Universidad del Desarrollo
Facultad de Gobierno
Doctorado en Ciencias en Complejidad Social

CICS UDD
CENTRO DE INVESTIGACIÓN EN COMPLEJIDAD SOCIAL

Copulation Call in Female Hamadryas Baboons (*Papio hamadryas*): Adaptive Function and Information Content

BY: MONTSERRAT BELINCHON ORTIZ

Thesis Project submitted to the Faculty of Government at Universidad del Desarrollo in partial fulfillment of the requirements for the degree of Doctor in Social Complexity Sciences

Supervisors:

Dr. Pablo Polo Rodrigo

December, 2024

Content

I. GENERAL ASPECTS

TITTLE:	Copulation Call in Female Hamadryas Baboons (*Papio hamadryas*): Adaptive Function and Information Content

Key words

Primate communication	*Female copulation calls*	*Hamadryas baboons*

CICS Research Line Associated with the Project	*Foundations of Cognition and Social Behaviour*

I.1. Student

Belinchón	Ortiz	Montserrat
First surname	Second Surname	Name

I.2. Supervisor

Enter the identification details of the program's professors who have participated in supervising this project.

Surnames	Name	Faculty
Polo Rodrigo	Pablo	Laboratorio de Comportamiento Animal y Humano, Centro de Investigación en Complejidad Social, Facultad de Gobierno

II. ABSTRACT:

Principal Investigator:	Montserrat Belinchón Ortiz
Project title:	Copulation Call in Female Hamadryas Baboons (*Papio hamadryas*): Adaptive Function and Information Content

Introduction: In primates, copulation calls are vocalizations emitted by females at the end of copulation, being common in promiscuous species organized in multi-male, multi-female groups. These calls are thought to increase male competition for access to females, enhancing either male guarding or sperm competition around ovulation, which could respectively increase or confuse paternity certainty and reduce the risk of infanticide. Female hamadryas baboons also produce these calls. However, this species is organized in one-male units, where leader males sexually monopolize the females in their units, resulting in high paternity certainty. Therefore, these vocalizations appear to provide no obvious benefit in hamadryas baboons regarding risk of infanticide, raising the question of their role in this species.

Objective: This study aims to investigate the adaptive function of copulation calls in hamadryas baboons by examining their use (chapter 2) and the information they convey (chapter 3). We propose that if these vocalizations increase male competition in other primate species, in hamadryas baboons, they might be related to the coercive takeovers of females, as this is the primary consequence of male competition.

Methods: This study was based on an observational design using behavioral sampling to collect data on copulations and their acoustic behavior in the Hamadryas baboon colony at Madrid Zoo during July and September 1999. Additionally, previous databases from the colony's longitudinal study and grooming interaction records were included. Using these data, we analyzed the presence of copulation calls in each event, their acoustic structure, the male's and female's social status, the occurrence of ejaculation, the female's reproductive status, the presence of related females in the unit, and female transfers to other units.

Results: We observed that copulation calls are more likely in peripheral females within large units and central females in small units, occurring more frequently when the male ejaculates and during female's maximal sexual swelling. These vocalizations were also associated with an increased likelihood of females transferring to other units, although such transfers occurred only in females belonging to small units. On the other hand, no evidence was found that copulation calls convey information about the male's or female's social status, but they did convey information about male ejaculation. Furthermore, significant acoustic variability was observed among females.

Conclusion: We conclude that copulation calls in hamadryas baboons are used and contain information different from that observed in other primates with promiscuous mating systems, suggesting a potentially distinct adaptive role. The evidence indicates that these vocalizations might be primarily related to promoting female transfers to other units, where their reproductive success could be increased. However, due to the limitations of our study, definitive conclusions cannot be drawn, and we highlight the need for longitudinal studies with longer observation periods to better understand their function.

III. PROPOSED RESEARCH CHAPTER 1: INTRODUCTION

Animal Communication and Copulation Calls in Primates

Communication systems in animals are complex and have evolved to meet the particular needs and characteristics of each species. Through these systems, individuals can exchange signals that allow them to make decisions based on the information they provide (Endler, 1993). There is a wide variety of signals depending on the ecology and sensory systems of each species, such as visual, chemical, acoustic, and other signals (Bradbury & Vehrencamp, 1998). In primates, studies on communication have predominantly focused on acoustic signals due to comparisons with human natural language use (e.g., Cäsar et al., 2012; Seyfarth et al., 1980; Züberbuhler et al., 1999). Acoustic communication includes a diversity of sounds and vocalizations produced in various contexts, such as foraging, predator presence, social play and reconciliation, and mating (Bradbury & Vehrencamp, 2011; Chen & Wiens, 2020; Hauser, 1996; Sebeok, 1977). Although there is considerable debate about the nature and type of information conveyed by these vocalizations—such as whether they transmit information about internal emotional states or, conversely, referential information about the environment—it is generally considered that acoustic signals can convey specific information about a particular individual or context. This is possible when there is a relationship between the vocalization and the individual or context, enabling receivers to learn the association and infer it through the signal (Seyfarth & Cheney, 2017).

During mating, many animal species produce vocalizations before, during, or immediately after copulations (e.g., *Loxodonta africana*: Poole et al., 1988; *Mirounga angustirostris*: Cox & LeBoeuf, 1977; *Macaca fascicularis*: Engelhardt et al., 2012; *Pan troglodytes*: Townsend et al., 2011; *Papio cynocephalus cynocephalus*: Semple et al., 2002), known as copulation calls. In primates, these calls are produced by females towards the end of or immediately after copulation (Gonzalez et al., 1998; Hamilton & Arrowood, 1978; Hohmann & Herzog, 1985; O'Connell & Cowlishaw, 1994) and are typical of cercopithecine monkeys and apes that form multi-male, multi-female groups with promiscuous mating systems in which females advertise their receptivity through anogenital swellings (Dixson, 2012; Engelhardt et al., 2012; Hauser, 1996; Hohmann & Herzog, 1985; Nunn, 1999; van Schaik et al., 1999). Depending on the species, these vocalizations can vary acoustically. For example, in chimpanzees (*Pan troglodytes*), these vocalizations are screams (Townsend et al., 2008), whereas in baboons (*Papio* spp.), they are emitted as a series of loud and rhythmic grunts (Kemp et al., 2017).

Although there is no definitive consensus on the adaptive function of these vocalizations in primates, copulation calls are considered a sexually selected trait that increases female reproductive success by stimulating male competition. This could point to different functions depending on the consequences and benefits of increasing male competition in each species (Bouquet et al., 2018; Hauser, 1990; O'Connell & Cowlishaw, 1994; Pradhan et al., 2006). Given the timing of these calls (towards the end of copulation), two primary hypotheses currently receive greater support. First, in certain species, it is suggested that copulation calls serve as a post-copulatory female choice strategy, where the calls encourage females to be guarded around ovulation by a high-ranking consort male, reducing sperm competition and favoring paternity certainty in these genetically superior males (Maestripieri et al., 2005; Vaglio et al., 2020). According to this hypothesis, females should emit more calls when mating with high-ranking males. Second, in other species with high levels of promiscuity where female monopolization is challenging, it has been proposed that copulation calls promote mating with multiple males, thereby increasing sperm competition and paternity confusion (Bouquet et al., 2018; O'Connell & Cowlishaw, 1994).

To explore the adaptive function of these calls, previous research has focused on two different approaches. The first investigates the use of the calls—specifically, which individuals produce them and in what contexts they are emitted—to determine the situations that promote their use. The second approach analyses the acoustic structure of the calls in relation to different contexts to understand the information they convey, which is, therefore, relevant to the audience. Studies have suggested that copulation calls may indicate the reproductive status of females, specifically the likelihood of ovulation, as their emission rate and acoustic form appear to correlate with the size of female sexual swellings (Maestripieri et al., 2005; O'Connell & Cowlishaw, 1994; Rigaill et al., 2013; Semple, 2000; 2002). Sexual swellings are perigenital region edemas whose size is related to the proportion of estrogen and progesterone and is considered a probabilistic signal of ovulation (e.g., Higham et al., 2008). However, studies with precise ovulation measurements have not found conclusive evidence that these vocalizations provide accurate information about the female fertile phase during the ovulatory cycle (Bernardo de Quiros et al., 2018; Engelhardt et al., 2012; Pfefferle et al., 2008; Townsend et al., 2011; Vaglio et al., 2020). Additionally, copulation calls have also been linked to the context of the copulatory interaction itself. On the one hand, these vocalizations are more likely to occur or are more intense during ejaculatory mounts (Dixson, 2012; Engelhardt et al., 2011; Maestripieri & Roney, 2005; Pfefferle et al., 2008; but see Semple et al., 2002). On the other hand, it has also been observed that these calls can convey information about the age and social status of the male with whom the female is mating, as these calls are more frequent and longer when females copulate with high-ranking males (Bouquet et al., 2018; Clay & Zuberbühler, 2011; Engelhardt et al., 2011; Maestripieri et al., 2005; Semple et al., 2002). However, other studies have not found such a relationship (Pfefferle et al., 2008). Finally, copulation calls have been shown to vary between females, and males can identify them based on the acoustic features of these calls (Clay & Zuberbühler, 2011; Semple & McComb, 2000; Townsend et al., 2011).

Considering this, it appears that copulation calls may primarily convey information about the likelihood of conception, as they are associated with larger sexual swellings and the occurrence of male ejaculation. This evidence could support both hypotheses (i.e., the female post-copulatory choice hypothesis and the sperm competition hypothesis). However, under the female post-copulatory choice hypothesis, these calls would be expected to be associated with copulations involving dominant males, as observed in some studies (e.g., Bouquet et al., 2018). In such cases, consort males would be more likely to approach and maintain closer proximity to calling females, thereby promoting paternal certainty (Maestripieri et al., 2005; Todt et al., 1995). On the other hand, under the sperm competition hypothesis, calls would be expected to occur regardless of male rank, encouraging subsequent copulations with other males and fostering paternal confusion (e.g., Semple, 1998). Given this mixed evidence, it has been proposed that these two functions are not mutually exclusive and that both strategies could coexist, depending on the mating system and selective pressures of each species (Bouquet et al., 2018; Pradhan et al., 2006).

Since these vocalizations tend to be more common in species that live in multi-male, multi-female groups with promiscuous mating systems (Dixson, 2012; Maestripieri & Roney, 2005; Pradhan et al., 2006; van Schaik et al., 1999; Zinner et al., 2004), it has been supported that copulation calls likely evolved as part of female mating strategies in polygynandrous species aiming to reduce infanticide by concentrating or confusing paternity (Pradhan et al., 2006). This would explain why females use these calls differently and transmit distinct information depending on the strategy—female post-copulatory choice or sperm competition—that was most effective during evolutionary history to prevent infanticide, based on the social system of each species (Pradhan et al., 2006). For instance, chacma baboons (*Papio ursinus*) or yellow baboons (*Papio cynocephalus*), which live in more promiscuous societies, produce copulation calls during 80% to 92% of copulations (Collins, 1981; Hall, 1962; Saayman, 1970; Semple, 2001; Semple et al., 2002). In contrast, hamadryas baboons (*Papio hamadryas*), where females are monandrous during a single ovulatory cycle, produce these calls less frequently, with rates of 18% to 26.1% (Nitsch et al., 2011; Swedell & Saunders, 2006). In this species, females would not gain any benefit from producing copulation calls related to infanticide risk, as they are sexually monopolized by the resident males of their units, who have high or absolute paternal certainty. This raises questions about the function of these calls in this species, suggesting they may have acquired a new role adapted to their specific social system.

Social Structure and Mating System in Hamadryas Baboons

Baboons are primates of the Cercopithecoidea family, belonging to the genus *Papio*, which comprises different species distributed mostly across Africa and adapted to a wide range of habitats, from the deserts of Namibia to the tropical forests of Uganda (Barret & Henzi, 2008). However, the taxonomy of baboons has been the subject of intense debate for decades (Hill, 1970; Groves, 2001; Jolly, 1993). Currently, six phylogenetic species are recognized (Anandam et al., 2013): chacma baboons (*Papio ursinus*) and kindae baboons (*Papio kindae*) inhabiting southern Africa; yellow baboons (*Papio cynocephalus*) and olive baboons (*Papio anubis*) in eastern Africa; guinea baboons (*Papio papio*) with a very limited geographic range in western Africa; and hamadryas baboons (*Papio hamadryas*), which inhabit regions in Ethiopia, Eritrea, and the Arabian Peninsula. Based on their habitat, baboons can be classified into two groups: the "savanna baboons," which include yellow, kindae, olive, guinea, and chacma baboons, and the "desert baboons," represented by hamadryas baboons, which inhabit desert climates (Barret & Henzi, 2008).

Hamadryas baboons exhibit a multi-level social organization based on one-male units (OMUs), consisting of a leader male, several females with their offspring, and, occasionally, a follower male (Kummer, 1968). These units aggregate into clans (Abegglen, 1984), and, along with non-affiliated males, form bands, the primary ecological unit. Finally, multiple bands may congregate at key resources, such as sleeping sites, forming troops (Schreier & Swedell, 2009). Leader and follower males tend to be maternally related and rarely disperse. In contrast, females transfer between units throughout their lives, mainly due to forced abductions by males (Abegglen, 1984; Amann et al., 2017; Pines et al., 2015; Polo et al., 2014; Sigg et al., 1982; Swedell et al., 2011), although studies have also shown that females within a unit tend to be more maternally related than would be expected by chance (Städele et al., 2016). In these units, leader males sexually monopolize females by guarding them to prevent other males from copulating with them (Amann et al., 2017; Kummer, 1968; Nitsch et al., 2011; Pines et al., 2015; Stammbach, 1987; Swedell and Saunders, 2006). As a result, females are monandrous within the same ovulatory cycle, which grants leader males high paternity certainty. This promotes the active protection of females and their offspring by the males, resulting in low levels of infanticide compared to other baboon species (Swedell & Saunders, 2006), thereby reinforcing the bond between females and their respective leader males.

On the other hand, leader males compete with one another to increase the size of their units through takeovers, recruiting females belonging to other OMUs into their own (Swedell

& Saunders, 2006). These events often occur when the original leader male becomes weakened, whether due to age, injury, or illness, making it easier for a competitor to challenge him (Swedell, 2000). During and after a takeover, the challenging male engages in coercive behaviors such as herding and aggressively controlling the movements of females, thereby restricting their opportunities to choose mates (Amann et al., 2017; Pines et al., 2015; Swedell & Saunders, 2009). Studies show that takeovers are not random: males tend to target nulliparous females, likely due to their higher long-term reproductive value, although females in any reproductive state—pregnant, lactating, or cycling—can also be targeted (Amann et al., 2017). Takeovers impose significant costs on females: there is a markedly increased risk of infant mortality (Polo et al., 2014; Swedell, 2000; Swedell & Saunders, 2006; Swedell et al., 2014), either due to direct infanticide or neglect by the new male, who does not provide protection (Amann et al., 2017). Furthermore, females may terminate their pregnancies as an adaptive response to avoid investing in offspring unlikely to survive (Amann et al., 2017). Takeovers also significantly lengthen interbirth intervals, as females require more time to conceive after being transferred to a new male (Polo et al., 2014).

Although takeovers impose substantial costs on females, their lifetime reproductive success may depend on certain characteristics related to the units they belong to (Polo et al., 2014). Firstly, the leader male's rank indicates his ability to acquire and maintain resources, which is directly related to the size of the OMU he can sustain (Pines et al., 2015). Females may benefit indirectly from being in a unit led by a high-ranking male by producing highly competitive and reproductively successful offspring, and directly through better access to valuable resources (Swedell & Saunders, 2006; Zinner, 1999). Secondly, since high-ranking males are expected to maintain larger units, competition among females for access to these males would also increase (Colmenares et al., 2002; Zinner et al., 1994). This is relevant because the degree of association between a female and the leader male could determine her social status. In this regard, females may benefit from belonging to units where they hold a high social status, as low-status females receive less protection from the male and face greater risks (Stammbach, 1987). Lastly, although females are the sex that disperses, kinship remains an important variable for explaining bonding patterns observed among females within units

(Ekeyanabe-Weber & Swedell, 2021; Städele et al., 2015, 2016; Swedell, 2002). Related females are more likely to be found in the same unit, suggesting that when females can transfer between units—or are opportunistically taken, as when a leader male dies—they prefer to move to units containing other related females (Städele et al., 2016). This preference allows them to gain advantages through nepotistic relationships in addition to potential direct benefits from close social bonds (Silk, 2007). Consequently, the ranking of males (measured by the size of their unit), the social status of females (measured by their bond with the leader male), as well as the presence of related females within the unit, are key factors that may impact the reproductive success of female hamadryas baboons.

