society B-Biological Sciences, 254*(1340), 93-96. doi:10.1098/rspb.1993.0132

Hauser, M. D., & Marler, P. (1993). Food-associated calls in rhesus macaques (Macaca mulatta): II. Costs and benefits of call production and suppression. *Behavioral Ecology, 4*(3), 206-212.

Hausfater, G. (1975). *Dominance and reproduction in baboons (Papio cynocephalus): A quantitative analysis* (Vol. 7). Basel: S. Karger.

Henzi, S. P. (1996). Copulation calls and paternity in chacma baboons. *Animal Behaviour, 51*, 233-234.

Henzi, S. P., & Lycett, J. E. (1995). Population-structure, demography, and dynamics of mountain baboons- an interim-report. *American Journal of Primatology, 35*(2), 155-163. doi:10.1002/ajp.1350350208

Higham, J. P., Heistermann, M., Ross, C., Semple, S., & MacLarnon, A. (2008). The timing of ovulation with respect to sexual swelling detumescence in wild olive baboons. *Primates, 49*(4), 295-299. doi:10.1007/s10329-008-0099-9

Higham, J. P., Heistermann, M., Saggau, C., Agil, M., Perwitasari-Farajallah, D., & Engelhardt, A. (2012). Sexual signalling in female crested macaques and the evolution of primate fertility signals. *Bmc Evolutionary Biology, 12*. doi:10.1186/1471-2148-12-89

Higham, J. P., MacLarnon, A. M., Ross, C., Heistermann, M., & Semple, S. (2008). Baboon sexual swellings: Information content of size and color. *Hormones and Behavior, 53*(3), 452-462. doi:http://dx.doi.org/10.1016/j.yhbeh.2007.11.019

Higham, J. P., Ross, C., Warren, Y., Heistermann, M., & MacLarnon, A. M. (2007). Reduced reproductive function in wild baboons (*Papio hamadryas anubis*) related to natural consumption of the African black plum (*Vitex doniana*). *Hormones and Behavior, 52*(3), 384-390. doi:10.1016/j.yhbeh.2007.06.003

Higham, J. P., Semple, S., MacLarnon, A., Heistermann, M., & Ross, C. (2009). Female reproductive signaling, and male mating behavior, in the olive baboon. *Hormones and Behavior, 55*(1), 60-67. doi:10.1016/j.yhbeh.2008.08.007

Higham, J. P., Warren, Y., Adanu, J., Umaru, B. N., MacLarnon, A. M., Sommer, V., & Ross, C. (2009). Living on the Edge: Life-History of Olive Baboons at Gashaka-Gumti National Park, Nigeria. *American Journal of Primatology, 71*(4), 293-304. doi:10.1002/ajp.20651

Hinde, R. A. (1981). Animal signals: Ethological and games-theory approaches are not incompatible. *Animal Behaviour, 29*(2), 535-542.

Hohmann, G. M., & Herzog, M. O. (1985). Vocal communication in lion-tailed macaques (*Macaca silenus*). *Folia Primatologica, 45*, 145-178.

Holekamp, K. E., & Smale, L. (1991). Dominance Acquisition During Mammalian Social Development: The “Inheritance” of Maternal Rank1. *American Zoologist, 31*(2), 306-317. doi:10.1093/icb/31.2.306

Hrdy, S. B. (1976). Care and exploitation of nonhuman primate infants by conspecifics other than mother. *Advances in the Study of Behavior, 6*, 101-158.

Hsu, M. J., Lin, J. F., Chen, L. M., & Agoramoorthy, G. (2002). Copulation calls in male Formosan macaques: Honest signals of male quality? *Folia Primatologica, 73*(4), 220-223. doi:10.1159/000065428

Humphrey, N. K. (1976). The social function of intellect *Growing points in ethology* (pp. 303-317): Cambridge University Press.

