Mating behaviour of a wild olive baboon population (*Papio anubis*) infected by *Treponema pallidum*

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“Back at Ndala camp it was as if life were beginning again with all the excitement of the unexpected”

Iain & Oria Douglas-Hamilton *in* Among the Elephants

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Chapter 4: General discussion

SUMMARY

According to the World Health Organization (2019), more than one million sexually transmitted infections (STIs) are acquired every day worldwide in the human population. These infections can have serious reproductive health consequences (e.g., infertility or mother-to-child transmission), and in nonhuman mammalian populations, are important selection agents that shape the evolution of immune defences. As such, individuals are expected to favour healthy mates instead of diseased ones.

The relation between pathogens and fitness consequences in nonhuman primates has been the subject of numerous research efforts focusing on social and reproductive behaviour. My dissertation sets out to add a piece to the puzzle of the complex relation between hosts and pathogens by testing whether conspicuous disease cues prompt avoidance behaviour towards diseased individuals. Specifically, I studied the sexual behaviour of a large population (approximately 170 individuals) of wild olive baboons (*Papio anubis*), at Lake Manyara National Park (LMNP), in East Africa, Tanzania. Here, nonhuman primates (NHPs) are infected by *Treponema pallidum* (*TP*), a bacterium known to cause conspicuous genital ulcerations in both males and females. Since genital ulcerations are mainly found in sexually mature individuals, it is likely to be sexually transmitted. *TP* also affects humans, and it is responsible for different diseases such as syphilis, bejel and yaws. Interestingly, nonhuman primate *TP* strains, are most closely related with human yaws (a disease mainly causing facial lesions), than to syphilis (known to cause genital ulcerations). This, together with the geographic overlap of the distribution of human yaws and simian *TP infection* in Sub-Saharan Africa, could indicate that NHPs may function as a natural reservoir for human *T. pallidum.*

The results of my study showed that genital ulcers have a major impact at a pre-copulatory level by influencing female mate choice. The likelihood of copulation decreased if the male mating partner had visible signs of *TP* infection (i.e. genital ulcers). Similarly, there was a decrease in the likelihood of copulation when females were infected (regardless of the genital health status of the male), which

hints towards potential pain avoidance. No evidence has been found for male mate choice, but individuals exhibiting genital ulcers, performed less pelvic thrusts than non-ulcerated individuals. This most likely results in reproductive fitness consequences, as ejaculation can be compromised if not enough pelvic thrusts are performed. To understand whether the impact of *TP*-associated genital ulcerations is only restricted to the pre-copulatory level, I extended the same analyses to the female post-copulatory behaviours. I investigated whether genital ulcers would alter the frequency of female copulation calls, post-copulatory withdraw (i.e. darting) and the occurrence of post-copulatory grooming. The post-copulatory behaviour of females was not altered in relation to visible signs of disease, which means *TP* does play role on a pre-copulatory level but not at a post-copulatory level.

This dissertation sheds light on behavioural avoidance in wild NHPs in relation to STIs and contributes to a better understanding of host-pathogen interactions and pathogen-avoidance. Additionally, it adds important data on baboon mating behaviour which is essential for comparative analyses. The close genetic relationship of simian and human *TP* strains, and the growing habitat encroachment of the human-NHP interface, supports the call for a more multidisciplinary approach linking humans and wildlife when investigating the impact of shared pathogens like *Treponema pallidum*.

GENERAL INTRODUCTION

1. Sociality and healthy in nonhuman primates

The effects of sociality on health and reproduction have long been recognized in humans (House *et al*. 1988; Uchino 2009; Holt-Lunstad *et al.* 2010). Similarly, in other animals including nonhuman primates (NHPs), social relationships or social bonds, have been also linked to enhanced longevity and reproduction (e.g., Silk *et al.* 2003, 2009, 2010; Cameron *et al.* 2009; Stanton & Mann 2012; Schülke *et al.* 2010; Kulik *et al.* 2012; Archie *et al*. 2014). Nonhuman primates, as many other social animals, live in groups that vary greatly (e.g. size, social organization) within and between species and populations. Group-living has been considered as one of the major transitions in evolution (Smith & Szathmary 1995), but it comes along with particular costs. Among them, increased feeding competition (Schülke & Ostner 2012), increased likelihood of pathogen transmission (Freeland 1976) and increased susceptibility to disease; as the bigger the groups, the greater is the infection risk (Altizer *et al.* 2003; Patterson & Ruckstuh 2013). Host-pathogen relationships are complex and dynamic (Irvine 2006; Knowles *et al.* 2013; Lello *et al.* 2004) and health parameters of wild nonhuman primates are poorly known (Nunn & Altizer 2006; Huffman & Chapman 2009). Thus, investigating the link between sociality and health enables a better understanding of the underlying processes of disease transmission in nonhuman primates. At the same time, this is of considerable relevance for human health, when considering zoonosis and emerging infectious diseases (Gillespie *et al.* 2008; Jones *et al.* 2008).