In this context, considering the social organization and mating system of hamadryas baboons, it does not appear that females would gain significant benefits by using copulation calls to reduce the risk of infanticide through concentrating or confusing paternity. On the one hand, opportunities to copulate outside the unit are very limited due to the coercive control exercised by resident males. Additionally, in the rare cases where extra-consort copulations occur, females may face aggression from their leader males, making such interactions highly costly (Kummer, 1968; Swedell & Saunders, 2006). However, females would also gain no additional benefit by encouraging paternity concentration, given that males already have a high paternity certainty due to their sexual monopolization of females. Thus, it seems that these signals do not provide benefits related to reducing the risk of infanticide, which might suggest that they lack an adaptive function in this species. Nevertheless, since these calls are suggested to be costly because they attract the attention of competitors or predators (Bouquet et al., 2018; Dixson, 1998; Dunbar, 1988; Hamilton & Arrowood, 1978; O'Connell & Cowlishaw, 1994), it is reasonable to think that their function may have shifted in response to selective pressures stemming from the social system of hamadryas baboons.

Since females may achieve greater reproductive success in certain units compared to others, it is expected that they would have individual preferences regarding them (Anderson, 1994). Although females lack opportunities to choose mates or voluntarily transfer to other units (Pines et al., 2015), they may have developed strategies to attract males, increasing male competition, which in turn results in coercive takeovers and the transfer of females between units. In this sense, the costs associated with promoting takeovers——may be counterbalanced if females are transferred to units where they can enhance their long-term reproductive success. If these signals serve to attract males and promote competition among them (O'Connell & Cowlishaw, 1994; Pradhan et al., 2006), as the primary consequence of intrasexual competition in hamadryas males are takeovers, it is possible that these calls have developed an adaptive role aimed at facilitating the transfer of hamadryas females between units.

The use of copulation calls and their acoustic structure in hamadryas baboons: objectives, hypotheses, and predictions

The main objective of this research is to understand the role of copulation calls in the mating strategies of hamadryas baboons. It has been suggested that in primates living in societies with polygynous mating systems—where males sexually monopolize females within their unit and the risk of infanticide is relatively low, as in the case of hamadryas baboons—these calls might be nearly absent, persisting merely as a phylogenetic vestige without any clear adaptive function (Pradhan et al., 2006). In fact, hamadryas baboons are characterized by a lower frequency of copulation calls compared to other primates (reviewed in Maestripieri & Roney, 2005). However, due to the costs associated with producing such signals, we hypothesize that copulation calls in hamadryas baboons, as in other primate species, function to increase male competition for access to females. However, given this species' social system, the consequence of this competition would be the transfer of females between units. If this general hypothesis holds, it would be expected that copulation calls occur more frequently in certain contexts than in others and that their acoustic structure varies depending on these contexts. Furthermore, we predict that the emission of copulation calls will be associated with future female transfers. Specifically, we will investigate, first, how these vocalizations are used and what consequences they have for females in terms of transfers (*chapter 2*), and second, what type of information they contain and convey to the audience (*chapter 3*).

To date, no studies have explored the potential function of copulation calls in hamadryas baboons— a species whose mating system renders previously proposed functions (such as sperm competition and female post-copulatory choice) unfeasible. However, to understand their function, it is crucial to determine how these calls are used and what information they convey. In this study, we conduct the first frequency and acoustic analysis of copulation calls in the hamadryas baboon colony residing at the Madrid Zoo. By examining which females produce copulation calls and the information conveyed through these calls, we can shed light on their role and function in hamadryas baboons, contributing to a deeper understanding of their adaptive significance in a polygynous species where female mate choice is constrained by male takeovers and reduced sperm competition.

In *chapter 2*, we will focus on investigating which females produce copulation calls and in what contexts, with the goal of understanding how they are used. If copulation calls in hamadryas baboons function to facilitate the transfer of calling females to other units, then we expect that they will be produced by females who would gain greater reproductive advantages by promoting such transfers. In this sense, we predict that the frequency of these calls will be higher in females belonging to units led by low-ranking males, in peripheral females residing in large units with high-ranking males, and in females living in units without the presence of related females. Additionally, we expect that copulation calls will occur more frequently when females exhibit maximum sexual swellings and during ejaculatory copulations, as has been observed in other primate species (e.g., Maestripieri et al., 2005; Rigaill et al., 2013; Saayman, 1970; Vaglio et al., 2020). Finally, if copulation calls facilitate female transfers between units, we predict that the use of these calls will increase the likelihood that the calling females will be transferred in the future.

In *chapter 3*, we will explore the factors determining the observed variability in the acoustic structure of these calls and, consequently, what information is conveyed to the audience. If hamadryas females use copulation calls to promote their transfer between units, it is likely that these calls convey at least information about the rank of the leader male of the unit, allowing other males to infer the intensity of intrasexual competition they would face when attempting to recruit the calling female. Additionally, these calls may also transmit information about the female's social status since peripheral females, who spend less time in proximity to the leader male, receive less surveillance, thereby presenting reduced competition for males attempting to recruit them compared to central females. Therefore, copulation calls may contain information about both male rank and female social status, enabling males to assess their probability of success in recruiting a particular female. Furthermore, we aim to explore whether these calls differ between females and whether they are related to the female's reproductive state and the male's ejaculation, factors that influence the acoustic structure of copulation calls in other primates (e.g., Engelhardt et al., 2011; O'Connell & Cowlishaw, 1994; Pfefferle et al., 2008; Semple, 2002).

CHAPTER 2: FEMALE COPULATION CALLS IN HAMADRUAS BABOONS (PAPIO HAMADRYAS): FEMALE CHOICE IN A POLYGYNOUS MATING SYSTEM WITH MALE SEXUAL COERCION?

Manuscript sent to International Journal of Primatology

Authors: Montserrat Belinchón[1], Pablo Polo[1], María Victoria Hernández-Lloreda[2], José Zamorano-Abramson[1], Fernando Colmenares[2]

Afilitations: [1]Centro de Investigación en Complejidad Social, Facultad de Gobierno, Universidad del Desarrollo, Chile; [2]Departamento de Psicobiología y Metodología del Comportamiento, Facultad de Psicología, Universidad Complutense de Madrid, Spain

Abstract

In primates, copulation calls are thought to increase male-male competition, leading to a decrease in infanticide risk through concentrating or confusing paternity. Accordingly, their function in species where females mate monandrously within sexual cycles and paternity is concentrated, such as hamadryas baboons (*Papio hamadryas*), is not well understood. We propose that copulation calls in hamadryas baboons could serve to promote male takeovers in females belonging to low-status one-male units (OMUs) and in peripheral females in highstatus OMUs, as they could get benefits from transferring to other units. We studied copulation calls in a colony of hamadryas baboons consisting of 8-11 OMUs that deployed the species' typical characteristics: multi-level social organization, harem-guarding polygyny, female transfers across OMUs via forced male takeovers, and intense coercion.

We recorded a total of 321 copulations through behavioral sampling and gathered the caller's reproductive state, the copulation outcome, the mating partner's social status (proxied by the OMU size), the calling female's social status (peripheral versus central), the presence of female relatives in the unit and whether she was transferred via male takeover in the next years. We found that copulation calls were more likely produced by central females in lowstatus (small) OMUs and by peripheral females in high-status (large) OMUs. Moreover, calling females were more likely to be transferred during a male takeover if they belonged to low-status OMUs. We argue that by calling, females instigate male-male competition, potentially resulting in male takeovers and thus expressing mate preferences even in a scenario of intense intersexual conflict.

Keywords

Sexual conflict, male takeovers, intrasexual competition, mate preferences

Introduction

The communicative repertoire of a wide variety of animal species includes the production of sounds and vocalizations (Bradbury & Vehrencamp, 2011; Chen & Wiens, 2020; Sebeok, 1977). Calls are uttered in a variety of contexts, including food, predation, social play, friendly social interaction, agonism, reconciliation, and mating (Bradbury & Vehrencamp, 2011; Hauser 1996). In several species of primates, including humans, females utter calls during or immediately after copulation, which are referred to as copulation calls (Brewer & Hendrie, 2011; Clutton-Brock, 2016; Dixson, 2012; Maestripieri & Roney, 2005; Pradhan et al., 2006; Prokop, 2021; Snowdon, 2004). Moreover, copulation calls in primates typically co-occur alongside other sexually selected traits such as exaggerated sexual swellings (Dixson, 2012; Maestripieri & Roney, 2005; Pradhan et al., 2006; van Schaik et al., 1999; Zinner et al., 2004), that are claimed to have evolved in response to the polygynandrous mating system commonly observed in multimale, multifemale social groups (Dixson, 2012, Clutton-Brock, 2016; van Schaik et al., 1999; Zinner et al., 2004). Although these vocalizations have been observed and described in many species of primates their function is still debated.

Previous studies have examined the use of copulation calls as well as male responses to them in order to investigate their function. First, copulation calls are more common in primate species that form multi-male, multi-female groups and mate promiscuously (Pradhan et al. 2006). Regarding the use of these calls, several studies reported that copulation calls are more frequently produced when the calling female's sexual swelling is larger (Henzi, 1996; Maestripieri et al., 2005; O'Connell & Cowlishaw, 1994; Rigaill et al., 2013; Saayman, 1970; Swedell, 2006; but see Vaglio et al., 2020) and during ejaculatory copulations (Deputte & Goustard 1980; Dixson, 2012; Engelhardt et al., 2012; Henzi, 1996; Maestripieri et al., 2005; Maestripieri & Roney, 2005; Pfefferle et al., 2008; Pradhan et al., 2006; Vaglio et al., 2020). Moreover, some studies suggest that the use of copulation calls is influenced by male partner's age and dominance status (Clutton-Brock, 2016; Dixson, 2012; Maestripieri & Roney, 2005; Pradhan et al., 2006), being these calls more frequent when females copulate with high-ranking males (Bouquet et al., 2018; Maestripieri et al., 2005; but see Pfefferle et al., 2008) and with males with greater competitive ability (Semple et al., 2002). Regarding male responses, some studies found that after copulation calls, consort males increased their proximity towards the caller and decreased the propensity to leave her, therefore increasing mate guarding (Maestripieri et al. 2005; Todt et al. 1995). Nonetheless, other studies found that females were mated sooner by non-consort males when they listened to the playback of their copulation calls compared to the control stimuli (Semple, 1998).

In line with this evidence, several hypotheses have been proposed to explain the occurrence and function of copulation calls in primates, which a common theme that these calls are a sexually selected trait that increases female fitness by promoting competition between males, leading to different potential effects (e.g., Bouquet et al., 2018; Hauser, 1990; Maestripieri & Roney, 2005; O’Connell & Cowlishaw, 1994; Pradhan et al., 2006). Two major hypotheses are considered the most plausible based on the context and timing of the occurrence of these calls (Bouquet et al., 2018; Pradhan et al., 2006). The postcopulatory female choice hypothesis claims that female copulation calls encourage mate-guarding by the female’s current mating partner, thus minimizing the probability of sperm competition and enhancing paternity concentration (Bouquet et al., 2018; Maestripieri et al., 2005). In contrast, the sperm competition hypothesis argues that by calling, females instigate polyandrous mating and, therefore, foster sperm competition and paternity confusion (Bouquet et al., 2018; O’Connell & Cowlishaw, 1994). According to these functions, copulation calls were proposed to emerge in species organized in multi-male, multi-female groups with polygynandrous mating systems where females can regularly mate with several males within ovarian cycles (Pradhan et al. 2006).

Given that evidence supports both hypotheses, it has been proposed that copulation calls can produce either effect, depending on the mating system and selective pressures related to the risk of infanticide in each species (Pradhan et al., 2006). This would explain the remarkable variability found in the use of copulation calls among primates (Bouquet et al., 2018; Pradhan et al., 2006). Nonetheless, hamadryas baboons (*Papio hamadryas*) represent an interesting exception. Despite hamadryas females reproduce polygynously in one-male units (OMUs), they produce copulation calls (Swedell & Saunders, 2006). In this context, copulation calls are unlikely to reduce the risk of infanticide through sperm competition or postcopulatory female choice, as females are already guarded by males in each OMU. This raises the question of what function, if any, copulation calls serve in this species of baboon.

Hamadryas baboons live in multilevel, fusion-fission societies (Abegglen, 1984; Colmenares, 1992; Colmenares et al., 2006; Kummer, 1984; Sigg et al., 1982; Schreier & Swedell, 2012a, 2012b; Swedell & Leigh, 2006; Swedell & Plummer, 2019). Their mating system is based on female defense polygyny: leader males compete to collect females individually into their units through forcibly coercive takeovers, guarding and herding them to prevent mounts from other males (Amann et al., 2017; Kummer, 1968; Nitsch et al., 2011; Pines et al., 2015; Stammbach, 1987; Swedell & Saunders, 2006). Therefore, females transfer across OMUs mainly due to coercive male takeovers, so female mate choice is highly constrained in this species (Abegglen, 1984; Amann et al., 2017; Pines et al., 2015; Polo et al, 2014; Sigg et al., 1982; Swedell et al., 2011).

However, female reproductive success in hamadryas baboons may depend on factors related to their OMU membership. In this sense, unit size denotes the capacity of a leader male to acquire and maintain resources, which might signal his social status (Pines et al., 2015). Accordingly, females in high-status OMUs could benefit indirectly by producing competitive offspring and directly by having preferential access to valuable resources (Swedell, 2006). However, since high-status males are expected to have larger OMUs, the female-female competition for access to them would be increased in that context (Colmenares et al., 2002; Zinner et al., 1994). This is relevant because the degree of association and grooming interactions with the male can impact the protection that the female and offspring receive from him (Colmenares, 1997). Central females, who spend more time in proximity with their leader male, would have a stronger association with him, thereby influencing the protection they and their offspring receive (Colmenares, 1997) and reducing the risks they might face compared to peripheral females (Stammbach, 1987). Finally, kinship remains an important variable accounting for the patterns of female bonding observed within OMUs (Ekanayake-Weber & Swedell, 2021; Städele et al., 2015, 2016; Swedell, 2002). Female relatives are present in the same OMU more likely than expected by chance (Städele et al., 2016), suggesting that when females can voluntarily transfer across units (e.g., after a leader male’s death), they prefer to move to OMUs that contain maternal relatives (Städele et al., 2016). This kinship can provide inclusive fitness benefits through nepotistic relationships and potential direct fitness benefits through close social bonds (Silk, 2007).

Therefore, the leader male’s and female’s social status, as well as the presence of female relatives, may significantly influence female reproductive success in a social system characterized by male sexual coercion.

Then, as females can gain more benefits by belonging to certain OMUs compared to others, they might have individual preferences over them (Anderson, 1994). Even if they do not typically have opportunities to voluntarily transfer to other groups (Pines et al., 2015), they could still attract mates, thereby enhancing male-male competition. This could lead to male takeovers and, consequently, increase their likelihood of being transferred to other units. In this regard, the costs associated with male takeovers (Polo et al., 2014; Swedell et al., 2014; Swedell & Saunders, 2006) might be counteracted by the long-term reproductive success gained by being transferred to more advantageous units. In this sense, we proposed that if copulation calls in primates are considered sexually selected traits that attract males to promote male-male competition (via sperm competition or female monopolization) (O'Connell & Cowlishaw, 1994; Pradham, 2006), it is possible that hamadryas females might use these calls similarly, thereby promoting transfers via male takeovers to other units where their fitness could be enhanced.