Johnson, C. A., Swedell, L., & Rothman, J. M. (2012). Feeding ecology of olive baboons (*Papio anubis*) in Kibale National Park, Uganda: preliminary results on diet and food selection. *African Journal of Ecology, 50*(3), 367-370. doi:10.1111/j.1365-2028.2011.01316.x

Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology & Evolution, 19*(2), 101-108. doi:https://doi.org/10.1016/j.tree.2003.10.013

Johnson, S. E. (2003). Life history and the competitive environment: trajectories of growth, maturation, and reproductive output among chacma baboons. *American Journal of Physical Anthropology, 120*(1), 83-98.

Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science, 153*(3735), 501-506.

Kalan, A. K., Mundry, R., & Boesch, C. (2015). Wild chimpanzees modify food call structure with respect to tree size for a particular fruit species. *Animal Behaviour, 101*, 1-9. doi:10.1016/j.anbehav.2014.12.011

Keil, A., & Sachser, N. (1998). Reproductive benefits from female promiscuous mating in a small mammal. *Ethology, 104*(11), 897-903.

Keller, L., & Reeve, H. K. (1995). Why do females mate with multiple males - the sexually selected sperm hypothesis. *Advances in the Study of Behavior, 24*, 291-315. doi:10.1016/s0065-3454(08)60397-6

Kitchen, D. M., Cheney, D. L., & Seyfarth, R. M. (2003). Female baboons' responses to male loud calls. *Ethology, 109*(5), 401-412. doi:10.1046/j.1439-0310.2003.00878.x

Kitchen, D. M., Seyfarth, R. M., Fischer, J., & Cheney, D. L. (2003). Loud calls as indicators of dominance in male baboons (Papio cynocephalus ursinus). *Behavioral Ecology and Sociobiology, 53*(6), 374-384. doi:10.1007/s00265-003-0588-1

Krunkelsven, E., Dupain, J., Van Elsacker, L., & Verheyen, R. (1996). Food calling by captive bonobos (Pan paniscus): an experiment. *International Journal of Primatology, 17*(2), 207-217.

Kummer, H., & Kurt, F. (1963). Social Units of a Free-living Population of Hamadryas Baboons. *Folia Primatologica, 1*(1), 4-19.

Laporte, M. N. C., & Zuberbühler, K. (2010). Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour, 80*(3), 467-473. doi:10.1016/j.anbehav.2010.06.005

le Roux, A., Snyder-Mackler, N., Roberts, E. K., Beehner, J. C., & Bergman, T. J. (2013). Evidence for tactical concealment in a wild primate. *Nature Communications, 4*. doi:10.1038/ncomms2468

Lowe, A. (2014). *The effect of reproductive state on the sociality of female olive baboons: Evidence from a field study in Nigeria.* (Master), UCL.

Maciej, P., Patzelt, A., Ndao, I., Hammerschmidt, K., & Fischer, J. (2013). Social monitoring in a multilevel society: a playback study with male Guinea baboons. *Behavioral Ecology and Sociobiology, 67*(1), 61-68. doi:10.1007/s00265-012-1425-1

Maestripieri, D. (1994). Social structure, infant handling, and mothering styles in group-living Old World monkeys. *International Journal of Primatology, 15*(4), 531-553.

Maestripieri, D., Leoni, M., Raza, S. S., Hirsch, E. J., & Whitham, J. C. (2005). Female copulation calls in guinea baboons: Evidence for postcopulatory female choice? *International Journal of Primatology, 26*(4), 737-758. doi:10.1007/s10764-005-5306-6

Maestripieri, D., Leoni, M., Roney, J. R., & Whitham, J. C. (2004). Copulation calls and female mate choice in Guinea baboons and other primates. *American Journal of Physical Anthropology*, 140-141.

Maestripieri, D., & Roney, J. R. (2005). Primate copulation calls and postcopulatory female choice. *Behavioral Ecology, 16*(1), 106-113. doi:10.1093/beheco/arh120

Manno, T. G., Nesterova, A. P., DeBarbieri, L. M., Kennedy, S. E., Wright, K. S., & Dobson, F. S. (2007). Why do male Columbian ground squirrels give a mating call? *Animal Behaviour, 74*(5), 1319-1327. doi:http://dx.doi.org/10.1016/j.anbehav.2007.02.033

Manson, J. H. (1999). Infant handling in wild *Cebus capucinus*: testing bonds between females? *Animal Behaviour, 57*(4), 911-921. doi:http://dx.doi.org/10.1006/anbe.1998.1052

Masataka, N. (1989). Motivational referents of contact calls in Japanese monkeys. *Ethology, 80*(1-4), 265-273.