1.2. Behavioural immunity & pathogen avoidance strategies

Infectious diseases have posed a threat to survival and reproduction (i.e. fitness) of organisms throughout time. As a consequence, organisms evolved a complex immune system to detect pathogens and mobilize defences against infectious agents. But triggering such responses has considerable energetic costs (Colditz 2008), and thus, an additional set of mechanisms that serves as a first line of defence against pathogens can be employed - the so called "behavioural immune system" (Schaller 2011, Tybur & O'Brien 2014). Behaviour plays a major role in modulating the exposure to pathogens. For instance, disgust is elicited by olfactory, visual and/or gustatory stimuli that are associated with infectious diseases and almost certainly evolved as a defence against pathogens (Curtis *et al.* 2011).

Pathogen avoidance strategies have been reviewed extensively elsewhere (Hart 1990, 1992, 1994, 2011; Curtis & Biran 2001; Curtis 2014; Curtis *et al.* 2011). Examples of pathogen avoidance include corpse removal from the nest in social insects (Diez *et al.* 2014), localized defecation sites in fish (Nicholson & Sikkel 2018), anointing behaviour in birds (Bush & Clayton 2018), avoidance of sick conspecifics in rodents (Boillat *et al.* 2015), grazing on non-faecal contaminated patches in ungulates and marsupials (Ezenwa 2004, Coulson *et al.* 2018) and avoidance of faecal contaminated items (Curtis 2014; Sarabian & MacIntosh 2015; Amoroso *et al.* 2017; Weinstein *et al.* 2018). For most social animals, the first set of preventive measures in order to avoid disease transmission is how an individual´s health status is perceived by its conspecifics. For example, Caribbean spiny lobsters (*Panulirus argus*), refuse sharing dens with lobsters infected with the lethal *PaV1* virus (Behringer *et al.* 2006). Other strategies of pathogen avoidance may include the alternation of sleeping and foraging sites in yellow baboons (*Papio cynocephalus*: Hausfater & Meade 1982) and white-cheeked mangabeys (*Cercocebus albigena*: Freeland 1980), or the use of specific defecation sites (red howler monkeys, *Alouatta seniculus*: Gilbert 1997; lemurs, *Lepilemur* sp., *Hapalemur griseus*: Irwin *et al.* 2004). Individuals might also avoid direct contact with conspecifics which are likely to transmit pathogens (Curtis 2014). Mice for instance, display a preference for non-parasitized mating partners (Ehman & Scott 2002), and mandrills (*Mandrillus sphinx*), avoid grooming individuals that carry high levels of oro-feacally transmitted protozoa (Poirotte *et al.* 2017).

Some pathogens are capable of altering and control specific aspects of their host's behaviour to enhance the frequency of encounters among suitable hosts, and consequently increase the rate of transmission (Holmes & Bethel 1972). An example of this "adaptive host manipulation hypothesis" is the "fatal attraction" observed in hosts carrying the protozoon *Toxoplasma gondii*. Infected individuals are known to increase exposure to predators and infected males become sexually more attractive to healthy females (Dass *et al.* 2011; Adamo 2013; Poirotte *et al.* 2016). In insects, the sexually transmitted bacterium *Wolbachia,* uses different strategies to ensure vertical transmission through the manipulation of the host reproductive system (Saridaki & Bourtzis 2010). Strategies such as feminization, parthenogenesis, male killing, and sperm–egg incompatibility are used to increase the frequency of infected females in a population (Saridaki & Bourtzis 2010). Additionally, sperm from an infected male does not result in offspring unless the female is infected with the same strain of *Wolbachia* (Werren et al. 2008). Dourine, a sexually transmitted trypanosome of horses, is also thought to increase sexual activity of infected stallions (Thrall *et al.* 1997), and the bovine genital campylobacteriosis, potentially increases the duration of oestrus in cattle (Roberts, 1979) thereby enhancing the likelihood of potential matings.

The type of response to disease cues depends on several factors. Among them, are the ecology of the species (i.e. type of environment, Behringer *et al.* 2018, Sarabian *et al.* 2018), the species' individual characteristics (i.e. age, sex and life-history stage), the mechanisms of infection (i.e. means by which the pathogen infects its host), virulence, incidence and pathogen load. Thus, depending of the factors involved in the host-pathogen interaction, there are cases where the benefits of avoidance are outweighed by the costs, and avoidance of sick conspecifics is inexistent. In banded mongooses infected with tuberculosis, clinically diseased individuals showed a significantly smaller proportion of time active and lower reciprocation of allogrooming, but still, no evidence was found for behavioural avoidance of sick group members (Fairbanks *et al.* 2015). Reaction towards sick conspecifics may vary even within the same species. In house finches, individuals preferred diseased feeding partners due to reduced feeding competition (Bouwman & Hawley 2010), but in another experiment, house finches spent less time in proximity with conspecifics showing disease symptoms (Zylberberg *et al.* 2012). Therefore, it is important to avoid generalizations in relation to pathogen avoidance, since the host's behavioural outcome seems to be intertwined to a wide array of factors leading to different responses.