The goal of the present study was to investigate the context in which copulation calls are produced and their consequences in terms of female transfers in a colony of hamadryas baboons to further understand its function. First, we predicted that copulation calls might be produced more frequently under maximal sexual swelling and in ejaculatory mounts, as observed in other primate species (e.g., Dixon 2012; Mastrepieri et al., 2005). Second, if copulation calls among hamadryas females could be used to promote female transfers, they would be produced by females who stand to benefit from being transferred into a different OMU. Consequently, we predicted the frequency of copulation calls would be higher in females belonging to OMUs of low-status males as well as in low-status (peripheral) females belonging to OMUs of high-status males, and the copulation calls would be more frequent in females with no relatives in their OMUs. Finally, if copulation calls in hamadryas promote male takeovers as we hypothesized, we predicted that the use of copulation calls would increase the probability of male takeovers in the callers.

Methods

Ethic statement

The research described in this paper was non-invasive, and nonexperimental, and strictly adhered to the legal requirements of Spain. No approval from any Research Committee was necessary because no special permission for the use of animals in purely observational studies is required in Madrid Zoo. Animal husbandry and research in the Madrid Zoo comply with the "EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria" and the "WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums." It also adhered to the American Society of Primatologists (ASP) principles for the ethical treatment of nonhuman primates. The Madrid Zoo and Aquarium granted permission to carry out this study.

Study Subjects and Housing

The subjects of this study were 36 adult females, members of the colony of hamadryas baboons (*Papio hamadryas*) housed at the Madrid Zoo, Spain, between July and October 1999. As described in previous reports (Colmenares, 1992), although individuals in the colony at that time comprised hamadryas and some hamadryas-anubis hybrids, they deployed the multi-level group structure, harem-defense polygynous mating system, cross-sex bonding, male takeovers and male coercive herding behavior of females observed in wild populations of hamadryas baboons (Erer-Gota: Abegglen, 1984; Kummer, 1984; Sigg et al., 1982; Filoha: Swedell & Saunders, 2006; Swedell and Schreier, 2009; Swedell & Plummer, 2019). At the beginning of the study period, i.e., 5th July 1999, the colony consisted of 11 OMUs containing 36 sexually mature females altogether. Between the 15th and 17th of July, most of the individuals from two OMUs were removed, and one leader male died.

Afterwards, the colony comprised 23 adult females reorganized into 8 OMUs (Table 1). All the colony members were recognized individually, and their kin relations were also known. The colony was housed in a large outdoor enclosure (36 m long, 26 m wide, and 7 m deep) and an attached indoor area. The outdoor enclosure was terraced and contained several climbing structures and a water-filled moat with up to 21 flat-circular islands (Colmenares, 1992). The indoor area consisted of four large rooms inaccessible to visitors that baboons could access freely at any time during the day. Baboons were fed once or twice per day and running water was available ad libitum.

TABLE 1. One-Male Units (OMUs) and its composition before and after the removal of individuals on July 15th-17th, 1999.

Before removal		After removal	
OMU	Unit females	OMU	Unit females
Fom	Crisi	Fom	Crisi, Ceres
Faruk	Gracita, Nabila, Goa	Faruk	Gracita, Nabila, Goa
Ramsés	Fez, Grama	Ramses	Crama, Grama*
Geb	Plo, Oyama, Nua, Gambia, Gaza	Geb	Plo, Oyama, Flavia, Nua, Gambia, Gaza
Netto	Grey, Nana, Inúa, Niba	Netto	Grey, Nana, Inúa, Niba
Gaos	Noma, Nyani, Galea	Gaos	Noma, Nyani, Galea
Gogh	Gilka, Cira	Gogh	Gilka, Cira
Perseo	Guereza, Olaya	Perseo	Guereza, Olaya
Ra	Crama, Flavia, Flo		
Chad	Giselle, Osaka, Gueisa, Fiona		
Amón	Chepka, Gala, Noa, Gizeth, Ceres, Namibia, Nube		

*This female was removed on September 9th, 1999 and reintroduced on January 12th, 2000.

Data Collection

This study involved the collection of behavioral, socio-demographic, and reproductive data. The *behavioral* records included copulations and copulation calls that were collected via behavior sampling (Bateson & Martin, 2021) from 5th to 31st July and from 3rd September to 1st October 1999, between 8:30 and 10:30, five days a week, amounting to a total of 82 hours of observation. Behavioral data were recorded by videotapes, providing information about the identity of participants (e.g., copulating male and female), the sequence and content of behavioral actions, and their context. The *behavioral* records also included data on femaleto-male grooming, extracted from a database (see below), collected between January and December 1999, via scan-sampling of OMUs and instantaneous sampling of grooming (Altmann, 1974; Bateson & Martin, 2021) at 30-min intervals.

The *socio-demographic* and *reproductive* data were extracted from the database of longterm records of the colony. These data were recorded about three to five days weekly throughout the entire long-term research project, which started in 1972 and finished in 2001. The *socio-demographic data* included parameters such as the composition of OMUs, the occurrence of female transfers across OMUs, typically via male takeovers, the males' social and reproductive careers, and the females' reproductive life history patterns. The *reproductive data* included records of each female's reproductive state, i.e., cycling, pregnant and lactating. Of the females undergoing ovarian cycles and engaging in copulations, information was further collected on their phase within the cycle and the identity of their mating partners (typically their unit's leader male). The baboon female's ovarian cycle comprises two major phases that can be estimated through clues provided by the color and especially the size of the swelling of the sex skin of her anogenital area (Saayman, 1970; Higham et al., 2008a, 2008b, see also Dixon, 2012). During the follicular phase, the sex skin increases in turgescence (inflating period) until it peaks for a few days (swollen period). After ovulation, the ovarian cycle's luteal phase begins signalled by a decrease of the sexual swelling (deflating period) which is finally followed by another time span of a few days during which the sexual skin is flat (flat period).

Study Variables

The study variables coded and then analyzed are defined as follows.

Copulation calls. Females produce copulation calls towards the end or right after copulation, defined as loud, low-pitched rhythmic vocalizations uttered as a series of staccato grunts (o-o-o-o) in baboons (Kemp et al., 2017). We coded the presence or absence of a copulation call in each registered copulation for any given female. A copulation was defined as a mount involving male intromission of the penis and pelvic thrusting. *Copulation outcome.* During an ejaculatory mount, there is a slowing down of pelvic thrusts, followed by muscular spasm, where the male remains rigid upon the female for a few seconds and the emission of semen presumably takes place (e.g., Saayman, 1970; Paciência et al., 2020). When possible ($N = 250$), we determined the copulation outcome, specifically whether or not ejaculation occurred. *Female's social status.* The amount (percentage of scans) of grooming that females directed to their unit leader males was used as a proxy of the females' social status within the unit, that we classified into two categories: central *versus* peripheral (see Sigg, 1980) based on two different criteria. We tested if grooming interactions were significantly unequally distributed between females within their units using Chi-square goodness-of-fit test. However, we found that grooming interactions were unequally distributed only in three OMUs. Hence, we used a more relaxed criterion according to which females were classified as central (or peripheral) if the proportions of scans they spent grooming their OMU´s male was higher (or lower) than the mean within that OMU. *Male's social status.* To assess the unit male's social status or resource-holding potential, i.e., RHP (e.g., Allen & Krofel, 2022) we used the OMU size as a proxy, that is, the number of sexually mature females in the OMUs at the time of copulation. *Presence of female relatives residing in the OMU.* We coded this variable as the presence or absence of the mother, female full siblings and female half-siblings in the OMU. *Male takeovers and female transfers.* We used the long-term database of the colony to check whether the studied females eventually transferred to another OMU via a male takeover until August 2001, excluding those females who were removed from the colony during the study period. *Female reproductive state.* We classified each female's cycle phase into three categories. *Tumescence (inflating)*, when the female's anogenital swelling was increasing; *maximum swelling (swollen)*, estimated considering the 5 days prior to the onset of detumescence; and a category labeled flat that combined several reproductive states: when the sex skin was deflating or flat during the luteal phase of the ovarian cycle, and when the sex skin was flat during the female's pregnancy or during the post-partum period of lactation.

Data Analyses

We included a total of 321 copulations after discarding copulations not completed because females ran away while being mounted (N = 2), when vocal behaviour could not be precisely determined (N = 8), or when individuals could not be accurately identified (N = 69). We first describe and characterize the observed copulations and the associated copulation calls produced during these events. Then to test our first and second predictions, we used a generalized linear mixed model (GLMM) with a logistic function to examine which factors influence the emission of copulation calls, including only copulations between mature females and adult males (N=301). We considered the presence/absence of copulation calls in each copulation as the dependent variable. Male's social status (OMU size) was included as a covariate in the model. Female's social status, the presence of female relatives in their OMUs, the female reproductive state and copulation outcome were included as fixed factors in the model. In addition, we included the interaction between female's and male's social status. In order to control for the unequal contribution of copulation by females to the data sample and the repeated measures, we included female ID as a random effect in the model. As the copulation outcome was only determined for 250 copulations, we ran a first model with the complete dataset without considering the copulation outcome (N = 301) and then a reduced model including it (N = 250). Given the difference in sample size between the models, we used Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) to choose the best model. We reported the reduced model as it yielded lower AIC and BIC values, indicating a better balance between the model fit and complexity (Raftery, 1995; Sakamoto et al., 1986). Moreover, the predictor variables got consistent results in terms of statistical significance compared to the model that employed the full dataset (see Table S1).

Regarding our third prediction, we could not use a generalized linear mixed model due to convergence errors. Instead, we decided to use a contingency table analysis to test whether producing copulation calls during the study was related to changing OMUs via male takeovers in the future. Given the small sample size and the low expected frequencies, we used non-parametric tests, including the Fisher's Exact test to assess relationships between categorical variables and Mann-Whitney U test to compare differences between groups.

For statistical analysis we used R (v.4.2.1 Core Team, 2022). The GLMMs were run using *glmer* function within lme4 package (v. 1.1-30, Bates et al., 2015) with the optimizer "*bobyqa*". We set the significant level at 0.05. Raw data are available at: https://osf.io/543r7/.

Results

Descriptive results

Out of the 321 copulations included, 311 involved 30 adult females, while the remaining 10 copulations involved non-sexually mature females. Considering only adult females, most of the copulations were with the females' leader males, representing 96.26% of the cases (299 copulations). In contrast, followers (adult males other than the leader attached to an OMU) or juveniles from their units accounted for 3.12% of the copulations (10 copulations), and only 0.62% involved other leader males (2 copulations). Among the 30 copulating adult females, 18 underwent ovarian cycles during the study period, while nine were pregnant and three were lactating. Most copulations occurred when the females' sexual swelling was inflating (31.2%; 97 copulations) or had reached maximal swelling (33.8%; 105 copulations). Of the copulations for which the outcome was accurately determined, 23% resulted in ejaculation (58 copulations), most of them when their sex skin was maximally swollen (65.5%; 38 copulations) or inflating (27.6%; 16 copulations). None of the 10 copulations that involved immature females were ejaculatory.

Copulation calls were exclusively produced by adult females and occurred in only 15.9% (48 copulations) of all copulations involving adult females and leader males (N = 301). Out of the 48 recorded copulation calls, only one vocalization was emitted during copulation with a leader male from a different OMU. Copulation calls were uttered by eight of the 30 copulating females (see Table 2). Three of these calling females belonged to OMUs led by low-status males (OMU size = 2) and had no other female relatives within their units. The remaining calling females belonged to OMUs led by higher-status males, with three out of five being peripheral females within their respective units. Notably, seven of these females were cycling except one female who was pregnant.

TABLE 2. Information on the calling females considering copulations between adult females and leader males.

Female	OMU size	Presence of female relatives	Female's social status	Male Takeover	No. copulation calls	No. copulations	Reproductive condition
Olaya	2/1	No	Central	Yes	23	41	Cycling
Ceres	2	No	Central	Yes	14	52	Cycling
Chepka	7	Yes	Peripheral	-	1	1	Cycling
Crisi	2	No	Peripheral	Yes	4	11	Cycling
Grey	4	Yes	Peripheral	No	2	3	Cycling
Guereza	4	No	Peripheral	Yes	1	6	Pregnant
Niba	4	Yes	Central	No	1	7	Cycling
Plo	6	Yes	Central	No	2	9	Cycling

Predictors of copulation calls

Table 3 presents the contributions of various predictors to the occurrence of copulation calls based on the reduced model (N = 250 copulations; see Methods for details). The model accounts for 63.5% of the variability observed in the production of copulation calls. Females were more likely to vocalize when their sexual swelling was at its maximum and when copulations resulted in ejaculation (Table 3). Notably, the significant interaction effect indicates that the vocal behavior of females in relation to their social status is influenced by the male's social status, as determined by the size of the OMU (Table 3). Figure 1 illustrates that females were significantly more likely to vocalize when they occupied central positions within small OMUs or by peripheral females in larger OMUs. That is, as OMU size increases, the likelihood of copulation call emissions among peripheral females rises in comparison to central females. Conversely, the presence of female relatives within the OMU did not have a statistically significant impact on the occurrence of copulation calls. We further tested if having females' relatives in the OMU was related to the emission of copulation calls without the presence of the other predictors, but the variable remained nonsignificant (B = -1.609, SE = 1.509, p = 0.286).

TABLE 3. GLMM with the reduced dataset considering copulation outcome (n=250).

variable	Reduced model (n=250) Predictor		
	B	Exp(B)	*p*
Intercept	-7.597	.000	.001
Reproductive state: tumescence	1.785	5.797	.051
Reproductive state: maximal swelling	1.881	6.700	.037
Copulation outcome: ejaculatory	1.184	3.741	.037
Female relatives: presence	-7.599	.187	.174
Male's social status (OMU size)	.716	2.084	.077
Female's social status: central	8.593	4815.703	.002
Male's social status * Female's social status	-2.098	.129	.002
AIC			159.09
BIC			184.71
Log lik			-67.543

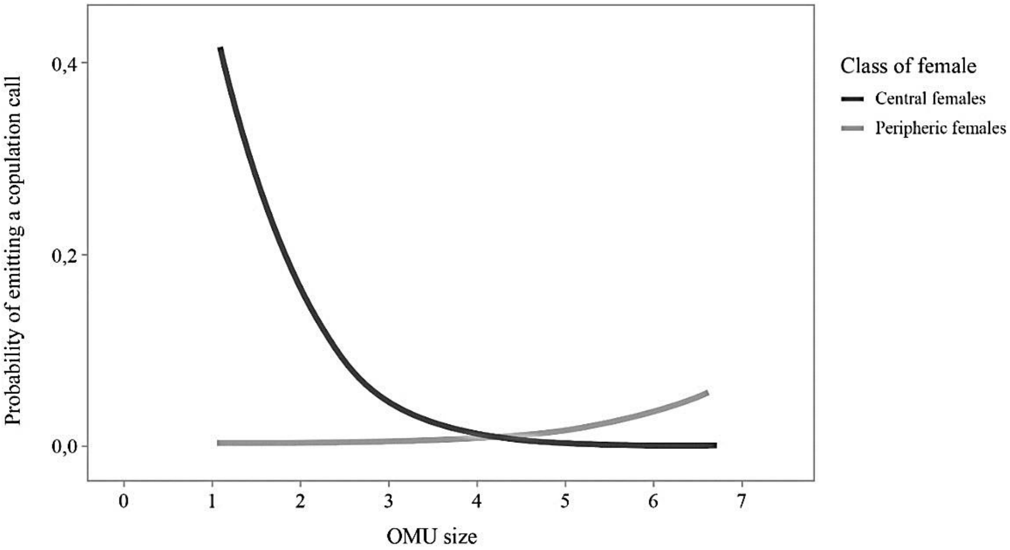

FIGURE 1. Probability of the occurrence of copulation calls in response to the interaction effect between female's social status and male's social status (OMU size).

Female transfers and copulation calls

Of the 23 females who remained in the colony until the end of the long-term study (i.e., year 2001), only five were transferred to other OMUs. Of these, four uttered copulation calls during the current study. Indeed, calling females were more likely to be transferred than expected by chance (Fisher exact test, *p* = .017, adjusted standardized residuals = 2.7, Table 4). In general, the females who were transferred to other OMUs belonged to smaller OMUs than those who stayed in their OMUs (mean OMU size 2.20 versus 4.16, respectively; *U* = 14, *p* = .014, *N* = 23).