Meise, K., Keller, C., Cowlishaw, G., & Fischer, J. (2011). Sources of acoustic variation: Implications for production specificity and call categorization in chacma baboon (Papio ursinus) grunts. *Journal of the Acoustical Society of America, 129*(3), 1631-1641. doi:10.1121/1.3531944

Mercier, S., Neumann, C., van de Waal, E., Chollet, E., Meric de Bellefon, J., & Zuberbühler, K. (2017). Vervet monkeys greet adult males during high-risk situations. *Animal Behaviour, 132*(Supplement C), 229-245. doi:https://doi.org/10.1016/j.anbehav.2017.07.021

Møller, A., & Jennions, M. D. (2002). How much variance can be explained by ecologists and evolutionary biologists? *Oecologia, 132*(4), 492-500. doi:10.1007/s00442-002-0952-2

Møller, A. P., Dufva, R., & Allander, K. (1993). Parasites and the evolution of host social behavior. *Advances in the Study of Behavior, 22*(65102), 60405-60402.

Muller, M. N., & Wrangham, R. W. (2004). Dominance, aggression and testosterone in wild chimpanzees: a test of the 'challenge hypothesis'. *Animal Behaviour, 67*(1), 113-123. doi:https://doi.org/10.1016/j.anbehav.2003.03.013

Nagel, U. (1973). A Comparison of Anubis Baboons, Hamadryas Baboons and Their Hybrids at a Species Border in Ethiopia. *Folia Primatologica, 19*(2-3), 104-165.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution, 4*(2), 133-142. doi:10.1111/j.2041-210x.2012.00261.x

Neumann, C. (2016). socialindices: social and association indices. Unpublished R package version 0.46-08.

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., . . . Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour, 82*(4), 911-921. doi:10.1016/j.anbehav.2011.07.016

Neumann, C., & Kulik, L. (2014). EloRating: Animal Dominance Hierarchies by Elo Rating. R package version 0.43. https://CRAN.R-project.org/package=EloRating.

Niemeyer, C. L., & Anderson, J. R. (1983). Primate harassment of matings. *Ethology and Sociobiology, 4*(4), 205-220. doi:10.1016/0162-3095(83)90010-9

Nikitopoulos, E., Arnhem, E., van Hooff, J., & Sterck, E. H. M. (2004). Influence of female copulation calls on male sexual behavior in captive *Macaca fascicularis*. *International Journal of Primatology, 25*(3), 659-677. doi:10.1023/B:IJOP.0000023579.30595.ae

Nunn, C. L. (1999). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behaviour, 58*, 229-246. doi:10.1006/anbe.1999.1159

O'Connell, S. M., & Cowlishaw, G. (1994). Infanticide avoidance, sperm competition and mate choice - the function of copulation calls in female baboons. *Animal Behaviour, 48*(3), 687-694. doi:10.1006/anbe.1994.1288

Oda, R., & Masataka, N. (1992). Functional significance of female Japanese macaque copulatory calls. *Folia Primatologica, 58*(3), 146-149. doi:10.1159/000156621

Oda, R., & Masataka, N. (1995). Function of copulatory vocalizations in mate choice by females of Japanese macaques (*Macaca fuscata*). *Folia Primatologica, 64*(3), 132-139. doi:10.1159/000156843

Oi, T. (1996). Sexual behaviour and mating system of wild pig-tailed macaque in West Sumatra. In J. E. Fa & D. G. Lindburg (Eds.), *Evolution and ecology of macaque societies* (pp. 342-368): Cambridge Unversity Press.

Overduin-de Vries, A. M., Olesen, C. U., de Vries, H., Spruijt, B. M., & Sterck, E. H. M. (2013). Sneak copulations in long-tailed macaques (*Macaca fascicularis*): no evidence for tactical deception. *Behavioral Ecology and Sociobiology, 67*(1), 101-111. doi:10.1007/s00265-012-1430-4

Owren, M. J., & Rendall, D. (2001). Sound on the rebound: bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews, 10*(2), 58-71.