1.2.1. Impact of infection on mating behaviour

Sexual interactions pose the highest infectious disease risk of any social behaviour due to the involvement of physical contact (i.e. skin and genitals) and exposure to multiple body fluids (e.g. saliva, semen, vaginal fluids, blood), all of which can contain pathogens (Curtis & Biran 2001). Given the high risk, infection avoidance and choice of pathogen-free partners are expected even if the mechanisms of mate choice are costly to implement (Pomiankowski 1987). However, these costs of infection avoidance via mate choice have to be counter-balanced by benefits, such as increased reproductive success and offspring with better survival (Iwasa *et al.* 1991). The assessment of the health status of potential mating partners appears to be a major force driving the evolution of behaviours associated with mate choice (Antonovics *et al.* 2011). At a pre-copulatory level, some bird species are known to perform cloacal inspection of their partners before mating (Sheldon 1993), and in mammals, genital inspection is an important step in assessing sexual receptivity (Dixson 1998), but it may also serve to identify infection (Antonovics *et al.* 2011). Genital self-grooming has been linked to a reduction of the risk of sexually transmitted infections (STI) in male rats (Hart et al. 1987), and in humans, post-copulatory urination is thought to reduce STI risk (Hooper *et al.* 1978; Donovan 2000). However, in a meta-analysis including several nonhuman primate species, no support was found for pre or post-copulatory behavioural counterstrategies (e.g. genital inspection prior to copulation, post-copulatory genital self-grooming or post-copulatory urination) related to risk factors for STI transmission (Nunn 2003).

In numerous species, males infected with directly transmitted parasites (e.g. bacteria, nematodes, protozoan, and viruses) are less preferred as mating partners by their conspecific females (Beltran-Bech & Richard 2014). Similarly, female rock doves (*Columba livia*) prefer to mate with louse-free males (Clayton 1990). However, when the costs of infection avoidance via mate choice are not offset by the benefits, avoidance of infected conspecifics might not be observed (Beltran-Bech & Richard 2014; Aguilar *et al.* 2008; Henderson *et al*. 1995; Ilmonen *et al.* 2009; Klein *et al.* 1999).

1.3. Sexually Transmitted Infections (STIs)

Sexually transmitted infections are mediated by a variety of pathogens, including viruses, bacteria, fungi, and protozoa, which cause a diverse array of clinical symptoms. STIs have several characteristics that distinguish them from other diseases. First, they tend to be slow developing diseases which normally cause sterility rather than mortality. Second, they may yield few or minor cues of infection (e.g. HIV, chlamydia and papillomavirus), thus limiting information that can be used by mate choosers to avoid mating with infected individuals. As a by-product, cryptic infections may also tend to be of relatively low virulence. Additionally, STIs are known to be persistent in the host, a trait that is useful to enable pathogen transmission in subsequent mating seasons and to enhance the likelihood of being carried with the host if it colonizes a new area or migrates into a new population (Antonovics *et al.* 2011).

STIs can be grouped into infections that produce genital lesions (e.g., herpes simplex viruses, *Treponema pallidum*, *Haemophilus ducreyi*, *Klebsiella granulomatis*) and those, which can be sexually transmitted, but which do not generally produce genital lesions (e.g. human immunodeficiency virus [HIV], simian immunodeficiency virus [SIV], human T-lymphotropic virus, cytomegalovirus, [HPV], Human papillomavirus infection). The presence of STIs in the human society needs no introduction. Accounts date back to the 15th century, when an epidemic disease appeared in Europe provoking incurable sores throughout the body in both women and men. What we know today as syphilis, was previously denominated by a variety of names including the 'Great Pox', 'French Disease' and 'Spanish Disease' mainly due to the war time period in which the disease appeared (Quétel 1990; Oriel 1994; Arrizabalaga *et al.* 1997; Cartwright & Biddis 2000; Meyer *et al.* 2002). Likewise, gonorrhoea, another STI that has afflicted humans for centuries, has ancient references in Chinese and Hebrew writings (Jones & Lopez 2013). Despite these early records, STIs are far from being a disease from the past. According to the WHO 2019, more than one million STIs are acquired everyday worldwide. The total number of distinct sexually transmitted or transmissible pathogens in humans now exceeds 35 (Holmes *et al.* 2008). From those, eight have the greatest incidence of illness among humans. Four of them are currently curable: syphilis, gonorrhoea, chlamydia and trichomoniasis. The other four are viral infections and are incurable: hepatitis B, herpes, HIV, and HPV, but can be mitigated or modulated through treatment (WHO 2019).