TABLE 4. Contingency table of copulation calls and male takeovers. Expected frequencies are shown in parenthesis.

		Male takeover	
		Occurrence	Absence
Copulation calls	Occurrence	4 (1.5)	3 (5.5)

	Absence	1 (3.5)	15 (12.5)

Discussion

This study investigates the use of copulation calls in hamadryas baboons to understand the role of these signals in this species of baboons. Given that copulation calls are thought to promote male-male competition for the access to receptive females in primates (Cox & Leboeuf, 1977; Hauser, 1990; Pradhan et al., 2006), we hypothesized that, if these signals serve a function in hamadryas baboons, they should be associated with male takeovers, the primary consequence of male-male competition in this species (Swedell & Saunders, 2006). Overall, we found partial evidence supporting our predictions since copulation calls were uttered more frequently by peripheral females in larger OMUs and by central females in small OMUs. In addition, we found that the reproductive state of the female and copulation outcome affected the likelihood of emitting a copulation call but the presence of female relatives did not. Finally, we found that females who emitted copulation calls, especially those in small OMUs, were more likely to be transferred between units in the future.

In our first prediction, we tested whether the female reproductive state and copulation outcome influence the production of copulation calls in hamadryas baboons, as has been observed in other baboons (Henzi, 1996; Maestripieri et al., 2005; O'Connell & Cowlishaw, 1994; Rigaill et al., 2013; Saayman, 1970; Swedell & Leigh, 2006; see, however, Vaglio et al., 2020) and other primates (see Dixon, 2012; Maestripieri & Roney, 2005; Pradhan et al., 2006; for reviews). We found that females were more likely to call under maximal sexual swelling and in ejaculatory mounts supporting the prediction. In general, it seems that copulation calls across most primate species tend to occur in conjunction with sexual swelling and male ejaculation (e.g., Dixon, 2012). In addition, considering reports of females emitting copulation calls during defecation (Boese, 1973; Hall, 1962), it is possible that copulation calls are a physiological response triggered by genital stimulation from the compression of the vaginal wall (Hauser, 1990; Henzi, 1996; Swedell & Saunders, 2006; Townsend et al., 2008), with females being more sensitive during higher tumescence and male ejaculation. However, it has also been suggested that this automatic response could be under voluntary control, serving as a tactic for deception (Bouquet et al., 2018). In this case, females might control or inhibit these vocalizations when they offer no benefits, which could explain why some females did not produce copulation calls.

In this line, in our second prediction, we tested whether copulation calls were uttered preferentially by females who could gain more benefits by transferring to other units. First, we found that the likelihood of emitting copulation calls was influenced by male's and female's social status: as higher the male's social status (larger OMU size), peripheral (lowstatus) females were more likely to produce copulation calls, whereas central (high-status) females were less likely to do so. In other words, peripheral females in large OMUs called at a greater rate than central ones supporting our prediction. Peripheral females would be at a competitive disadvantage regarding access to resources and protection (Swedell, 2006; Stammbach, 1987), especially in those larger OMUs (Zinner et al., 1994). Thus, these females would benefit from transferring to other units where they could form preferential relationships with the dominant male, thereby increasing the protection they and their offspring would receive (Colmenares, 1992, 1997). We also found that central females in small OMUs called at higher rates than peripheral ones; however, we expected that both peripheral and central females would call indistinctly since females who belong to small OMUs might indirectly benefit from moving to larger OMUs with dominant males by producing highly competitive male offspring and directly by being able to access better resources and protection (Swedell, 2006). This outcome could be explained if we consider that small OMUs were sometimes composed of just one female, which is automatically the central one, or of two females, where the grooming interactions between them with their leader male were not significantly different. Accordingly, the categorization of peripheral and central females could be arbitrary in these cases.

Second and contrary to our prediction, females without female relatives in their units did not produce copulation calls at higher rates. Female kin is more important in the hamadryas society than it was once thought (Kummer, 1968, 1990; Swedell, 2006), and in general, kinship provides nepotistic benefits and the opportunity to establish strong social bonds (Silk, 2007). However, hamadryas baboons are also characterized as a cross-sex bonded species, where the most significant bond is between females and the unit male (Barton, 1996). Consequently, the lack of a relationship between copulation calls and the presence of other female relatives suggests that, at least for females in this band, establishing a strong association with the leader male to prevent aggression toward themselves or their offspring is more crucial than forming affiliative relationships with other females.

Finally, and in relation to our third prediction, if copulation calls in hamadryas baboons promote female transfers between OMUs, we expected females who utter copulation calls to be more likely to transfer than non-calling females. Our results showed that four out of five females who were transferred over the next two years uttered copulation calls during the study period supporting our prediction. However, the effect of copulation calls was influenced by males' social status. Only calling females from small OMUs transferred across OMUs while calling females from larger OMUs did not transfer. It is possible that, as males compete to monopolize these females, only high-status males might display effective takeovers, so these events would only involve females in small OMUs. Then, according to the membership of the female, the consequence of the copulation calls may differ. In large OMUs, attracting competing males may lead to an increased and successful mate guarding toward the caller female, thus reinforcing and strengthening the pair bond with their leaders. However, as male guarding in hamadryas implies high levels of aggression toward females (Polo & Colmenares, 2012), this is still a costly strategy, so just low-status females would counteract these costs by promoting a better association with their resident males, whereas high-status females would not display this strategy. In small OMUs, attracting competing males may lead to successful takeovers by higher-status males. Indeed, if we assume that copulation calls are general vocalizations that are not particularly directed to specific males, then promoting transfers would not guarantee females their joining a better, preferred unit where they would improve their reproductive success. However, if we consider that only high-status males display effective takeovers, this would guarantee that at least females in low-status OMUs could move into higher-status units. However, we acknowledge that this is a speculative explanation for our results and that future studies are needed to test this.

Overall, our results partially supported our general hypothesis since the emission of copulation calls was biased toward females who would benefit most from promoting malemale competition. Specifically, of the 30 females observed during copulations, only eight emitted copulation calls. These calls were rare in pregnant females or those with lactating infants, with only one female out of 11 using the call which aligns with the high costs related to male takeovers. When excluding these females from the sample, 36.84% (7 out of 19) of the remaining females produced copulation calls, a similar rate to previous studies in wild populations (30% in Filoha: Swedell & Saunders, 2006). In addition, copulation calls were uttered in only 15.9% of observed copulations, a similar rate to previous studies in the wild (18% in Folia: Swedell & Saunders, 2006) and in captive populations (26.1%: Nitsch et al., 2011). This low calling rate could also suggest that copulation calls in hamadryas baboons serve no significant function (Pradhan et al., 2006). Since female hamadryas baboons are sexually monogamous within ovarian cycles, these vocalizations may not offer advantages in preventing infanticide and these calls may be conserved by phylogenetic inertia (Pradhan et al., 2006), possibly produced involuntarily due to genital stimulation. Nevertheless, this low percentage of calling females may still align with our hypothesis if we consider that only a subset of females benefits from leaving and joining other units.

According to our results hamadryas females, traditionally seen as having a passive mating strategy, could potentially exhibit an active mate choice by using sexual signals to influence male behavior. However, due to the limitations of our study, further research is needed to draw definitive conclusions and to discard the phylogenetic inertia explanation. The limited duration of the data collection and the unbalanced copulatory behavior across all females could have led to biased results. Then, future longitudinal studies should investigate whether these females continue calling until transferred and if the calls cease afterward or whether they are linked to female traits such as genotype, as some females appear to produce longer and more intense calls. Finally, it would be necessary also to assess the direct effect of copulation calls on male behavior and their potential impact on female reproductive success.

In conclusion, our study contributed new evidence to understand the use of copulation calls across primates and the evolution of this signal according to different selective pressures. In general, as copulation calls seem to foster male-male competition for the sexual access of the receptive mates, females would promote male competition according to the benefits they could get in accordance to their social system, leading to different functions which in turn is reflected in the divergent use of copulation calls across them. Therefore, it is possible that there is not a unitary function to explain the use of these calls (Henzi, 1996), neither within the same genus nor species, so its use varies in relation to changes in ecological factors and their social structure (Bouquet et al., 2018) by controlling its production. This also denotes a high degree of vocal flexibility in acoustic behavior among primates, as females would need a certain degree of cognitive control to guide their production.

CHAPTER 3: INFORMATION CONTENT OF FEMALE COPULATION CALLS IN HAMADRYAS BABOONS (*PAPIO HAMADRYAS*)

Authors: Montserrat Belinchón[1], Pablo Polo[1], María Victoria Hernández-Lloreda[2], José Zamorano-Abramson[1], Fernando Colmenares[2]

Afilitations: [1]Centro de Investigación en Complejidad Social, Facultad de Gobierno, Universidad del Desarrollo, Chile; [2]Departamento de Psicobiología y Metodología del

Comportamiento, Facultad de Psicología, Universidad Complutense de Madrid, Spain

Abstract

In many primate species, females produce copulation calls during or immediately after mating. They have been hypothesized to be sexually selected signals that instigate male-male competition for access to the calling female. In this study, we aimed to understand the role of copulation calls within a captive population of hamadryas baboons (*Papio hamadryas*) by exploring which information is encoded in their acoustic structure and made available to the audience. We proposed that if copulation calls also incite male-male competition in hamadryas baboons, they might convey information about male rank and female social status, enabling males to assess the likelihood of a successful takeover. In addition, we explore whether these vocalizations encode information about female reproductive state, and the occurrence of ejaculation as previously reported for other species of baboons. Our findings indicate that these calls only provide information about male ejaculation, but their acoustic form is distinctive among females. This suggests that males might gain information at the very least about the mating outcome and the copulating female's identity, potentially providing additional social clues useful to decide whether or not to challenge the current male for the female. This study enhances our understanding of the adaptive significance of copulation calls in hamadryas baboons, implying that there may not be a singular function for these calls, as their adaptative roles likely evolved under varying selective pressures.

Keywords: *Copulation calls, Hamadryas baboons, Acoustic structure, Information content*

Introduction

In primates, females produce vocalizations known as copulation calls during the final stage of the mount or immediately after copulation (Gouzoules et al., 1998; Hamilton & Arrowood, 1978; Hohmann & Herzog, 1985; O'Connell & Cowlishaw, 1994). Even though they are widespread among primates, these calls are particularly common in Old World species that live in multi-male multi-female groups with a polygynandrous mating system (e.g., Dixon, 2012). Several adaptative hypotheses have been proposed to explain their occurrence, sharing the idea that copulation calls are sexually selected signals that potentially enhance the female's reproductive success (Bouquet et al., 2018; Cox & Leboeuf, 1977; Hamilton & Arrowood, 1978; Hauser, 1990; Maestripieri & Roney, 2005; Pradhan et al., 2006; Semple, 1998). Although there is no tight consensus on the functions of copulation calls, most widely invoked hypotheses suggest that they play a role in attracting mates, increasing male-male competition; however, the consequences of this competition (mainly sperm competition and mate guarding) differ among proposals (Bouquet et al., 2018; Dixon, 2012; Maestripieri & Roney, 2005; Pradhan et al., 2006; Semple, 1998).

In order to investigate the adaptative function of primate copulation calls, researchers have examined which information these signals could provide to the audience (e.g., Semple et al., 2002; Townsend et al., 2011). In general, calls can convey precise information when their acoustic structure varies predictably according to a specific individual or social situation (Seyfarth & Cheney, 2017). In this line, some researchers reported that female copulation calls covaried acoustically with some features of the caller, such as its dominance rank, age (Gouzales et al., 1998), or the size of their sexual swelling (O'Connell & Cowlishaw, 1994; Semple et al., 2002, but see Clay & Zuberbühler, 2011), a graded signal of female's fertility (Higham et al., 2008). Specifically, the length of copulation calls and the number of call units increase with sexual swelling (e.g., O'Connell & Cowlishaw, 1994; Semple et al., 2002). Other studies, however, that accurate measured the timing of ovulation through the assessment of reproductive hormones failed to find that copulation calls contain reliable information about female fertility (Engelhardt et al., 2012; Pfefferle et al., 2008; Bernaldo de Quiros et al., 2018; Townsend et al., 2011), thus suggesting that these calls could contain only probabilistic information about the timing of ovulation. Moreover, in some cases, these calls have also been found to be related to the dominance rank of the mating partner as they tended to be longer or had a higher fundamental frequency when mating with high-ranking mates compared to subordinates (Engelhardt et al., 2012; Semple et al., 2002; but see Clay & Zuberbühler, 2011; Pfefferle et al., 2008). In addition, copulation calls can be significantly more intense (e.g., longer call duration, higher exhale rate or peak frequency) during ejaculatory mounts (Engelhardt et al., 2012; Pfefferle et al., 2008, but see Semple et al., 2002).

Finally, these calls are individually distinct among females as they exhibit significant acoustic variation between them (Clay & Zuberbühler, 2011; Semple, 2001; Townsend et al., 2011), allowing males to discriminate the callers' identity based on the acoustic form of these vocalizations (Semple & McComb, 2000). This information might help males to assess the level of intrasexual competition they might face when attempting to mate with a particular female, considering the dominance rank of her consort partner and the intensity of sperm competition (Semple et al., 2002). Consequently, males could use this information to strategically allocate their mating effort (Semple et al., 2000).

As for females, they might use copulation calls to influence male behavior in ways that enhance their own reproductive success (Pradhan et al., 2006). Since females might derive different benefits from attracting mates and promoting male-male competition depending on the characteristics of their mating system and social structure, the use of copulation calls and the information they encode might be species and context-related. For instance, in species where males can temporarily monopolize the reproductive access to a female, females might use copulation calls as a strategy of postcopulatory female choice to promote mate guarding by dominant preferred males (Maestripieri et al., 2005; Pradhan et al, 2006). In this context, copulation calls can signal the probability of conception, thereby increasing paternity certainty and simultaneously advertising other males about the mating partner' dominance status (Bouquet et al., 2018). In contrast, in species where mate guarding is less effective, as when mating is highly promiscuous, copulation calls can instigate sperm competition (Pradhan et al., 2006). Here, females would signal their receptivity to attract multiple mates and indicate a high probability of ovulation and the occurrence of ejaculation to all potential partners, thereby reducing paternity certainty and mitigating the risk of infanticide (O'Connell & Cowlishaw, 1994; Pradhan et al., 2006). Therefore, it is possible that there is no unified function to explain the occurrence of copulation calls across primates and that females might use them strategically according to the benefits they can obtain through these signals (Bouquet et al., 2018).

Although at a rather low frequency, a female hamadryas baboons have also been reported to utter copulation calls (Nitsch et al., 2011; Swedell & Saunders, 2006). The hamadryas baboon's mating system is unique in that males typically have exclusive reproductive access to a group of females forming a one-male unit (OMU) and actively and aggressively prevent their females from mating with other males (Swedell & Saunders, 2006). At the same time, males compete to recruit additional females into their OMUs through forcibly coercive takeovers that cause female transfers across units (Kummer, 1968; Swedell & Saunders, 2006; Pines et al., 2015; Nitsch et al., 2011). In this sense, copulation calls could increase male-male competition in hamadryas baboons, as observed in other primates (e.g. Hauser, 1990; O'Connell & Cowlishaw, 1994); however, since female mate choice is constrained by male coercive behavior and sperm competition is limited, it is possible that females might derive other benefits from uttering copulation calls in contrast to primates living in multi-male multi-female groups. The potential benefits for hamadryas' females in inciting male-male competition could be to facilitate their transfers across units since this might be the main consequence of this competition (Swedell & Saunders, 2006). This strategy could enable females to gain benefits from exerting some sort of mate choice by facilitating their transfer to OMUs with high-status males, as these units typically offer priority of access to valuable resources such as food (e.g., Swedell, 2006; Zinner, 1999); and similarly, by being transferred to OMUs where they can become central females, as peripheral females may experience reduced protection and face greater risks (Stammbach, 1987). Accordingly, if copulation calls in hamadryas reflect the willingness of the female to change the OMU, these calls may carry information about the leader male rank allowing other males to infer the intensity of intrasexual competition they may face in attempting to recruit that female, similar to observations in other primate species (Semple et al., 2002). Additionally, these calls may provide information into female social status, as peripheral females spend less time in proximity with their leader male and have a weaker social bond with him (Stammbach, 1987). Consequently, peripheral females may experience reduced vigilance from leader males, which renders them more accessible and heightens the likelihood of takeover attempts by other males. Nonetheless, it remains unclear what specific information is conveyed through the acoustic form of these calls in hamadryas baboons, as no studies have investigated this aspect to date.