Owren, M. J., Seyfarth, R. M., & Cheney, D. L. (1997). The acoustic features of vowel-like grunt calls in chacma baboons (Papio cyncephalus ursinus): Implications for production processes and functions. *Journal of the Acoustical Society of America, 101*(5), 2951-2963. doi:10.1121/1.418523

Pagel, M. (1994). The evolution of conspicuous oestrous advertisement in Old World monkeys. *Animal Behaviour, 47*(6), 1333-1341. doi:https://doi.org/10.1006/anbe.1994.1181

Palombit, R. (2003). Male infanticide in wild savanna baboons: Adaptive significance and intraspecific variation. In C. B. Jones (Ed.), *Sexual selection and reproductive competition in primates: New perspectives and directions* (C.B Jones ed., pp. 367-412). Norman, Oklahoma: American society of primatologists.

Palombit, R., Cheney, D., Fischer, J., Johnson, S., Rendall, D., Seyfarth, R., & Silk, J. B. (2000). Male infanticide and defense of infants in chacma baboons. In C. P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp. 123-152): Cambridge University Press.

Palombit, R. A., Cheney, D. L., & Seyfarth, R. M. (1999). Male grunts as mediators of social interaction with females in wild chacma baboons (Papio cynocephalus ursinus). *Behaviour, 136*, 221-242. doi:10.1163/156853999501298

Palombit, R. A., Cheney, D. L., & Seyfarth, R. M. (2001). Female-female competition for male 'friends' in wild chacma baboons, Papio cynocephalus ursinus. *Animal Behaviour, 61*, 1159-1171. doi:10.1006/anbe.2000.1690

Palombit, R. A., Seyfarth, R. M., & Cheney, D. L. (1997). The adaptive value of 'friendships' to female baboons: experimental and observational evidence. *Animal Behaviour, 54*, 599-614. doi:10.1006/anbe.1996.0457

Patzelt, A., Kopp, G. H., Ndao, I., Kalbitzer, U., Zinner, D., & Fischer, J. (2014). Male tolerance and male-male bonds in a multilevel primate society. *Proceedings of the National Academy of Sciences of the United States of America, 111*(41), 14740-14745. doi:10.1073/pnas.1405811111

Patzelt, A., Zinner, D., Fickenscher, G., Diedhiou, S., Camara, B., Stahl, D., & Fischer, J. (2011). Group Composition of Guinea Baboons (Papio papio) at a Water Place Suggests a Fluid Social Organization. *International Journal of Primatology, 32*(3), 652-668. doi:10.1007/s10764-011-9493-z

Paul, A., & Kuester, J. (1996). Infant handling by female Barbary macaques (Macaca sylvanus) at Affenberg Salem: testing functional and evolutionary hypotheses. *Behavioral Ecology and Sociobiology, 39*(2), 133-145. doi:10.1007/s002650050275

Petrie, M., Marion, H., Halliday, T., Helen, B., & Chris, P. (1992). Multiple Mating in a Lekking Bird: Why Do Peahens Mate with More than One Male and with the Same Male More than Once? *Behavioral Ecology and Sociobiology, 31*(5), 349-358.

Petrie, M., Tim, H., & Carolyn, S. (1991). Peahens prefer peacocks with elaborate trains. *Animal Behaviour, 41*(2), 323-331. doi:https://doi.org/10.1016/S0003-3472(05)80484-1

Pfefferle, D., Brauch, K., Heistermann, M., Hodges, J. K., & Fischer, J. (2008). Female Barbary macaques (*Macaca sylvanus*) copulation calls do not reveal the fertile phase but influence mating outcome. *Proceedings of the Royal Society B-Biological Sciences, 275*(1634), 571-578. doi:10.1098/rspb.2007.1499

Pfefferle, D., Heistermann, M., Hodges, J. K., & Fischer, J. (2008). Male Barbary macaques eavesdrop on mating outcome: a playback study. *Animal Behaviour, 75*(6), 1885-1891. doi:https://doi.org/10.1016/j.anbehav.2007.12.003