1.3.1. The bacterium *Treponema pallidum*

Treponemes are gram-negative bacteria belonging to the family Spirochaetaceae within the order Spirochaetales. This family comprises several important human diseases (e.g., syphilis, Lyme disease, and relapsing fever), animal pathogens, as well as symbionts. Several symbiotic (i.e. mutualists) treponemes species have been identified in the digestive tract of cattle, termites and in the human gut microbiota of the Hadza hunther-gatherers (Lukehart 2008, Schnorr *et al.* 2014). These organisms appear to be important for host nutrition by increasing the ability to digest food items with high fibre content. A second family, Leptospiraceae, includes the agents of leptospirosis; a proposed third family, Brachyspiraceae, includes several species associated with gastrointestinal illnesses in humans and other mammals (Lukehart 2008). All members of the order Spirochaetales are characterized by their spiral shape, corkscrew motility, and the existence of periplasmic flagella known as endoflagella (Lukehart 2008). The three morphologically identical subspecies of *Treponema pallidum* (*TP*) are subsp. *pallidum* (causing syphilis in humans), subsp. *pertenue* (causing yaws), and subsp. *endemicum* (causing bejel). *T. carateum* is a closely related organism causing infections responsible for a nowadays rare disease called ‘pinta’ (Meheus & Ndowa 2008). Further, these three treponemes subspecies cannot be distinguished serologically.

Many pathogenic treponemes are uncultivable and slow-growing microorganisms (Radolf *et al.* 2016), making them difficult to study. The bacterium *TP* is an obligate pathogen which thrives in moist regions of the body of its host and will survive and reproduce in environments with little oxygen, being killed by heat, dehydration, and sunlight (Jones & Lopez 2013). In contrast to other spirochetes or other gram-negative bacteria, the outer membrane of *TP* lacks lipopolysaccharide

(Hardy & Levin 1983, Fraser *et al.* 1998) and it has a deficiency of integral membrane proteins (Radolf *et al.* 1989; Walker *et al.* 1989). It was suggested that the surface of the bacterium is covered by a mucopolysaccharide “slime layer” (Christiansen 1963, Fitzgerald & Johnson 1979) or by host-derived proteins (Alderete & Baseman 1979), thus blocking the binding of specific antibodies to surface antigens. This relative antigenic inertness of the *T. pallidum* surface led to the coining of the term “stealth pathogen” (Radolf 1994).

1.3.2. *Treponema pallidum* in humans

Syphilis (caused by *TP* subsp. *pallidum*), has been recognized as a sexually transmitted infection for at least five centuries (Dennie 1962). In most cases, infections are acquired through sexual contact with an actively infected partner. The treponemes enter the host tissue through mucosal surfaces or microscopic skin abrasions. Syphilis manifests itself in three main stages: primary, secondary and tertiary. Transmission requires exposure to the moist mucosal or cutaneous ulcers of primary or secondary syphilis. Genital ulcers, known as hard chancre, are the most common manifestation of primary syphilis which becomes clinically apparent within 3–4 weeks following infection (Salazar *et al.* 2002). These primary ulcers have a clear base, without exudate and are painless, an important feature contributing to the successful spread of this disease. In the absence of treatment, syphilitic chancres heal spontaneously within 3–6 weeks where the patient enters into a period of latency and no infection can be transmitted (Sparling *et al.* 2006). Within a few weeks or months a systemic illness develops, characterized by low-grade fever, malaise, sore throat, headache, adenopathy, and cutaneous or mucosal rash. The development of secondary lesions is a result of the haematogenous and lymphatic dissemination of *TP* (Sparling *et al.* 2006). Subsequently, these symptoms disappear after a few weeks, and the individual progresses to the latency stage after an average of about 15 weeks. After this stage, if untreated, patients could progress to the tertiary stage (gummatous, cardio- and/or neurosyphilitic) which appeared in approximately 30% of infected persons in the preantibiotic era (Lukehart 2008), but nowadays this stage is rarely observed, due to advances in medical treatment. Moreover, syphilis can be transmitted vertically to the foetus via transplacental invasion or amniotic fluid infection leading to congenital syphilis (Wendel *et al.* 1991).

Yaws (caused by *TP* subsp. *pertenue*), as opposed to syphilis, is a non-venereal disease that is transmitted by direct skin contact through open lesions, bites and excoriations. Yet, as in syphilis, the clinical manifestations of yaws are divided into early (including primary and secondary lesions) and late stage disease (Engelkens *et al.* 1991). Yaws occurs primarily in warm, humid, tropical areas of Africa, Asia, Latin America and some Pacific islands and it is usually contracted during childhood (Meheus & Ndowa 2008; WHO 2019). An initial lesion (mother yaws) develops at the point of entry of the pathogen and it produces a lesion exudate rich in treponemes which is highly infectious. Secondary lesions are characterized by large, raised papillomas and papules from which exudation of highly infectious lesions is a feature. Early lesions on the palms and soles include hyperkeratotic or squamous macular lesions, which may be combined with a papilloma. If such papillomas develop on the soles of the feet, walking becomes very painful. The late stage of disease develops in about 10% of patients circa 5–10 years after the initial infection. Treponemes are microscopically scanty or absent in late lesions. Late lesions may affect the skin and subcutaneous tissues, including the skin of the palms and soles, the mucosae, and the bones and joints (Meheus & Ndowa 2008).