In this study, we conducted the first acoustic analysis of female copulation calls in hamadryas baboons to determine the information content conveyed by these calls. We aimed to explore which aspects of the mating context are relevant to communicate to the audience studying whether these calls vary according to male rank, female social status, and if they are individually distinctive across females. We also explored if these calls contain information about the female's reproductive status and the outcome of the copulation, as has been reported in other primates (e.g., Engelhardt et al., 2012; O'Connell & Cowlishaw, 1994; Pfefferle et al., 2008; Semple et al., 2002). Our results would help to shed light on the role and function of copulation calls in hamadryas baboons, contributing to a better understanding of their adaptive significance in a polygynous species where males constraint the expression of female mate choice through coercive behavior and sperm competition is limited.

Methods

Ethic statement

The research described in this paper was noninvasive, and nonexperimental, and strictly adhered to the legal requirements of Spain. No approval from any Research Committee was necessary because no special permission for the use of animals in purely observational studies is required in Spain. Animal husbandry and research in the Madrid Zoo comply with the "EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria" and the "WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums." It also adhered to the American Society of Primatologists (ASP) principles for the ethical treatment of nonhuman primates. The Madrid Zoo and Aquarium granted permission to carry out this study.

Study site and subjects

We conducted our study on the colony of hamadryas baboons (*Papio hamadryas*) housed at the Madrid Zoo during July and September 1999. Details of the zoo enclosure are provided elsewhere (Polo et al., 2014). At the onset of the study period, 5th July 1999, the colony consisted of 11 OMUs with 34 sexually mature females distributed among them. Between the 15th-17th of July, most individuals from two units were removed and one leader male died. After that date, the band comprised 24 adult females distributed into 8 OMUs which ranged from 6 to 2 adult females and, following one transfer, from 6 to 1 (see Table S1). Despite the presence of some hamadryas-anubis hybrids, the colony exhibited the harem-defense polygynous mating system and the social behavior characteristic of hamadryas' wild populations (Erer-Gota: Abegglen, 1984; Filoha: Schreier & Swedell, 2009).

The colony was established in June 1972 and studied interruptedly until August 2001 (Colmenares, 2004). During this study period, long-term data were collected two to four days weekly, covering the demographic and social status of each individual and the composition of the colony, including memberships and individual trajectories between units, births, deaths, and females' reproductive state (i.e., cycling, pregnant and lactating) as well as their phase within the cycle (Colmenares, 1992). All the individuals in the colony during the study period were individually recognizable.

Data collection

We recorded copulations and the associated copulation calls using behavioral sampling (Bateson & Martin, 2021) from 5th to 31st July and from 3rd September to 1st October 1999, between 8:30 and 10:30, five days a week (82 hours of observation). These calls were collected and tape-recorded by VH with the assistance of one student using a Sony TC-D5 PRO cassette tape recorder with a Sennheiser directional microphone (ME80 head with a K3 power module). Using videotapes, we also recorded the context of the copulation, providing information about the identity of participants (e.g., copulating male and female) as well as the outcome of the copulation. Examples of these copulation calls are available at:

https://figshare.com/projects/Information_Content_of_Female_Copulation_Calls_in_Hamadryas_Baboons_Papio_hamadryas_/216376. To assess the females' social status, we extracted data on the female-to-male grooming database (see below) collected between January and December 1999. This data was gathered using scan-sampling of OMUs and instantaneous sampling of grooming behavior (Altmann, 1974; Bateson & Martin, 2021) at 30-min intervals. Finally, the reproductive state of females was assessed employing the longterm data from the colony.

Study variables

Male rank. To assess the leader's male rank, we used the OMU size as a proxy, defined as the number of sexually mature females in the OMUs at the time of copulation. *Female social status.* The proportion of grooming behavior (expressed as a percentage of scans) that females directed toward their unit leader males was used as a proxy for females' social status within the unit. We classified females as either central or peripheral based on whether the time they spent grooming their leader male was above or below the average within that OMU. *Copulation outcome.* Copulation outcome was determined according to the presence or absence of male ejaculation, considering that males change their position and pause before dismounting (Nikitopoulos et al., 2004). We could only assign accurate male ejaculation for 38 out of 48 copulation calls. *Female reproductive status (FRS).* Cycling baboon females show changes in the size and brightness of the red/pink color of the perineal sex skin related to hormonal activity (Dixson, 2012). The inflation of the sexual swelling (tumescence period) corresponds to the follicular phase stimulated by estrogen levels, while the onset of detumescence sex skin corresponds to the luteal phase of the oestrus cycle, which is characterized also by a loss of color and the increase of wrinkles (Higham, MacLarnon, Ross, Heistermann, & Semple, 2008). As these are noticeable signals, we measured female reproductive state using the size of their sexual swelling, which was registered every two to four days as a part of the long-term data record from the colony. Following previous studies, we assume that ovulation was more likely during maximum swelling, that is, along 5 days before detumescence (Higham, Heistermann, Ross, Semple, & MacLarnon, 2008).

Therefore, according to the size of the sexual swelling and whether females were pregnant or lactating, we classified each female's reproductive status as tumescence, maximum swelling, detumescence, flat, pregnant, and lactating. We combined detumescence, flat, pregnant and lactating categories because of their low or null probability of fecundation.

Acoustic analysis

A baboon copulation call was defined as a series of loud, low-pitched rhythmic vocalizations consisting of staccato grunts emitted by females towards the end or right after copulation (Kemp et al., 2017). In this study, we adopted the terminology of Deputte and Goustard (1980), where copulation call bouts are referred to as copulation calls and the individual copulation calls within the bout are termed call units, as used in previous studies (e.g., Semple et al., 2002). A total of 48 copulation calls were recorded, of which 47 had sufficient signal-to-noise ratio, enabling visual identification of the call units. Therefore, our sample consisted of 47 copulation calls from seven different cycling females (OL: N= 22; CE: N=14; CR: N=4; CH: N=1; GR: N=2; NI: N=1; PL: N=2) and one non-cycling female (GU: N=1).

To characterize the acoustic structure of copulation calls, we performed temporal and spectral analyses using Raven Pro 1.6.5 (www.birds.cornell.edu/raven). First, MB visually segmented the calls at a sampling rate of 44,100 Hz by marking the start and end of each call unit using the cursor on the spectrogram at two different time points, with an interval of three months. Following this segmentation, we extracted several temporal acoustic parameters: copulation call length, number of call units, rate of call unit delivery (number of call units per second), mean duration of call units, the total duration of call units, and the mean duration of the intervals between call units. Subsequently, we reduced the sampling frequency to 11,025 Hz to achieve higher frequency resolution using the R package "seewave" (Sueur, Aubin & Simonis, 2008) and extracted spectral parameters from the resampled calls. Most of these call units were brief and showed no apparent frequency modulation, as no harmonics were detected (Fig. 1), aligning with previous findings on baboon's copulation calls (Semple et al., 2002). Therefore, our spectral analysis focused on variables describing the distribution of amplitudes in the frequency spectrum (i.e., the mean frequency at which the amplitude distribution reaches the first (Q25), second (Q50) and third (Q75) quartiles in the frequency spectrum), and the peak frequency (the frequency with the highest amplitude in a time segment), considering all call units within each bout without background noise. We excluded two copulation calls in the spectral analysis because another animal (a bird) was vocalizing simultaneously during the majority of the call units. The absolute agreement of the acoustic analyses, based on intra-observer reliability for the two time-point segmentation, was high: copulation call length (ICC = 0.922), mean duration of call units (ICC = 0.998), total duration of call units (ICC = 0.994), mean duration of intervals between call units (ICC = 0.975), Q25 (ICC = 0.997), Q50 (ICC = 0.997), Q75 (ICC = 0.998), and peak frequency (ICC = 0.996).

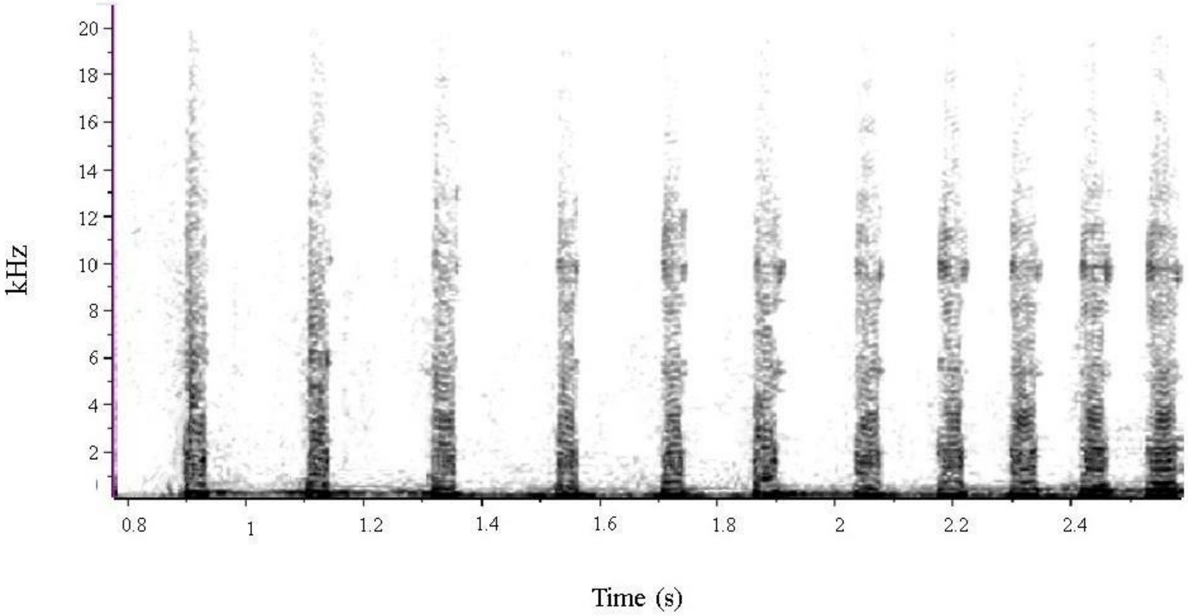

Fig. 1. Spectrogram illustrating a copulation call of a female hamadryas baboon. Filter bandwidth: 124 Hz, frequency range: 22,050 Hz.

Statistical analysis

Initially, we assessed the normality of the acoustic parameters and applied logarithmic transformations to correct deviations from normality. Then, we evaluated collinearity among the parameters and removed those exhibiting high multicollinearity. This process resulted in the selection of three temporal parameters (i.e., copulation call length; number of call units, and mean call unit duration) and three spectral parameters (i.e., Q25, Q75, and peak frequency) all of which had variance inflation factors below 8, an acceptable threshold for inclusion in the analysis (Kennedy, 1992). For log-transformed variables, the beta coefficients were back-transformed for interpretability. To investigate the contextual information embedded in the acoustic structure of copulation calls, we employed general linear mixed models (GLMM). Male rank and female social status, copulation outcome, and female reproductive status were included as fixed effects, while acoustic parameters served as response variables. To account for repeated observations from the same subjects, we included the identity of the females as a random effect across the models. To determine whether female hamadryas baboons produce copulation calls that are individually distinctive, first, we visually inspected the intraclass correlation coefficient obtained for each GLMM. To assess whether the acoustic parameters of copulation calls varied significantly among females, we first conducted a Permutational Multivariate Analysis of Variance (PERMANOVA). This method evaluates group differences in multivariate data by partitioning the variance based on a distance matrix and testing its significance through permutation (Anderson, 2005). We used PERMANOVA because it is robust to violations of normality and the homogeneity of variance-covariance matrices, particularly in cases where some categories (females) have low sample sizes. Additionally, we conducted a KruskalWallis test to determine which acoustic parameters exhibited significant differences among females. The Kruskal-Wallis test is a non-parametric method that compares medians across groups, suitable for addressing heteroscedasticity and non-normal data distributions (Conover, 1999). P-values were adjusted for multiple statistical tests using the BenjaminiHochberg correction (Benjamini & Hochberg, 1995), a procedure that controls the expected proportion of false discoveries among the rejected null hypotheses.

Statistical analyses were performed using R version 4.2.1 (R Core Team, 2022), employing the *lme4* package (v. 1.1-30; Bates, Mächler, Bolker, & Walker, 2015), the *lmerTest* package (Kuznetsova, Brockhoff, & Christensen, 2017), the *vegan* package (Oksanen et al., 2013) and the default *stats* package (R Core Team, 2022). Intra-observer reliability was assessed in SPSS using Intraclass Correlation Coefficients (ICC). We set the significance level at α = 0.05. ICC estimates and their 95% confident intervals were calculated using SPSS statistical package version 23 (SPSS Inc, Chicago, IL) based on a mean-rating (*k* = 3), absolute-agreement, 2-way mixed-effects model. The script and dataset employed are available at: https://figshare.com/projects/Information_Content_of_Female_Copulation_Calls_in_Hamadryas_Baboons_Papio_hamadryas_/216376.

Results

Table 1 shows descriptive statistics for each acoustic parameter tested in this study. The results of the GLMM are presented in Table 2. We found that the copulation outcome had a significant effect on the temporal structure of copulation calls. Specifically, copulation calls were longer (b = 2.036, t = 2.42, p < 0.01) and contained more call units (b = 1.474, t = 1.573, p = 0.038) when males ejaculated. On the contrary, neither male rank, female social status, nor female reproductive status had a significant impact on the acoustic structure of these calls. The Intraclass Correlation Coefficient across models showed that female identity accounted for a substantial portion of the variance within these parameters (see Table 2).

Table 1. Descriptive statistics for each acoustic parameter.

	Copulation calls length (s)	Number of call units	Mean call unit duration (s)	Q25 (Hz)	Q75 (Hz)	Peak frequency (Hz)
Mean	3.031	10.260	0.126	417.457	832.454	516.360
Standard deviation	1.859	8.334	0.148	173.71	292.499	191.492

Table 2. Results of the GLMM for each acoustic parameter tested are presented. P-values were adjusted using the Benjamini-Hochberg procedure. Values below the alpha threshold are indicated in italics. ICC refers to intraclass correlation coefficient for the full model.

	Beta	*Sd*	*t*	*Adj. p*	*ICC*
Copulation call length					
Intercept	0.805	0.672	1.197	0.133	
Male rank	-0.028	0.118	-0.242	0.912	
Copulation outcome: ejaculatory mount	0.711	0.293	2.42	*<0.001*	
FRS: tumescence	-0.417	0.619	-0.674	0.825	
FRS: maximal swelling	-0.018	0.611	-0.031	0.556	
Female social status: central	-0.103	0.576	-0.18	0.859	
Female ID					0.186
Number of call units					
Intercept	1.609	0.570	2.823	0.322	
Male rank	-0.068	0.107	-0.641	0.362	
Copulation outcome: ejaculatory mount	0.388	0.221	1.753	*0.038*	
FRS: tumescence	0.253	0.487	0.520	0.877	
FRS: maximal swelling	0.534	0.474	1.127	0.321	
Female social status: central	0.082	0.505	0.163	0.876	

Female ID					0.342
Mean call unit duration					
Intercept	9.096	4.955	-1.836	0.313	
Male rank	-0.905	0.794	-.140	0.516	
Copulation outcome: ejaculatory mount	1.251	1.999	0.626	0.669	
FRS: tumescence	-3.596	4.683	-0.768	0.583	
FRS: maximal swelling	-0.424	4.691	-0.090	0.970	
Female social status: central	-1.248	2.945	-0.879	0.882	
Female ID					0.072
Q25					
Intercept	5.704	0.378	12.058	*0.025*	
Male rank	0.061	0.078	0.78	0.319	
Copulation outcome: ejaculatory mount	0.184	0.132	1.399	0.086	
FRS: tumescence	0.021	0.288	0.074	0.588	
FRS: maximal swelling	-0.28	0.279	-0.406	0.426	
Female social status: central	0.310	0.341	0.911	0.393	
Female ID					0.589
Q75					
Intercept	6.451	0.296	21.769	*0.0137*	
Male rank	0.047	0.059	0.797	0.4871	

Copulation outcome: ejaculatory mount	0.057	0.111	0.515	0.6903	
FRS: tumescence	0.169	0.238	0.710	0.6443	
FRS: maximal swelling	-0.078	0.231	-0.034	0.3175	
Female social status: central	0.182	0.267	-0.681	0.516	
Female ID					0.243
Peak frequency					
Intercept	237.882	196.929	1.208	0.195	
Male rank	81.74	41.872	1.952	0.970	
Copulation outcome: ejaculatory mount	62.837	54.872	1.145	0.383	
FRS: tumescence	79.731	125.736	0.634	0.536	
FRS: maximal swelling	-52.109	122.774	.0.424	0.456	
Female social status: central	-271.495	178.99	-1.517	0.177	
Female ID					0.751

Note: the beta coefficients for the log-transformed variables (copulation call length, number of call units, Q25 and Q75) were back-transformed for interpretability.