Pfefferle, D., Heistermann, M., Pirow, R., Hodges, J. K., & Fischer, J. (2011). Estrogen and Progestogen Correlates of the Structure of Female Copulation Calls in Semi-Free-Ranging Barbary Macaques (Macaca sylvanus). *International Journal of Primatology, 32*(4), 992-1006. doi:10.1007/s10764-011-9517-8

Poole, J. H., Payne, K., Langbauer, W. R., & Moss, C. J. (1988). The social contexts of some very low-frequency calls of African elephants. *Behavioral Ecology and Sociobiology, 22*(6), 385-392. doi:10.1007/bf00294975

Pradhan, G. R., Engelhardt, A., van Schaik, C. P., & Maestripieri, D. (2006). The evolution of female copulation calls in primates: a review and a new model. *Behavioral Ecology and Sociobiology, 59*(3), 333-343. doi:10.1007/s00265-005-0075-y

Price, T., Wadewitz, P., Cheney, D., Seyfarth, R., Hammerschmidt, K., & Fischer, J. (2015). Vervets revisited: A quantitative analysis of alarm call structure and context specificity. *Scientific Reports, 5*, 13220. doi:10.1038/srep13220

R Core Team. (2017). R: A language and environment for statistical computing (version 3.4.0). http://www.R-project.org/. Vienna, Austria: R Foundation for Statistical Computing.

Ransom, T. (1981). *Beach troop of Gombe*. East Brunswick, NJ: Associated University Presses.

Rendall, D. (2003). Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalizations of baboons. *Journal of the Acoustical Society of America, 113*(6), 3390-3402. doi:10.1121/1.1568942

Rendall, D., Seyfarth, R. M., Cheney, D. L., & Owren, M. J. (1999). The meaning and function of grunt variants in baboons. *Animal Behaviour, 57*, 583-592. doi:10.1006/anbe.1998.1031

Rigaill, L., Higham, J. P., Lee, P. C., Blin, A., & Garcia, C. (2013). Multimodal Sexual Signaling and Mating Behavior in Olive Baboons (Papio anubis). *American Journal of Primatology, 75*(7), 774-787. doi:10.1002/ajp.22154

Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal Behaviour, 51*(5), 1077-1086. doi:https://doi.org/10.1006/anbe.1996.0109

Robinson, J. G. (1982). Intrasexual competition and mate choice in primates. *American Journal of Primatology, 3*(S1), 131-144. doi:doi:10.1002/ajp.1350030520

Ron, T., Henzi, P., & Motro, U. (1996). Do female chacma baboon compete for a safe spatial position in a southern woodhland habitat? *Behaviour, 133*(5), 475-490.

Ross, C., Warren, Y., MacLarnon, A., & Higham, J. P. (2011). How different are Gashaka's baboons? Forest and open populations compared. In Springer (Ed.), *Primates of Gashaka:hh Socioecology and conservation in Nigeria's biodiversity hotspot* (pp. 333-359).

Rowell, T. E. (1966). Forest living baboons in Uganda. *Journal of Zoology, 149*.

Rowell, T. E. (1972). Female Reproduction Cycles and Social Behavior in Primates. In D. S. Lehrman, R. A. Hinde, & E. Shaw (Eds.), *Advances in the Study of Behavior* (Vol. 4, pp. 69-105): Academic Press.

Saayman, G. S. (1970). The menstrual cycle and sexual behaviour in a troop of free ranging chacma baboons (*Papio ursinus*). *Folia Primatologica, 12*(2), 81-110.

Schel, A. M., Machanda, Z., Townsend, S. W., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour, 86*(5), 955-965. doi:10.1016/j.anbehav.2013.08.013

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution, 1*(2), 103-113. doi:10.1111/j.2041-210X.2010.00012.x

Schino, G. (2001). Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour, 62*(2), 265-271. doi:https://doi.org/10.1006/anbe.2001.1750

Semple, S. (1998). The function of Barbary macaque copulation calls. *Proceedings of the Royal Society B-Biological Sciences, 265*(1393), 287-291. doi:10.1098/rspb.1998.0294

Semple, S. (2001). Individuality and male discrimination of female copulation calls in the yellow baboon. *Animal Behaviour, 61*, 1023-1028. doi:10.1006/anbe.2001.1692

Semple, S., & McComb, K. (2000). Perception of female reproductive state from vocal cues in a mammal species. *Proceedings of the Royal Society B-Biological Sciences, 267*(1444), 707-712.