Bejel (caused by *TP* subsp. *endemicum*), also known as endemic syphilis, is essentially a disease of hot, dry countries and was until recently considered as a non-venereal disease where transmission occurred only via infectious lesions on the skin and mucous membranes, often through the use of common feeding utensils (Meheus & Ndowa 2008). However, recently sexual transmission of bejel has been reported as well, along with the presence of genital ulcers (Noda *et al.* 2018). Similarly to syphilis and yaws, it is divided in early and late stage of infection but primary lesions are rarely seen and tend to favour moist areas of the body such as mouth corners and armpit. In a late stage severe destruction of the skin, bones and cartilage may occur especially in the nose and palate (gangosa).

1.3.3. *Treponema pallidum* in animal populations

Treponemal infections have been recognized in different nonhuman species. *Treponema paraluisleporidarum ecovar Cuniculus* and *Treponema paraluisleporidarum ecovar Lepus* are natural venereal infections of rabbits and hares, respectively (Šmajs *et al.* 2018). The critically endangered Australian Gilbert's potoroo (*Potorous gilbertii*) harbours a treponemal infection causing a green discharge on the male's genitalia (Vaughan *et al.* 2009, Vaughan-Higgins *et al.* 2011; Hallmaier-Wacker *et al.* 2019). In nonhuman primates, large numbers of infected individuals with *Treponema pallidum* (e.g., baboons [*Papio* sp.], green monkeys [*Chlorocebus* sp.] or guenons [*Cercopithecus* sp.], red colobus [*Piliocolobus* sp.], and chimpanzees [*Pan trogoldytes*]) have been reported in West Africa (Fribourg-Blanc *et al.* 1963; Fribourg-Blanc & Mollaret 1969). Clinical symptoms (when present at all) were usually described as small keratotic lesions and ulcers on the muzzle, eyelids and armpits (Baylet *et al.* 1971a, b; Fribourg-Blanc & Mollaret 1969; Fribourg-Blanc & Siboulet 1972). However, yaws-like orofacial and limb lesions or ulcerative anogenital skin lesions are also reported from NHPs in West Africa (Knauf et al. 2018). Similarly, in Central Africa, extensive facial lesions are the most common clinical symptoms in great apes resembling symptoms seen in humans affected by yaws (Lovell *et al.* 2000; Levrero *et al.* 2007).

In East Africa, genital lesions were observed in olive baboons (*Papio anubis*) in Gombe Stream National Park in Western Tanzania. Wallis & Lee (1999) suspected that *TP* was the agent causing this genital disease in the baboons. Later, similar genital lesions were found in olive baboons in Lake Manyara National Park (Mlengeya 2004). Harper *et al.* (2012) and Knauf et al. (2012) were able to confirm that a *TP* subsp. *pertenue*-like organism (*TPE*) was causing the disease. Clinical manifestations of *TPE* infection in NHPs range from asymptomatic to severe skin ulcerations, mainly affecting the face or genitalia (Harper & Knauf 2013). The high frequency of observed genital ulcerations in sexually mature individuals suggests that the pathogen is sexually transmitted (Mlengueya 2014; Knauf *et al.* 2012; Knauf *et al.* 2018). NHPs in other parts of Tanzania such as yellow baboons (*Papio cynocephalus*), blue monkeys (*Cercopithecus mitis*) and vervet monkeys (*Chlorocebus pygerythrus*) are also infected with the same bacterium (Chuma *et al.* 2018). Interestingly, in Tanzania, in contrast to the great apes of Central Africa, clinical symptoms appear mainly in the ano-genital region, resembling more a syphilis-like infection, although facial lesions also occur (Chuma *et al.* 2018).

1.3.4. The link between human & nonhuman treponemes

Treponemes, causing yaws, bejel and syphilis are pathogens of global importance for human and animal health (Šmajs *et al.* 2018). Genetically, the strains infecting baboons in West and East Africa are closely related to *TP pertenue*, which causes yaws in humans (Harper *et al.* 2008, Harper *et al.* 2012, Knauf *et al.* 2018). A first indication of potential cross-species infection is the obvious spatial overlap of areas of NHP infection in sub-Saharan Africa with areas where yaws is common in humans (Knauf *et al.* 2013). Additionally, in an ethical questionable study, a strain isolated from a baboon in Guinea (the Fribourg-Blanc simian strain, Fribourg-Blanc *et al.* 1966) caused sustainable infection in humans after experimental inoculation (Smith *et al.* 1971). A major source of zoonotic infection might be the processing and the consumption of bush meat by humans as *TPE* is mainly transmitted through direct contact with the exudate of infectious lesions (Richard *et al.* 2017). An alternative route of infection of *TP* by flies as vectors has been proposed (Kumm & Turner 1936; Satchell & Harrison 1953). In a recent study, DNA of *TP* was actually found on necrophagous flies (*Chrysomya putoria* and *Musca sorbens*) in areas of high prevalence of the disease in NHPs of Lake Manyara National Park (Knauf *et al.* 2016). However, the risk of acquiring treponemal infection through fly vectors was not examined in this study. Despite being theoretically possible for NHPs (and humans) to acquire the infection through flies, direct mucosa contact (i.e. sexual contact) should be considered the most likely way of transmission at an intraspecific level. Since Tanzania is among the 76 countries with a known history of human yaws (despite the lack of recent epidemiologic data, Marks 2016), studies on the spatial distribution of NHP infection with *T. pallidum* and genetic characterization of simian strains, are crucial for identifying whether NHPs might be acting as possible disease reservoirs for human infection (Hallmaier-Wacker *et al.* 2017).