The PERMANOVA test revealed significant differences in the acoustic structure of copulation calls among females (F(7, 37) = 7.86, R² = 0.60, p = 0.001). Kruskal-Wallis univariate analysis indicated significant differences in the acoustic structure of copulation calls among females for spectral parameters (i.e., Q25, Q75 and peak frequency) as well as copulation call length and number of call units (Table 3).

Table 3. Results of Kruskal Wallis testing in which acoustic variables contributed to the overall discrimination between female copulation calls. Values below the alpha threshold are indicated in italics. P-values were adjusted using the Benjamini-Hochberg procedure.

Acoustic parameter	*Kruskal-Wallis*	*df*	*Adj. p*
Bout length	16.596	7	*0.024*
Number of call units	19.14	7	*0.016*
Mean call unit duration	4.965	7	0.664
Q25	22.243	7	*0.006*
Q75	18.095	7	*0.016*
Peak frequency	23.042	7	*0.006*

Discussion

Explanations suggest that copulation calls in primates are sexually selected traits evolved to incite male-male competition for the access of the calling females, promoting either mate guarding as a form of postcopulatory female choice (Henzi, 1996; Oda & Masataka, 1992; Semple, 1998) or sperm competition (O'Connell & Cowlishaw, 1994; Semple, 1998b). However, these explanations typically apply to promiscuous species where strategies of paternity confusion or concentration play a significant role in mating strategies (Pradhan et al., 2006). In hamadryas baboons, a species organized in one-male units (OMUs) where leader males already monopolize female reproductive access and sperm competition is unlikely, the result of male-male competition is generally limited to instances of takeovers and attempted takeovers, which ultimately result in female transfers across units (Swedell & Saunders, 2006). Given the potential limitations of existing explanations about the role of copulation calls when applied to polygynous species as hamadryas baboons, the aim of this study was to explore the information encoded in the acoustic structure of female copulation calls in this species to clarify its role. Our acoustic analysis revealed that the temporal structure of copulation calls is influenced by copulation outcome and that these calls are individually distinctive among females in temporal and spectral parameters. These findings suggest that copulation calls in hamadryas baboons may provide males with information, at the very least, regarding which female is involved in the copulation and the outcome of that mating event.

In this study we proposed that, if copulation calls serve to promote male-male competition in hamadryas baboons as in other primate species, these calls might provide information regarding the rank of the mating male (i.e., the rank of the leader male) and the female social status, which would reflect the strength of the bond between the male and the caller and the vigilance that the male exerts over her (Swedell, 2006). This information would provide clues about the likelihood of a successful takeover, allowing males to make decisions about whether to invest resources in competing for a particular female. However, our findings did not reveal any relationship between the acoustic structure of copulation calls and the rank of the mating male or female social status. Conversely, some studies have shown that copulation calls are more intense (e.g., longer calls, more call units, or more inhales per exhale length) when mating with high-ranking males (long-tailed macaques: Engelhardt et al., 2012; yellow baboons: Semple et al., 2002), while others align with our data and do not support this association (bonobos: Clay & Zuberbühler, 2011; barbary macaques: Pfefferle et al., 2008). Although the reasons for these mixed results are not well understood, a possible explanation is based on the differences in dominance styles among males of different species. It is reasonable to think that copulation calls may provide information on male rank in those species in which rank is relevant because males are organized in steep linear dominance hierarchies, like stump-tail macaques or yellow baboons (Thierry, 2000; Watts, 2010), compared to others in which hierarchies are more egalitarian like barbary macaques (Preuschoft et al., 1998; Thierry, 2000; Watts, 2010). In addition, it is possible that in hamadryas baboons, females do not need to signal the rank of the mating partner as they mate monogamously within ovulatory cycles with their leader males, so that other males could infer the rank of the mating male.

In contrast, we found that copulation calls were individually distinct across females, consistent with previous studies (Clay & Zuberbühler, 2011; Semple, 2001; Townsend et al., 2011;), with differences in acoustic structure particularly related to pitch (frequency parameters), the duration of the call and the number of call units. In general, primate vocalizations tend to differ among individuals (Fisher et al., 2002; Owren et al., 1997; Rendall, 2003), and receivers can distinguish the identity of callers based on these variations, including also copulation calls (Cheney & Seyfarth, 1997; Fisher et al., 2000; Semple & McComb, 2000). Therefore, because primate copulation calls are intrinsically linked to the identity of the caller, which encompasses relevant knowledge of her social status, family membership, or group composition (Seyfarth & Cheney, 2012, 2014), it is likely that males infer information as male ranking or female social status from their broader knowledge of the individual, making explicit vocal signalling of this information unnecessary.

Moreover, our findings revealed that copulation calls were longer and contained more call units when males ejaculated, which aligns with previous studies in other primate species (Engelhardt et al., 2012; Pfefferle et al., 2008). However, we did not find evidence that the acoustic structure of these calls signals the female's reproductive state, though previous studies have found correlations between them and the size of the sexual swelling (O’Connell & Cowlishaw, 1994; Semple & McComb, 2000; Semple et al., 2002). Hamadryas females may not derive additional benefits from signalling the mating outcome or their fertile phase—information that essentially reflects the probability of conception. In hamadryas baboons, paternity is already guaranteed with the leader male. As such, there is no advantage in confusing or reaffirming paternity, which reduces the necessity for females to broadcast such information. Nevertheless, hamadryas females might signal some of these aspects even if they don’t have a clear adaptative role due to a physiological mechanism, as it has been suggested that the occurrence of copulation calls may be driven by genital stimulation (Hall, 1962; Hauser, 1990; Henzi, 1996; Swedell & Saunders, 2006; Townsend et al., 2008).

Given that copulation calls in hamadryas baboons do not contain relevant information about the mating context other than female identity and the occurrence of ejaculation, it is also possible that these calls do not provide any additional benefits to females in hamadryas baboons, indicating that they may lack any function in this species and are instead preserved through phylogenetic inertia. Indeed, it has been suggested that female copulation calls may not occur at all or occur at low rates in low promiscuous species because they would not have selective pressures to use them (Pradhan et al., 2006). However, given that copulation calls are generally considered costly signals for females (Dunbar, 1988; Dixson, 1998; O'Connell & Cowlishaw, 1994; Bouquet et al., 2018; Hamilton & Arrowood, 1978), it is reasonable to hypothesize that these signals may still play a role in sexual selection in hamadryas baboons. Indeed, our ongoing study has revealed that the emission of copulation calls in hamadryas baboons is biased towards certain females. Specifically, copulation calls were more frequently uttered by central females belonging to units led by low-ranking males, as well as by peripheral females in larger units led by high-ranking males. In lower-ranking units, malemale competition can facilitate transfers of females to higher-ranking males, thereby enhancing their fitness as they would have preferential access to valuable resources (Swedell, 2006; Zinner, 1999). Conversely, in larger one-male units with dominant males, promoting competition may not result in female transfers due to the leader male's superior fighting ability. Nevertheless, he must increase vigilance to prevent potential takeovers of the calling females, thereby spending more time in proximity to them, which could benefit these females by providing greater protection and reducing risks compared to peripheral females (Stammbach, 1987). These findings suggest that females who emit copulation calls at higher rates are the ones who benefit the most from promoting male-male competition. Therefore, it is possible that the function of copulation calls in hamadryas females is related to the emission of the call in certain contexts rather than to the specific information that may be conveyed by the acoustic structure of the call.

Our findings raise important questions regarding the mating strategies of female hamadryas baboons, who have traditionally been viewed as following a passive strategy with limited movement between units, thus constraining their mate choice (Pines et al., 2015;

Swedell et al., 2011. Nonetheless, this study has certain limitations that must be acknowledged, particularly the limited observation hours, which led to an uneven distribution of recorded copulation calls across females. In this context, some females might have individual traits to be more predisposed to produce copulation calls. For example, hybrid females may have a genetic predisposition toward increased copulation calling, inherited from other promiscuous baboon species. However, since half of the calling females were non-hybrids, no clear relationship can be established. Thus, increasing the number of recordings across females would be essential before drawing definitive conclusions. Additionally, it remains to be empirically tested whether females derive reproductive benefits from uttering these calls and what direct effects these calls have on male behaviour.

In conclusion, this study contributes to a growing body of evidence indicating that copulation calls in primates might be used differently and contain distinct information across species. Consequently, it is likely that there is no singular function to explain the use of these calls as their adaptative role might have been shaped by different selective pressures (Henzi, 1996). Moreover, it is essential to incorporate additional studies across a diverse range of primate species with varying mating strategies to deepen our understanding of the broader evolution of these signals depending on specific selective pressures.

CHAPTER 4: INTEGRATIVE DISCUSSION

Over many years, researchers have sought to understand the adaptive function of copulation calls in primates (reviewed in Maestripieri & Roney, 2005; Pradhan et al., 2006), focusing on their usage and the information they contain. These calls have been primarily studied in promiscuous species facing a high risk of infanticide (e.g., Deputte & Goustard, 1980; Engelhardt et al., 2011; Pfefferle et al., 2008; Townsend et al., 2008). Consequently, various hypotheses consistent with the mating strategies of these species have been proposed, based on the idea that copulation calls are sexually selected traits that enhance female reproductive success by attracting males, thereby promoting male-male competition for sexual access to these females. In this context, the most widely accepted functions to date are the sperm competition hypothesis (O'Connell & Cowlishaw, 1994) and the female postcopulatory choice hypothesis (Maestripieri et al., 2005), functions that ultimately mitigate the risk of infanticide by promoting different strategies of paternity confusion or concentration, respectively (e.g., Bouquet et al., 2018; Maestripieri et al., 2005; O'Connell & Cowlishaw, 1994; Oda & Masataka, 1992; Pradhan et al., 2006).

However, copulation calls are also observed in hamadryas baboons, a primate species organized in one-male units (OMUs) (Nitsch et al., 2011; Swedell & Saunders, 2006), where unit leader males sexually monopolize females, leaving few opportunities for them to mate with other males within the same ovulatory cycle (Kummer, 1968; Swedell & Saunders, 2006). In this species, leader males compete to incorporate females from other units into their own through forced and coercive takeovers, compelling males to monitor and herd their females to prevent matings or takeovers by other males (Amann et al., 2017; Kummer, 1968; Nitsch et al., 2011; Pines et al., 2015; Stammbach, 1987; Swedell & Saunders, 2006). In this regard, the hypotheses proposed for other primates are not consistent with the benefits that hamadryas females would gain by using these calls. On one hand, these signals would not provide any advantage in terms of protection against infanticide, as unit leader males have certainty about their paternity; on the other hand, females would not promote promiscuous mating since they reproduce almost exclusively with their leader male within the same ovulatory cycle. Therefore, the aim of this study is to investigate the use and content of copulation calls in this species to understand the role these signals play in the mating strategies of hamadryas baboons.

In this context, we propose that if copulation calls in primates serve to foster malemale competition (Cox & LeBoeuf, 1977; Hauser, 1990; Pradhan et al., 2006), hamadryas females would also use them for this purpose, though the consequences of promoting competition would result in facilitating their transfer to other units through coercive takeovers. This would allow them to increase their reproductive success by accessing valuable resources by belonging to more dominant units or by becoming central females, thereby mitigating the risks associated with being a peripheral female (Stammbach, 1987; Swedell, 2006; Zinner, 1999). Therefore, our hypothesis posits that the function of copulation calls in the reproductive strategies of hamadryas baboons is to promote the transfer of calling females to other units. Based on our general hypothesis, we first expect these calls to occur more frequently in females that can increase their reproductive success by changing units, outweighing the costs of such takeovers. In this sense, our prediction is that the rate of copulation call emission will be higher in females from less dominant units or in peripheral females in large units, as well as in females residing in units without the presence of related females. Secondly, we expect these calls to provide males with information about the rank of the consort male (leader male) and the social status of the female, as both factors would inform males about the likelihood of success in attempting to abduct the calling female. Finally, we anticipate that if copulation calls indeed promote transfers, then females that emit them more frequently will have a higher probability of being transferred to other units.

Our predictions were partially confirmed. Firstly, the results showed that the emission of copulation calls is biased towards certain females. Specifically, central females in small units and peripheral females in larger units were more likely to emit these calls. However, the absence of related females within the unit did not influence the likelihood of emitting these calls. We also found no relationship between the acoustic structure of these calls and the rank of the male or the social status of the female, although we did observe acoustic differences between females. Finally, we found a positive relationship between the emission of copulation calls and the transfer of females to other units.

Overall, these results support the hypothesis that copulation calls in hamadryas baboons promote the transfer of females to other units. Firstly, and in relation to the predictions proposed in Chapter 2, the calls do not appear to be emitted randomly among copulating females; rather, their use is concentrated in certain females, specifically, central females in small units and peripheral females in large units, who would gain greater benefits by promoting their transfer to other units. On the one hand, females belonging to small units could benefit indirectly by moving to larger units with higher-ranking males, producing more competitive offspring, and directly by gaining access to better resources and protection (Swedell & Saunders, 2006). It is important to note that the results indicate that, in lowranking units, central females call more than peripheral ones. However, since some lowranking units were composed of a single female, categorized as central, and in units with two females, the degree of association with the male was similar, it is possible that the central and peripheral categorization in such OMUs is not relevant. On the other hand, females in large units face higher levels of competition among themselves to form stronger bonds with the leader male (Zinner et al., 1994). Since peripheral females usually face greater risks than central females (Stammbach, 1987), they could benefit by moving to other units where they can become central females, thus receiving preferential treatment from the leader male, which would influence the protection the female and her offspring receive (Colmenares, 1992, 1997). Finally, we did not observe that females residing in units without related females emitted copulation calls more frequently. However, it is likely that the most relevant bond females establish is with their leader male to prevent aggression towards themselves or their offspring (Barton, 1996). Therefore, associations that could be established with other related females would be less important than the potential benefits of forming relationships with leader males.

Acoustically, the copulation calls emitted by females did not convey information about the rank of the male they were mating with or their own social status, suggesting that this information is not communicated to the audience through these vocalizations. It's possible that the calls lack this information if their function is to indiscriminately promote female transfers. However, the calls are acoustically distinct among females, and studies in other primate species have shown that males can recognize females through these calls (Cheney & Seyfarth, 1997; Fisher et al., 2000; Semple & McComb, 2000). Therefore, given that primate vocalizations are intrinsically linked to the identity of the emitting female, males might infer relevant information about the social status, family membership, or group composition of the callers (Seyfarth & Cheney, 2012; 2014), making it unnecessary to signal this information through copulation calls. Nonetheless, in more promiscuous primate species like yellow baboons or long-tailed macaques, providing information about the male a female is mating with can be crucial, as males might not be able to infer it in situations with limited visual access, which could explain the difference found in this study compared to previously published ones (e.g., Engelhardt et al., 2011; Semple et al., 2002).