Semple, S., McComb, K., Alberts, S., & Altmann, J. (2002). Information content of female copulation calls in yellow baboons. *American Journal of Primatology, 56*(1), 43-56. doi:10.1002/ajp.1062

Seyfarth, R., & Cheney, D. (1986a). Complexities in the study of vervet monkey grunts.

Seyfarth, R. M., & Cheney, D. L. (1984). The acoustic features of vervet monkey grunts. *The Journal of the Acoustical Society of America, 75*(5), 1623-1628.

Seyfarth, R. M., & Cheney, D. L. (1986b). Vocal development in vervet monkeys. *Animal Behaviour, 34*(6), 1640-1658.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls - Semantic communication in a free-ranging primate. *Animal Behaviour, 28*(NOV), 1070-1094. doi:10.1016/s0003-3472(80)80097-2

Shopland, J. M., & Altmann, J. (1987). Fatal intragroup kidnapping in yellow baboons. *American Journal of Primatology, 13*(1), 61-65. doi:10.1002/ajp.1350130108

Silk, J. B. (2002). Using the 'F'-word in primatology. *Behaviour, 139*, 421-446. doi:10.1163/156853902760102735

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science, 302*(5648), 1231-1234. doi:10.1126/science.1088580

Silk, J. B., Alberts, S. C., & Altmann, J. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology, 61*(2), 197-204. doi:10.1007/s00265-006-0250-9

Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology, 61*(2), 183-195. doi:10.1007/s00265-006-0249-2

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., . . . Cheney, D. L. (2009). The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B-Biological Sciences, 276*(1670), 3099-3104. doi:10.1098/rspb.2009.0681

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., . . . Cheney, D. L. (2010). Strong and Consistent Social Bonds Enhance the Longevity of Female Baboons. *Current Biology, 20*(15), 1359-1361. doi:10.1016/j.cub.2010.05.067

Silk, J. B., Cheney, D., & Seyfarth, R. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology, 22*(5), 213-225. doi:10.1002/evan.21367

Silk, J. B., Kaldor, E., & Boyd, R. (2000). Cheap talk when interests conflict. *Animal Behaviour, 59*, 423-432. doi:10.1006/anbe.1999.1312

Silk, J. B., Rendall, D., Cheney, D. L., & Seyfarth, R. M. (2003). Natal attraction in adult female baboons (Papio cynocephalus ursinus) in the Moremi Reserve, Botswana. *Ethology, 109*(8), 627-644. doi:10.1046/j.1439-0310.2003.00907.x

Silk, J. B., Seyfarth, R. M., & Cheney, D. L. (2016). Strategic Use of Affiliative Vocalizations by Wild Female Baboons. *Plos One, 11*(10). doi:10.1371/journal.pone.0163978

Simpson, B. S. (1984). Tests of habituation to song repertoires by Carolina wrens. *The Auk*, 244-254.

Slocombe, K. E., Kaller, T., Turman, L., Townsend, S. W., Papworth, S., Squibbs, P., & Zuberbuehler, K. (2010). Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. *Behavioral Ecology and Sociobiology, 64*(12), 1959-1966. doi:10.1007/s00265-010-1006-0

Slocombe, K. E., & Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences of the United States of America, 104*(43), 17228-17233. doi:10.1073/pnas.0706741104

Smith, E. O., & Whitten, P. L. (1988). Triadic interactions in Savanna-dwelling baboons. *International Journal of Primatology, 9*(5), 409-424. doi:10.1007/bf02736217

Smith, K. S. (1986). *Dominance and mating strategies of chacma baboons, Papio ursinus, in the Okavango delta.* (Ph.D. thesis), University of California.

Smuts, B. (1985). *Sex and friendship in baboons*. New York: Aldine de Gruyter.