1.4. Mating systems in nonhuman primates and its relation to STIs

Social and mating behaviour are major determinants of close contact among individuals within populations, and thus constitute major pathways for disease transmission. In NHPs various mating systems can be found (i) monogamy, where males and females typically mate with only one member of the opposite sex and have roughly equal variances in reproductive success (MacKinnon & MacKinnon 1980; Robinson *et al.* 1987; Rutberg 1983; Sommer & Reichard 2000); (ii) polyandry, in which one female mates with several males and each male mates only with that female (Garber 1997; Goldizen 1987; Tardif & Garber 1994); (iii) different forms of polygyny (i.e spatial polygyny, Charles-Dominique 1977; scramble-competition polygyny, Kappeler, 1997; female defense polygyny, Gerloff *et al.* 1999;) and (iv) polygynandry, where both sexes typically mate with several partners (Bercovitch 1989; Brockman & Whitten 1996; Altmann *et al.* 1997).

Other aspects of disease manifestation (e.g., effects on host fertility vs. mortality) and host mating systems (monogamy vs. promiscuity) might influence disease transmission patterns. Sexually transmitted infections are considered frequency dependent, in contrary to other diseases like measles which are density-dependent, where host contact rate varies linearly with density (Earn *et al*., 2000). In the first, the transmission is constant, as it is not dependent on the density but rather on the mean number of sexual partners per host and its associated variance (Smith & Dobson 1992; Lockhart *et al.* 1996; Thrall *et al.* 1997, 2000).

Since infection risk differs among species and covaries with different host features such as social and mating systems, an increased risk of infectious diseases should be accompanied by a greater immune defence (Harvey *et al.* 1991). In mammals, quantitative measures of immune defence include spleen size (Larson 1985), and numbers of circulating leukocytes (Bennett & Hawkey 1988). In primates, spleen mass does not seem to be a useful predictor of disease risk and it appears not to be related to increased promiscuity (Nunn 2002b). However, higher leukocyte counts have been found to be more prevalent in promiscuous than monogamous NHPs (Nunn *et al.* 2000*,* Nunn 2002a; Andersson *et al.* 2004). Lastly, promiscuous species show faster evolving immune genes (for the subset of genes that interact closely with pathogens) which was hypothesized to be an adaptive response to sexually transmitted infections (Wlasiuk & Nachman 2010).

1.5. Study aims and approach

The overall aim of this study is to provide a detailed analysis of the mating behaviour of a group of olive baboons (*Papio anubis*) afflicted with a putative sexually transmitted infection (*Treponema pallidum*). Specifically, I want to test whether genital ulcerations have an impact at the (i) pre-copulatory level more precisely on whether mating avoidance occurs and thus leading to mate choice (Chapter 2) and on the (ii) post-copulatory level, specifically the behaviours following a mating event (Chapter 3). The mating behaviour of wild baboons was first described and analysed in detail in Altmann & Altmann (1970) and Hausfater (1975). However, the following decades focused more on the study of the social systems, and despite early accounts on baboon sexual behaviour and behavioural changes of males and females in relation to menstrual cycling (e.g. Rowell 1967, 1969a,b; Saayman 1970; Hausfater 1975), recent quantitative reports on sexual behaviour and copulatory patterns are scarce. In chapter 2 and chapter 3 I aimed to fill this gap.

The unique constellation of a large population combined with a high *TPE*-infection associated with genital ulcerations provides an exceptional opportunity to test the impact of STIs on the mating behaviour of a group of a wild nonhuman primate and to get a better insight of the complex interaction between host-pathogen in wild populations.

1.5.1. Study site

This study was conducted at Lake Manyara National Park (LMNP) located in Northern Tanzania, during two field seasons (April-December 2015 and 2016). I was based inside the park at the Endala Research Camp. LMNP is a small protected area (approx. 580 km^2) with almost 220 km^2 of lake coverage and it is characterized by different ecosystems such as the ground water forest, acacia woodland, mixed woodland and rift escarpment (Snelson 1986). It also contains a wide diversity of large mammals like the African elephant (*Loxodonta africana*), African buffalo

(*Syncerus caffer*), Masai giraffe (*Giraffa camelopardalis tippelskirchii*), hippopotamus (*Hippopotamus amphibious*), lion (*Panthera leo*), leopard (*Panthera pardus*) and spotted hyena (*Crocuta crocuta*) (Snelson 1986). Additionally it is home to five primate species: lesser bushbaby (*Galago senegalensis*), large-eared greater galago (*Otolemur crassicaudatus*), vervet monkey (*Chlorocebus pygerythrus*), blue monkey (*Cercopithecus mitis*) and olive baboon (*Papio anubis*). In 2016 we conducted a survey and estimated that approximately 5,200 olive baboons live in the park (excluding the recently added area of 250 km^2 from the Marang forest), making LMNP one of the parks with the highest baboon densities in East Africa.