On the other hand, these calls do contain information about male ejaculation. Specifically, the calls seem to be more intense (comprising more units and, on average, longer) when males ejaculate. Additionally, we observed that copulation calls occur more frequently in females with greater anogenital swelling. These two findings are consistent with evidence reported in previous studies (Engelhardt et al., 2011; Pfefferle et al., 2008). In hamadryas baboons, females might not gain any additional benefit from informing the male about ejaculation or their reproductive status, as leader males have paternal certainty of their offspring and can monitor the females' reproductive status through other sexual signals. Therefore, it's possible that these two factors are related to copulation calls in hamadryas baboons simply due to a potential production mechanism. Both male ejaculation and female sexual swelling are linked to the level of physiological arousal due to genital stimulation from penetration, leading to a possible physiological response such as copulation vocalization (Hauser, 1990; Henzi, 1996; Swedell & Saunders, 2006; Townsend et al., 2008). This is further supported by the timing of these calls, as they usually occur towards the end of the mount. Therefore, it's possible that these calls are triggered upon reaching a stimulation threshold and that the intensity of the calls varies depending on the degree of stimulation, resulting in higher-pitched or prolonged vocalizations. However, since not all females who might be stimulated during copulation emit these vocalizations, it's possible that their use is under voluntary control, allowing inhibition when they don't provide any benefit to the emitting females (Bouquet et al., 2020).

Considering the above, these results are not incompatible with our hypothesis, as it could be feasible that the mere emission of the call promotes its function, attracting males to these females with the aim of recruiting them, without the need to include any specific information in these vocalizations. It's likely that any information males require to assess the competition for a particular female can be extracted from their social knowledge about that female (Seyfarth & Cheney, 2014). Additionally, we've observed that females more likely to be transferred are those emitting copulation calls; however, the data indicate that only females from low-ranking units (small units) were actually transferred, while females from high-status units with dominant males did not experience transfers. In light of this result, we propose that copulation calls act to encourage male competition; however, within the context of hamadryas females, this could have different consequences. On one hand, since the success in male takeover may be closely related to the dominance and strength of the male, this would facilitate females from low-ranking units being taken and transferred to other units by high-status males. However, for peripheral females belonging to high-ranking units with more dominant males, it's more challenging for other males to recruit them. Nonetheless, males might attempt to do so, forcing the leader male to intensify protection and vigilance over that female, thereby increasing proximity time and allowing the strengthening of their bond. Therefore, it's plausible that these calls are used for different purposes depending on the unit to which the females belong: those in low-status units would seek to transfer to higher-ranking units, while peripheral females in high-ranking units would aim to strengthen their bond with the male.

In contrast, it is possible that these calls do not offer additional benefits to female hamadryas baboons, suggesting they may lack function in this species. Indeed, it has been proposed that in species with low levels of infanticide risk and limited sperm competition opportunities, there are no selective pressures to use these signals, and they may have been retained as a mechanism of phylogenetic inertia, resulting in low emission frequencies (Pradhan et al., 2006). In our study, we found that hamadryas baboons produced copulation calls in 16.2% of observed copulations, a rate similar to previous studies in wild populations (18% in Filoha: Swedell & Saunders, 2006) and captive populations (26.1%: Nitsch et al., 2011). However, this rate remains notably low compared to other baboons living in promiscuous societies; for example, between 84% and 92% in chacma baboons (*Papio ursinus*: Saayman, 1970; Hall, 1962), 39% to 60% in Guinea baboons (*Papio papio*: Maestripieri et al., 2005; Boese, 1973), 60% to 68% in olive baboons (*Papio anubis*: Bouquet et al., 2018; Bercovitch, 1985), and 80% to 97% in yellow baboons (*Papio cynocephalus*: Collins, 1981; Semple, 2001; Semple et al., 2002). Nevertheless, copulation calls are considered costly signals for females (Bouquet et al., 2018; Dixson, 1998; Dunbar, 1988; Hamilton & Arrowood, 1978; O'Connell & Cowlishaw, 1994), suggesting that if they have been conserved, these signals could still play a role in sexual selection in hamadryas baboons. In fact, if these calls were maintained as a phylogenetic vestige, we might expect them to occur infrequently and randomly among copulating females, as they would not provide any additional benefit. However, our data show that these calls are concentrated in certain females, suggesting that there must be some control over the decision to emit them, evaluating the benefits that compensate for the costs associated with call production. Additionally, this low emission frequency could be explained by the fact that male competition in hamadryas baboons is considerably lower than in other baboons (Swedell & Saunders, 2006), reinforcing our hypothesis.

However, it is essential to consider the limitations of our data, as they may affect the statistical power needed to observe certain differences and bias our results. Firstly, the sample is small and presents little variability, as data were collected over a period of only two months. In this context, we highlight the need for longitudinal studies to confirm that the concentration of copulation calls in just a few females does not simply correspond to individual differences in the expression of acoustic behaviors. Furthermore, to support our hypothesis, it is necessary to expand our data with new information to, on the one hand, verify that females indeed obtain benefits from emitting these calls, i.e., that they are transferred to other units or that their bond with the male increases, and to assess the behavioral response of males to these vocalizations, i.e., that they actually increase competition to recruit females. Additionally, both the sample size and the quality of acoustic data could be improved by reducing environmental noise. This could be achieved by controlling factors that contribute to acoustic interference, such as the presence of water sources in the environment, or by collecting data at times that do not coincide with feeding events, when animals tend to be more acoustically active. This environmental noise, when inconsistent, causes many calls to be excluded from analyses due to the inability to clearly determine their beginning and end. In our case, we encountered a considerable amount of environmental noise characterized by low frequencies that overlap with copulation vocalizations. This suggests that the extracted spectral parameters may be skewed from the call's true value. However, it is important to note that this interference did not directly affect the observed differences, as environmental noise remained constant throughout all analyzed calls.

CONCLUSIONS

In conclusion, this study provides the first data on the use and content of copulation calls in hamadryas baboons, bringing us closer to a deeper understanding of the role these vocalizations play in this species. Considering the function of these signals in other primates and in light of the data obtained, we believe that these calls could serve to increase competition among males, acting as a means to promote the transfer of calling females to more dominant units or to strengthen their bonds with leader males, which could improve access to resources and, consequently, increase their reproductive success. However, it is plausible that this function is achieved simply by the emission of the call, without the need to provide specific information beyond the identity of the female. Our findings raise important questions about the role and reproductive strategies of female hamadryas baboons, as it has been suggested that they follow a passive strategy, with limited mobility between units, which would restrict their mate choice (Pines et al., 2015; Swedell et al., 2011).

However, despite the intense sexual coercion to which female hamadryas baboons are often subjected (Amann et al., 2017; Evans et al., 2022; Kummer, 1968; Polo & Colmenares, 2012; Swedell & Saunders, 2006; Swedell & Schreier, 2009; Swedell et al., 2014), our results suggest that females may subtly and indirectly exercise mate choice. Nevertheless, longitudinal studies are needed to corroborate whether females gain benefits from emitting these vocalizations and to investigate how males respond to them. Finally, our study suggests that copulation calls in hamadryas baboons may have a different function than those previously proposed in other primates. While copulation calls and other sexual signals can promote male competition, the repercussions of this competition may vary between species, leading to different patterns of emission and information content. Therefore, it is likely that these vocalizations do not serve a single function within the context of primates but rather adapt to the needs of females depending on the social structure and predominant mating strategies in each species. Ultimately, conducting research with other primate species will enrich our understanding of the evolution of copulation calls in these animals, but to do so, we must address the diversity in mating systems and the selective pressures that shape the use of sexual signals across species.

REFERENCES

Abegglen, J. J. (1984). *On socialization in hamadryas baboons*. Associated University Presses.

Allen, M. L., & Krofel, M. (2022). Resource Holding Potential. In J. Vonk & T. K. Shackelford (Eds.), *Encyclopedia of Animal Cognition and Behavior* (pp. 5990-5992). Springer International Publishing. https://doi.org/10.1007/978-3-319-55065-7_444

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*(3), 227267. https://doi.org/10.1163/156853974X00534

Amann, A. L., Pines, M., y Swedell, L. (2017). Contexts and consequences of takeovers in hamadryas baboons: Female parity, reproductive state, and observational evidence of pregnancy loss. *American Journal of Primatology*, *79*(7), e22649. https://doi.org/10.1002/ajp.22649

Anandam, M. V., Bennett, E. L., Davenport, T. R. B., Davies, N. J., Detwiler, K. M., Engelhardt, A., Eudey, A. A., Gadsby, E. L., Groves, C. P., Healy, A., & others. (2013). Species accounts of Cercopithecidae. In R. A. Mittermeier, A. B. Rylands, & D. E. Wilson (Eds.), *Handbook of the mammals of the world: Vol. 3. Primates* (pp. 628–753). Lynx Edicions.

Anderson, M. J. (2005). Permutational multivariate analysis of variance. *Department of Statistics, University of Auckland, Auckland*, *26*, 32-46.

Andersson, M. B. (1994). *Sexual selection*. Princeton University Press.

Barrett, L., y Henzi, S. P. (2008). Baboons. *Current Biology*, *18*(10), R404-R406.

Barton, R. A., Byrne, R. W., & Whiten, A. (1996). Ecology, feeding competition and social structure in baboons. *Behavioral Ecology and Sociobiology*, *38*(5), 321-329. https://doi.org/10.1007/s002650050248

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). “Fitting Linear Mixed-Effects Models Using lme4.” *Journal of Statistical Software*, 67(1), 1–48.

Bateson, M., & Martin, P. (2021). *Measuring behaviour: an introductory guide*. Cambridge university press.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B*, 57, 289–300. doi:10.1111/j.2517-6161.1995.tb02031.x.

Bercovitch, F. B. (1985). *Reproductive tactics in adult female and adult male olive baboons* (Doctoral dissertation, University of California, Los Angeles--Anthropology).

Bernaldo de Quirós, E., Wheeler, B. C., Hammerschmidt, K., Heistermann, M., & Tiddi, B. (2018). Do sexual calls in female black capuchin monkeys (Sapajus nigritus) vary with fertility? An acoustic analysis. *American Journal of Primatology*, *80*(9), e22920.

Boese, G. K. (1973). *Behavior and social organization of the Guinea baboon (Papio papio)*. The Johns Hopkins University.

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

Bradbury, J. W., y Vehrencamp, S. L. (1998). *Principles of animal communication* (Vol. 132). Sunderland, MA: Sinauer Associates.

Bradbury, J. W., y Vehrencamp, S. L. (2011). Principles of animal communication. 2nd. *Sunderland, Massachusetts: Sinauer*.

Brewer, G., & Hendrie, C. A. (2011). Evidence to Suggest that Copulatory Vocalizations in Women Are Not a Reflexive Consequence of Orgasm. *Archives of Sexual Behavior*, *40*(3), 559-564. https://doi.org/10.1007/s10508-010-9632-1

Cäsar, C., Byrne, R. W., Hoppitt, W., Young, R. J., y Zuberbühler, K. (2012). Evidence for semantic communication in titi monkey alarm calls. *Animal Behaviour*, *84*(2), 405-411.

Chen, Z., & Wiens, J. J. (2020). The origins of acoustic communication in vertebrates. *Nature Communications*, *11*(1), 369. https://doi.org/10.1038/s41467-020-14356-3

Cheney, D. L., & Seyfarth, R. M. (1997). "Reconciliatory grunts by dominant female baboons influence victims' behaviour."

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

Clutton-Brock, T. (2016). *Mammal societies*. John Wiley & Sons.

Collins, D. A. (1981). *Social behaviour and patterns of mating among adult yellow baboons (Papio c. cynocephalus. L. 1766)*. The University of Edinburgh (United Kingdom).

Colmenares, F. (1992). Clans and harems in a colony of hamadryas and hybrid baboons: male kinship, familiarity and the formation of brother-teams. *Behaviour*, *121*(1), 61-94. https://doi.org/10.1163/156853992X00444

Colmenares, F. (1992b). Primate social systems and the social and reproductive decisions of males: constraints on and consequences of alternative individual strategies. In: Bateson PPG, Gomendio M, editors. *Behavioural mechanisms in evolutionary perspective*. Madrid: Instituto Juan March, Centro de Reuniones Internacionales sobre Biología. 7477

Colmenares, F. (1997). Grooming for protection in baboons: two tests of the hypothesis. In M. Taborsky & B. Taborsky (Eds.), *Advances in Ethology* (Vol. 32 pp. 269). Blackwell Wissenschafts.

Colmenares, F. (2004). Kinship structure and its impact on behavior in multilevel societies. In B. Chapais & C. M. Berman (Eds.), *Kinship and behavior in primates* (pp. 242-270). Oxford University Press.

Colmenares, F., & Gomendio, M. (1988). Changes in females reproductive condition following male take-overs in a colony of hamadryas and hybrid baboons. *Folia Primatologica*, *50*(3-4), 157-174. https://doi.org/10.1159/000156343

Colmenares, F., Esteban, M. M., & Zaragoza, F. (2006). One male units and clans in a colony of hamadryas baboons (*Papio hamadryas hamadryas*): effect of male number and clan cohesion on feeding success. *American Journal of Primatology*, *68*, 21-37. https://doi.org/10.1002/ajp.20204

Colmenares, F., Zaragoza, F., & Hernández-Lloreda, M. V. (2002). Grooming and coercion in one-male units of hamadryas baboons: market forces or relationship constrains? *Behaviour*, *139*(11), 1525-1553. https://doi.org/10.1163/15685390260514753

Conover, W. J. (1999). *Practical nonparametric statistics*. Wiley.

Cox, C. R., y Le Boeuf, B. J. (1977). Female incitation of male competition: a mechanism in sexual selection. *The American Naturalist*, *111*(978), 317-335.

Deputte, B. L., & Goustard, M. (1980). Copulatory vocalizations of female macaques (*Macaca fascicularis*): Variability factors analysis. *Primates*, *21*(1), 83-99. https://doi.org/10.1007/BF02383826

Dixson A (2012) *Primate sexuality: comparative studies of the prosimians, monkeys, apes and human beings*. Oxford: Oxford University Press.

Dixson AF. (1998). *Primate sexuality: comparative studies of the prosimians, monkeys, apes and human beings.* New York: Oxford University Press.

Dunbar, R. I. M. (1988). *Primate social systems*. Croom Helm.

Ekanayake-Weber, M., & Swedell, L. (2021). An agent-based model of coercive female transfer in a multilevel society. *Animal Behaviour*, *182*, 267-283. https://doi.org/10.1016/j.anbehav.2021.10.004

Endler, J. A. (1993). Some general comments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *340*(1292), 215-225.

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. https://doi.org/10.1007/s00265-011-1260-9

Evans, K. D., Swedell, L., y Chowdhury, S. (2022). Respect for males amid suppression of females: Selective use of aggression and fitness correlates in the male-dominated society of hamadryas baboons. *Journal of Human Evolution*, *165*, 103151. https://doi.org/10.1016/j.jhevol.2022.103151

Fischer, J., Cheney, D. L., y Seyfarth, R. M. (2000). Development of infant baboons' responses to graded bark variants. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1459), 2317-2321.

Fischer, J., Hammerschmidt, K., Cheney, D. L., & Seyfarth, R. M. (2002). Acoustic features of male baboon loud calls: Influences of context, age, and individuality. *The Journal of the Acoustical Society of America*, *111*(3), 1465-1474.

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

Groves, C.P. *Primate Taxonomy*; Smithsonian Institution Press: Washington, DC, USA, 2001.

Hall, K. R. L. (1962). The sexual, agonistic and derived social behaviour patterns of the wild chacma baboon, *Papio ursinus*. *Proceedings of the Zoological Society of London*, *139*(2), 283-327. https://doi.org/10.1111/j.1469-7998.1962.tb01831.x

Hamilton, W. J., y Arrowood, P. C. (1978). Copulatory Vocalizations of Chacma Baboons (Papio ursinus), Gibbons (Hylobates hoolock). In *New Series* (Vol. 200, Issue 4348).

Hauser, M. D. (1990). Do chimpanzee copulatory calls incite male-male competition? *Animal Behaviour*, *39*(3), 596-597. https://doi.org/10.1016/S0003-3472(05)80427-0

Hauser, M. D. (1996). *The evolution of communication*. MIT press.