Smuts, B., & Nicolson, N. (1989). Reproduction in wild female olive baboons. *American Journal of Primatology, 19*(4), 229-246. doi:10.1002/ajp.1350190405

Smuts, B. B., & Watanabe, J. M. (1990). Social relationships and ritualized greetings in adult male baboons (*Papio cynochephalus anubis*). *International Journal of Primatology, 11*(2), 147-172. doi:10.1007/bf02192786

Stephan, C., & Zuberbühler, K. (2008). Predation increases acoustic complexity in primate alarm calls. *Biology Letters, 4*(6), 641-644. doi:10.1098/rsbl.2008.0488

Stephan, C., & Zuberbühler, K. (2014). Predation affects alarm call usage in female Diana monkeys (Cercopithecus diana diana). *Behavioral Ecology and Sociobiology, 68*(2), 321-331.

Stephan, C., & Zuberbühler, K. (2016). Social familiarity affects Diana monkey (Cercopithecus diana diana) alarm call responses in habitat-specific ways. *Royal Society Open Science, 3*(2), 150639.

Struhsaker, T. T. (1967). Auditory communication among vervet monkeys (Cercopithecus aethiops). In S. A. Altmann (Ed.), *Social communication among primates* (pp. 281-324): University of Chicago Press.

Strum, S. C. (1982). Agonistic dominance in male baboons: An alternative view. *International Journal of Primatology, 3*(2), 175. doi:10.1007/bf02693494

Strum, S. C. (1983). Use of females by male olive baboons (Papio anubis). *American Journal of Primatology, 5*(2), 93-109. doi:10.1002/ajp.1350050202

Strum, S. C. (1991). Weight and age in wild olive baboons. *American Journal of Primatology, 25*(4), 219-237. doi:doi:10.1002/ajp.1350250403

Strum, S. C., & Western, J. D. (1982). Variations in fecundity with age and environment in olive baboons (*Papio anubis*). *American Journal of Primatology, 3*(1-4), 61-76. doi:10.1002/ajp.1350030106

Stumpf, R. M., & Boesch, C. (2005). Does promiscuous mating preclude female choice? Female sexual strategies in chimpanzees (Pan troglodytes verus) of the Taï National Park, Côte d'Ivoire. *Behavioral Ecology and Sociobiology, 57*(5), 511-524. doi:10.1007/s00265-004-0868-4

Stumpf, R. M., & Boesch, C. (2006). The efficacy of female choice in chimpanzees of the Taï Forest, Côte d'Ivoire. *Behavioral Ecology and Sociobiology, 60*(6), 749-765. doi:10.1007/s00265-006-0219-8

Swedell, L. (2011). African Papionins: Diversity of Social Organization and Ecological Flexibility. In C. Campbell, A. Fuentes, S. MacKinnon, S. Bearder, & R. Stumpf (Eds.), *Primates in Perspective* (pp. 241-277). New York: Oxford University Press.

Symington, M. M. (1988). Food Competition and Foraging Party Size in the Black Spider Monkey (Ateles Paniscus Chamek). *Behaviour, 105*(1), 117-134. doi:doi:https://doi.org/10.1163/156853988X00476

Symonds, M. R., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology, 65*(1), 13-21.

Todt, D., Hammerschmidt, K., Ansorge, V., & Fischer, J. (1995). The vocal behaviour of Barbary macaques (*Macaca sylvanus*): Call features and their performance in infants and adults. In U. Jürgens, J. Newman, & E. Zimmermann (Eds.), *Current topics in primate vocal communication* (pp. 141-160): New York: Plenum Press.

Tomasello, M. (2007). Ape gestures and the origins of language. *The gestural communication of apes and monkeys*, 221-240.

Tomasello, M. (2014). *A natural history of human thinking*: Harvard University Press.

Townsend, S., & Zuberbühler, K. (2009). Audience effects in chimpanzee copulation calls. *Communicative & integrative biology, 2*(3), 282-284.