1.5.2. Study species

The radiation of modern baboons (genus *Papio*) began about 2 million years ago (Zinner *et al*. 2013). Currently six phylogenetic species are recognised: hamadryas (*P. hamadryas*), Guinea (*P. papio*), Kinda (*P. kindae*), yellow (*P. cynocephalus*), chacma (*P. ursinus*) and olive baboon (*P. anubis*). The last four species are characterized by their multi-male multi-female social organization, promiscuous mating and male-biased dispersal (Packer 1975; Smuts 1985; Melnick & Pearl 1987; Swedell 2011). In contrast, hamadryas and Guinea baboons are characterized by their multi-level society consisting of one-male units, clans and gangs. Their mating system is classified as polygyn-monandric and with female-biased dispersal (Kummer 1968; Schreier & Swedell 2009; Boese 1973, 1975; Galat-Luong *et al.* 2006; Kopp *et al.* 2015; Goffe *et al.* 2016, Fischer *et al.* 2017).

Olive baboons have been extensively studied with regard to their ecology, social behaviour and reproduction (e.g. Rowell 1967; Packer 1980; Bercovitch 1983, 1987, 1988, 1989; Strum 1983, 1991; Higham *et al.* 2008; Walz 2016, Silk *et al.* 2018; Städele *et al.* 2019). Olive baboon females (as females of other *Papio* species) exhibit typical oestrogen dependent ano-genital sexual swellings around the time of ovulation. During this period, females also show an increased proceptive behaviour (i.e. presenting the genital area to the male, Rowel 1967). Both, conspicuous swellings and proceptive behaviour attracts males and most copulations happen during the peak swelling period (Hausfater 1975; Saayman 1970, Gesquiere *et al.*

2007). Also males and females establish consortships during this period, which involve close spatial association between the female and the consorting male, and mating monopolization by the male (Seyfarth 1978; Packer 1979; Bercovitch 1985; Smuts 1985).

Before starting the data collection I had to habituate the study group to human presence using daily follows on foot. This process lasted approximately four months. To enhance group location, licensed wildlife veterinarians placed radio-collared on three adult females (Advanced Telemetry Systems, ATS), Inc. (Isanti, MN, USA). Our olive baboon study group is the largest studied to date, with approximately 170 individuals (including at least 35 adult males and 53 adult females). I conducted focal follows (Altmann 1974) from dawn to dusk on cycling (oestrous) subadult and adult females and prioritized following females in their peak oestrus (denoted by maximal tumescence of the anogenital area and bright pink colour, Zinner *et al.* 2004) to maximize the number of mating events observed.

1.5.3. Assessing age and genital health status of the group

In my study, I focused on reproductively active individuals, i.e. adult and subadults of both sexes. Age categories used followed Rowell (1969b). Adult males were identified by their large body size and fully developed secondary sexual traits (e.g., large shoulder mane, elongated canines). Subadult males were larger than females but lacked secondary sexual characteristics. Adult females were identified as individuals that have reached full body size, whereas subadult females were smaller and lacked elongated nipples (i.e. nulliparous but already cycling).

In order to assess the genital heath status (GHS) of the group, all adults and subadults were assigned a category of either “ulcerated” or “non-ulcerated” (as in Knauf *et al.* 2012). I also categorized immature individuals when possible but these were not used for the analysis. Genital ulcerations could be observed ranging from small lesions to a progressive scarification of the anogenital tissue leading to a severe mutilated vagina and anus in females, while males could display a substantial to complete loss of the penis. Ulcerated individuals were observed in most baboon groups in the national park, and thus were not restricted to any specific areas.

CHAPTER 2: MATING AVOIDANCE IN FEMALE OLIVE BABOONS (*PAPIO ANUBIS*) INFECTED BY *TREPONEMA PALLIDUM*

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Author contributions: FMDP, SK, and DZ designed the study. FMDP, ISC, IFL and SK performed field work including the collaring of the baboon females. FMDP collected the data in the field. FMDP, JR and DC performed the data analyses. FMDP, JR, DC, SK and DZ wrote the paper.