Henzi, P. (1996). Copulation calls and paternity in chacma baboons. *Animal Behaviour*, *51*(1), 233-234. https://doi.org/10.1006/anbe.1996.0021

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

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

Hill, W.C.O. *Primates: Comparative Anatomy and Taxonomy, Vol. 8*; Edinburgh University Press: Edinburgh, UK, 1970.

Hohmann, G. M., y Herzog, M. O. (1985). Vocal communication in lion-tailed macaques (Macaca silenus). *Folia primatologica*, *45*(3-4), 148-178.

Huberty, C. J., & Smith, J. D. (1982). The study of effects in MANOVA. *Multivariate Behavioral Research*, *17*(3), 417-432.

Jolly, C.J. Species, Subspecies and Baboon Systematics. In *Species, Species Concepts and Primate Evolution*; Kimbel, W.H., Martin, L.B., Eds.; Plenum Press: New York, NY, USA, 1993; pp. 67–107.

Kemp, C., Rey, A., Legou, T., Boë, L. J., Berthommier, F., Becker, Y., & Fagot, J. (2017). In Vocal Repertoire of Captive Guinea Baboons (Papio papio). *Origins of Human Language: Continuities and Discontinuities with Nonhuman Primates*, 15.

Kennedy, P. (2008). *A guide to econometrics*. John Wiley & Sons.

Kummer, H. (1968). *Social organization of hamadryas baboons*. University of Chicago Press.

Kummer, H. (1990). The social system of hamadryas baboons and its presumable evolution. *Baboons: Ecology and behaviour. Use and care*, 43-60

Kuznetsova A, Brockhoff P.B., Christensen R.H.B (2017). “lmerTest Package: Tests in Linear Mixed Effects Models.” *Journal of Statistical Software*, 82(13), 1–26. doi:10.18637/jss.v082.i13.

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

Maestripieri, D., Leoni, M., Raza, S. S., Hirsch, E. J., & Whitham, J. C. (2005). Female Copulation Calls in Guinea Baboon: Evidence for Postcopulatory Female Choice? *International Journal of Primatology*, *26*(4), 737-758. https://doi.org/10.1007/s10764-005-5306-6

Nikitopoulos, E., Arnhem, E., van Hooff, J. A. R. A. M., & Sterck, E. H. M. (2002). Influence of Female Copulation Calls on Male Sexual Behavior in Captive Macaca fascicularis. In *International Journal of Primatology* (Vol. 25, Issue 3).

Nitsch, F., Stueckle, S., Stahl, D., & Zinner, D. (2011). Copulation patterns in captive hamadryas baboons: a quantitative analysis. *Primates*, *52*(4), 373-383. https://doi.org/10.1007/s10329-011-0258-2

Nunn, C. L. (1999). The evolution of exaggerated sexual swellings in primates and the gradedsignal hypotesis. *Animal Behaviour*, *58*(2), 229-246. https://doi.org/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*, 687694. https://doi.org/10.1006/anbe.1994.1288

Oda, R., y Masataka, N. (1992). Functional significance of female Japanese macaque copulatory calls. *Folia Primatologica*.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., ... & Oksanen, M. J. (2013). Package 'vegan'. *Community ecology package, version*, *2*(9), 1-295. Retrieved from https://CRAN.R-project.org/package=vegan

Owren, M. J., Seyfarth, R. M., & Cheney, D. L. (1997). "The acoustic features of vowel-like grunt calls in chacma baboons (Papio cynocephalus ursinus): Implications for production processes and functions. *The Journal of the Acoustical Society of America*, *101*(5), 29512963.

Paciência, F. M., Chuma, I. S., Lipende, I. F., Knauf, S., & Zinner, D. (2020). Post-copulatory behavior of olive baboons (*Papio anubis*) infected by *Treponema pallidum*. *bioRxiv*, 2020.2002. 2023.961326.

Pfefferle, D., Brauch, K., Heistermann, M., Hodges, J. K., & Fischer, J. (2008). Female Barbary macaque (*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. https://doi.org/doi:10.1098/rspb.2007.1499

Pines, M., Chowdhury, S., Saunders, J., & Swedell, L. (2015). The rise and fall of leader males in a multi-level society: Takeovers and tenures of male hamadryas baboons. *American Journal of Primatology*, *77*(1), 44-55. https://doi.org/10.1002/ajp.22309

Polo, P., & Colmenares, F. (2012). Behavioural processes in social context: female abductions, male herding and female grooming in hamadryas baboons. *Behavioural Processes*, *90*(2), 238-245. https://doi.org/10.1016/j.beproc.2012.02.004

Polo, P., & Colmenares, F. (2016). Seasonality of reproductive events and early mortality in a colony of hamadryas baboons (*Papio hamadryas hamadryas*) over a 30-year period: Capital breeding and life history patterns in a food-provisioned population seasonally thermally stressed. *American Journal of Primatology*, *78*(11), 1149-1164. https://doi.org/https://doi.org/10.1002/ajp.22570

Polo, P., Hernández-Lloreda, V., & Colmenares, F. (2014). Male takeovers are reproductively costly to females in hamadryas baboons: a test of the sexual coercion hypothesis. *PloS One*, *9*(3), e90996. https://doi.org/10.1371/journal.pone.0090996

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

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*, 333-343. https://doi.org/10.1007/s00265-005-0075-y

Preuschoft, S., Paul, A., & Kuester, J. (1998). Dominance styles of female and male Barbary macaques (*Macaca sylvanus*). *Behaviour*, *135*(6), 731-755.

Prokop, P. (2021). Factors Influencing Sexual Vocalization in Human Females. *Archives of Sexual Behavior*, *50*(8), 3809-3820. https://doi.org/10.1007/s10508-021-02018-4

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. URL https://www.R-project.org/

Raftery, A. E. (1995). Bayesian model selection in social research. *Sociological methodology*, 111-163.

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

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. https://doi.org/10.1002/ajp.22154

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. https://doi.org/10.1159/000155283

Sakamoto, Y., Ishiguro, M., & Kitagawa, G. (1986). Akaike information criterion statistics. *Dordrecht, The Netherlands: D. Reidel*, *81*(10.5555), 26853.

Schreier, A. L., & Swedell, L. (2009). The fourth level of social structure in a multi-level society: ecological and social functions of clans in hamadryas baboons. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *71*(11), 948955.

Schreier, A., & Swedell, L. (2012a). The socioecology of network scaling ratios in the multilevel society of hamadryas baboons (*Papio hamadryas hamadryas*). *International Journal of Primatology*, *33*(5), 1069-1080. https://doi.org/10.1007/s10764-011-9572-1

Schreier, A. L., & Swedell, L. (2012b). Ecology and sociality in a multilevel society: Ecological determinants of spatial cohesion in hamadryas baboons. *American Journal of Physical Anthropology*, *148*(4), 580-588. https://doi.org/10.1002/ajpa.22076

Sebeok, T. A. (1977). 10. Ecumenicalism in Semiotics. In *A perfusion of signs* (pp. 180-206). Indiana University Press.

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

Semple, S. (2001). Individuality and male discrimination of female copulation calls in the yellow baboon. *Animal Behaviour*, *61*(5), 1023–1028.

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

Semple, S., McComb, K., Alberts, S. C., & Altmann, J. (2002). Information Content of Female Copulation Calls in Yellow Baboons. *American Journal of Primatology*, *56*, 43-56. https://doi.org/10.1002/ajp.1062

Seyfarth, R. M., & Cheney, D. L. (2012). The evolution of concepts about agents. In M. R. Banaji & S. Gelman (Eds.), Navigating the social world: What infants, children, and other species can teach us (pp. 27–30). Oxford: Oxford University Press.

Seyfarth, R. M., & Cheney, D. L. (2014). The evolution of concepts about agents: Or, what do animals recognize when they recognize an individual? In E. Margolis (Ed.), *The conceptual mind* (pp. 57– 76). Cambridge: MIT Press.

Seyfarth, R. M., & Cheney, D. L. (2017). The origin of meaning in animal signals. *Animal Behaviour*, *124*, 339-346.

Seyfarth, R. M., Cheney, D. L., y Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*, *28*(4), 1070-1094.

Sigg, H., Stolba, A., Abegglen, J.-J., & Dasser, V. (1982). Life history of hamadryas baboons: physical development, infant mortality, reproductive parameters and family relationships. *Primates*, *23*(4), 473-487. https://doi.org/10.1007/BF02373959

Silk, J. B. (2007). Social components of fitness in primate groups. *Science*, *317*(5843), 13471351. https://doi.org/10.1126/science.1140734

Snowdon, C. T. (2004). Sexual selection and communication. In P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp. 5770).

Städele, V., Pines, M., Swedell, L., & Vigilant, L. (2016). The ties that bind: Maternal kin bias in a multilevel primate society despite natal dispersal by both sexes. *American Journal of Primatology*, *78*(7), 731-744. https://doi.org/10.1002/ajp.22537

Städele, V., Van Doren, V., Pines, M., Swedell, L., & Vigilant, L. (2015). Fine-scale genetic assessment of sex-specific dispersal patterns in a multilevel primate society. *Journal of Human Evolution*, *78*, 103-113. https://doi.org/10.1016/j.jhevol.2014.10.019

Stammbach, E. (1987). Desert, forest and montane baboons: Multi-level societies. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., & Struhsaker, T. T. (Eds.), *Primate societies*, (pp. 112–120). Chicago: University of Chicago Press

Sueur, J., Aubin, T., & Simonis, C. (2008). Seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics*, *18*(2), 213-226.

Swedell, L. (2000). Two takeovers in wild hamadryas baboons. *Folia Primatologica*, *71*(3), 169172.

Swedell, L. (2002). Affiliation among females in wild hamadryas baboons (*Papio hamadryas hamadryas*). *International Journal of Primatology*, *23*(6), 1205-1226. https://doi.org/10.1023/A:1021170703006

Swedell, L. (2006). *Strategies of sex and survival in hamadryas baboons: through a female lens*. Pearson Prentice Hall. Partes

Swedell, L., & Leigh, S. R. (2006). Perspectives on Reproduction and Life History in Baboons. In L. Swedell & S. R. Leigh (Eds.), *Reproduction and Fitness in Baboons: Behavioral, Ecological, and Life History Perspectives* (pp. 1-15). Springer.

Swedell, L., & Plummer, T. (2019). Social evolution in Plio-Pleistocene hominins: Insights from hamadryas baboons and paleoecology. *Journal of Human Evolution*, *137*, 102667. https://doi.org/10.1016/j.jhevol.2019.102667

Swedell, L., & Saunders, J. (2006). Infant mortality, paternity certainty, and female reproductive strategies in hamadryas baboons. In L. Swedell & S. R. Leigh (Eds.), *Reproduction and fitness in baboons: behavioral, ecological, and life history perspectives* (pp. 19-51). Springer.

Swedell, L., & Schreier, A. (2009). Male aggression towards females in hamadryas baboons:

conditioning, coercion, and control. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females* (pp. 244-268). Harvard University Press.

Swedell, L., Leedom, L., Saunders, J., & Pines, M. (2014). Sexual conflict in a polygynous primate: costs and benefits of a male-imposed mating system. *Behavioral Ecology and Sociobiology*, *68*(2), 263-273. https://doi.org/10.1007/s00265-013-1641-3

Swedell, L., Saunders, J., Schreier, A., Davis, B., Tesfaye, T., & Pines, M. (2011). Female "dispersal" in hamadryas baboons: transfer among social units in a multilevel society. *American Journal of Physical Anthropology*, *145*(3), 360-370. https://doi.org/10.1002/ajpa.21504

Thierry, B. (2000). Covariation of conflict management patterns across macaque species. In F. Aureli & F. B. M. De Waal (Eds.), *Natural conflict resolution* (pp. 106-128). University of California Press.

Todt, D., Hammerschmidt, K., Ansorge, V., & Fischer, J. (1995). The Vocal Behavior of Barbary Macaques (*Macaca sylvanus*): Call Features and Their Performance in Infants and Adults. In E. Zimmermann, J. D. Newman, & U. Jürgens (Eds.), *Current Topics in Primate Vocal Communication* (pp. 141-160). Springer US. https://doi.org/10.1007/9781-4757-9930-9_7

Townsend, S. W., Deschner, T., & Zuberbühler, K. (2008). Female Chimpanzees Use Copulation Calls Flexibly to Prevent Social Competition. *PloS One*, *3*(6), e2431. https://doi.org/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. https://doi.org/10.1007/s10764-011-9510-2

Vaglio, S., Ducroix, L., Rodriguez Villanueva, M., Consiglio, R., Kim, A. J., Neilands, P., Stucky, K., & Lameira, A. R. (2020). Female copulation calls vary with male ejaculation in captive olive baboons. *Behaviour*, *157*(8-9), 807-822. https://doi.org/10.1163/1568539X-bja10024 van Schaik, C. P., van Noordwijk, M. A., y Nunn, C. L. (1999). Sex and social evolution in primates. In P. C. Lee (Ed.), *Comparative primate socioecology* (pp. 204-231).

Cambridge University Press.

Watts, D. P. (2010). Dominance, power, and politics in nonhuman and human primates. In P. M. Kappeler & J. B. Silk (Eds.), *Mind the gap: tracing the origins of human universals* (pp. 109-138). Springer.

Zinner, D. (1999). Relationship between feeding time and food intake in hamadryas baboons (Papio hamadryas) and the value of feeding time as predictor of food intake. *Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association*, *18*(6), 495505.

Zinner, D., Schwibbe, M. H., & Kaumanns, W. (1994). Cycle synchrony and probability of conception in females hamadryas baboons *Papio hamadryas*. *Behavioral Ecology and Sociobiology*, *35*(3), 175-183. https://doi.org/10.1007/BF00167957

Zinner, D., van Schaik, C. P., Nunn, C. L., & Kappeler, P. M. (2004). Sexual selection and exaggerated sexual swellings of female primates. In P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp. 71-89). Cambridge University Press.

Zuberbühler, K., Cheney, D. L., y Seyfarth, R. M. (1999). Conceptual semantics in a nonhuman primate. *Journal of Comparative Psychology*, *113*(1), 33.

SUPPLEMENTARY MATERIAL

TABLE S1. Multicollinearity between parameters[a]

	B	**t**	**p value**	**Tolerance**	**VIF**
Constant		3.157	0.003		
rate of delivery (unit per second)	-0.371	-3.523	0.001	0.260	13.262
number of call units	0.391	1.999	0.054	0.152	6.589
mean call unit duration	-0.009	-1.445	0.885	0.725	1.378

total duration	0.159	1.549	0.128	0.053	18.905
min duration	-0.113	-1.561	0.126	0.551	14.814
max duration	-0.124	-2.094	0.039	0.178	15.624
mean interval duration	0.129	1.129	0.267	0.220	13.540
Q25	0.033	0.182	0.857	0.089	11.237
Q50	0.255	1.002	0.324	0.044	22.482
Q75	-0.236	-1.435	0.154	0.106	9.406
Fpeak	-0.090	0.499	0.621	0.088	11.304

[a] Dependent variable was bout lenght

Universidad del Desarrollo
Facultad de Gobierno
Doctorado en Ciencias en Complejidad Social

CICS UDD
CENTRO DE INVESTIGACIÓN EN COMPLEJIDAD SOCIAL

Dra(c).
Montserrat Belinchón
Centro de Investigación en Complejidad Social
Facultad de Gobierno

<u>Presente</u>

A través de la presente, se deja constancia que el proyecto de título "Las llamadas de cópula en las hembras de babuino hamadríades: significado funcional y contenido informativo." a su cargo como Investigadora Responsable, fue aprobado en cuanto a las consideraciones de nuestro Comité de Ética Institucional de Investigación (CEII) corresponde.

A la IR se le realizaron observaciones menores al protocolo del proyecto, en cuanto a permisos para utilización del material. Las respuestas fueron revisadas y aprobadas por nuestro comité por lo que el proyecto se encuentra debidamente en regla según lo establecido por el comité de ética.

Sin otro particular, saluda cordialmente a usted,

Ceric G.

06 enero 2025
COMITÉ DE ÉTICA

Dr. Francisco Ceric G.
Presidente
Comité de Ética Institucional en Investigación
Universidad del Desarrollo