Townsend, S. W., Deschner, T., & Zuberbühler, K. (2008). Female chimpanzees use copulation calls flexibly to prevent social competition. *Plos One, 3*(6). doi:10.1371/journal.pone.0002431

Townsend, S. W., Deschner, T., & Zuberbühler, K. (2011). Copulation Calls in Female Chimpanzees (Pan troglodytes schweinfurthii) Convey Identity but Do Not Accurately Reflect Fertility. *International Journal of Primatology, 32*(4), 914-923. doi:10.1007/s10764-011-9510-2

van Noordwijk, M. A., & van Schaik, C. P. (1987). Competition among female long-tailed macaques, Macaca fascicularis. *Animal Behaviour, 35*(2), 577-589. doi:https://doi.org/10.1016/S0003-3472(87)80284-1

Vannoni, E., & McElligott, A. G. (2009). Fallow bucks get hoarse: vocal fatigue as a possible signal to conspecifics. *Animal Behaviour, 78*(1), 3-10.

Viljoen, S. (1977). Factors affecting breeding synchronization in an African bush squirrel (Paraxerus cepapi cepapi. *The journal of society for reproduction and fertility, 50*(1), 125-127.

Warren, Y., Higham, J. P., MacLarnon, A., & Ross, C. (2011). Crop-raiding and commensalism in olive baboons: The costs and benefits of living with humans. In V. Sommer & C. Ross (Eds.), *Primates of Gashaka: Socioecology and conservation in Nigeria's biodiversity hotspot* (pp. 307-333): Springer.

Waser, P. M., & Waser, M. S. (1977). Experimental studies of primate vocalization: Specializations for long-distance propagation. *Zeitschrift für Tierpsychologie, 43*(3), 239-263.

Wasserman, M. D., Chapman, C. A., Milton, K., Gogarten, J. F., Wittwer, D. J., & Ziegler, T. E. (2012). Estrogenic plant consumption predicts red colobus monkey (Procolobus rufomitratus) hormonal state and behavior. *Hormones and Behavior, 62*(5), 553-562. doi:10.1016/j.yhbeh.2012.09.005

Wasserman, M. D., Milton, K., & Chapman, C. A. (2013). The Roles of Phytoestrogens in Primate Ecology and Evolution. *International Journal of Primatology, 34*(5), 861-878. doi:10.1007/s10764-013-9699-3

Whitham, J. C., & Maestripieri, D. (2003). Primate rituals: The function of greetings between male Guinea baboons. *Ethology, 109*(10), 847-859. doi:10.1046/j.0179-1613.2003.00922.x

Wich, S. A., & Sterck, E. H. M. (2003). Possible audience effect in Thomas Langurs (Primates; Presbytis thomasi): An experimental study on male loud calls in response to a tiger model. *American Journal of Primatology, 60*(4), 155-159. doi:10.1002/ajp.10102

Wiley, R. H., & Douglas, G. R. (1982). Adaptations for acoustic communication in birds: sound transmission and signal detection. *Acoustic communication in birds, 1*, 131-181.

Wittig, R. M., & Boesch, C. (2003). Food Competition and Linear Dominance Hierarchy Among Female Chimpanzees of the Taï National Park. *International Journal of Primatology, 24*(4), 847-867. doi:10.1023/a:1024632923180

Wittig, R. M., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior, 54*(1), 170-177. doi:10.1016/j.yhbeh.2008.02.009

Yorzinski, J. L., & Anoop, K. R. (2013). Peacock copulation calls attract distant females. *Behaviour, 150*(1), 61-74. doi:10.1163/1568539x-00003037

Young, C., Majolo, B., Schülke, O., & Ostner, J. (2014). Male social bonds and rank predict supporter selection in cooperative aggression in wild Barbary macaques. *Animal Behaviour, 95*, 23-32. doi:https://doi.org/10.1016/j.anbehav.2014.06.007

Zinner, D., Buba, U., Nash, S., & Roos, C. (2010). Pan-African voyagers: The phylogeny of baboons. In V. Sommer & C. Ross (Eds.), *Primates of Gashaka. Socioecology and conservation in Nigeria's biodiversity hotspot* (pp. 267-306): Springer.

Zuberbühler, K., & Jenny, D. (2002). Leopard predation and primate evolution. *Journal of Human Evolution, 43*(6), 873-886.