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ECOLOGY

Mating avoidance in female olive baboons (*Papio anubis*) infected by *Treponema pallidum*

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Sexually transmitted infections (STIs) are ubiquitous within wild animal populations, yet it remains largely unknown whether animals evolved behavioral avoidance mechanisms in response to STI acquisition. We investigated the mating behavior of a wild population of olive baboons (*Papio anubis*) infected by the bacterium *Treponema pallidum*. This pathogen causes highly conspicuous genital ulcerations in males and females, which signal infectious individuals. We analyzed data on 876 mating attempts and associated acceptance or rejection responses in a group of about 170 baboons. Our findings indicate that females are more likely to avoid copulation if either the mating partner or females themselves have ulcerated genitals. We suggest that this outcome is linked to the overall higher choosiness and infection-risk susceptibility typically exhibited by females. Our results show that selection pressures imposed by pathogens induce individual behavioral modifications, leading to altered mate choice and could reduce promiscuity in a wild nonhuman primate population.

INTRODUCTION

Infectious diseases are pervasive in the animal kingdom and pose a serious threat to many wildlife populations (*1*). Fitness costs associated with infectious diseases (e.g., reduced fecundity and increased mortality rates) constitute important selection pressures on individuals and have driven the evolution of sophisticated physiological defenses through complex immune systems (*2*). In addition, many species also exhibit behavioral strategies (e.g., grooming avoidance of parasitized conspecifics and selective foraging to avoid contaminated grazing areas) that can serve as the first line of defense against directly or environmentally transmitted pathogens (*3*–*6*).

Sexually transmitted infections (STIs) represent a particularly interesting case, as they are tightly linked to mating behavior and consequently to reproductive fitness. Costs associated with STIs include chronic infections with low recovery rates, reduced offspring survival, sterility, and costly immune defenses (*7*, *8*). However, unexpectedly, little is known whether individuals avoid mating with infectious partners.

Syphilis, a disease caused by the bacterium *Treponema pallidum* subsp. *pallidum*, is one of the most common STIs in humans. Individuals become infected by direct contact, usually sexual, with an infectious lesion (i.e., primary chancre) in the genital area (*9*). In Tanzania, at Lake Manyara National Park (LMNP), olive baboons (*Papio anubis*) are infected with a closely related bacterium [*T. pallidum* subsp. *pertenue* (*TPE*) (*10*, *11*)]. Other nonhuman primates (NHPs) such as yellow baboons (*Papio cynocephalus*), blue monkeys (*Cercopithecus mitis*), and vervet monkeys (*Chlorocebus pygerythrus*) are also found infected (*11*). In humans, *TPE* is known to cause yaws, a nonvenereal disease that spreads via skin-to-skin contact and causes skin ulcers in different body regions [e.g., on the face, arms, and legs (*9*)]. In contrast, clinical signs of *TPE* in NHPs in Tanzania mainly manifest themselves in the anogenital region, resembling a syphilis-like infection. Infected individuals can be identified by the appearance of genital ulcerations that lead to partial or complete mutilation of the external genitalia (Fig. 1) (*10*, *12*, *13*). Nevertheless, in rare cases, facial lesions can also be observed among TPE-infected baboons (*13*). *T. pallidum* is very sensitive to temperature changes and desiccation outside of its host (*9*). Therefore, genital skin-to-skin transmission is a highly effective transmission pathway as the genital area provides a constant moist environment compared to other regions of the body. This, together with the high frequency of observed genital ulcerations in sexually mature NHPs in Tanzania, suggests that *TPE* in those is most likely sexually transmitted (*10*, *12*).

Every time a susceptible individual mates with an infectious partner, it exposes itself to pathogens and subsequent loss of fitness, but the overall benefit of avoidance behavior might be counterbalanced by the cost of missed mating opportunities. Theoretical models have analyzed the potential impacts that STIs might have on mate choice and on the evolution of mating systems (*14*–*17*), but empirical data on animal host–STI interactions are lacking.

In this study, we investigated the sexual behavior of a wild olive baboon population to test whether the genital health status (GHS) had an impact on mate choice and mating behavior. We hypothesized that olive baboons at LMNP can discriminate between genitally ulcerated and non-ulcerated individuals and consequently adapt their mating behavior according to the GHS of the sexual partner. We assumed that individuals were infectious when genital ulcers were present, as is the case in humans infected with *T. pallidum* (*9*). We postulated that (i) non-ulcerated individuals avoid mating with ulcerated conspecifics and that (ii) mating patterns (i.e., the number of mating attempts and copulations) of ulcerated individuals are reduced when compared to non-ulcerated individuals.

RESULTS

Frequency of genital ulcers

The prevalence of genitally ulcerated individuals, determined visually, remained almost stable throughout the 18-month study period. At

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Fig. 1. Genital ulcerations caused by *Treponema pallidum*. Clinical signs of infection in adult females (top) and males (bottom) of our study group. Photo credit: F. M. D. Paciência, German Primate Center.

the end of the study, 44% of the 53 adult and subadult females and 47% of the 35 adult and subadult males displayed genital ulcers and were therefore considered as infectious (Fig. 1). Six baboons (three males and three females) that showed no ulcers at the beginning of the study developed genital ulcers, and no recovery was observed. No clinical signs were detected in infants, but five juveniles (one female and four males) were observed with genital ulcerations (of an estimated 70 immature individuals). Genital ulcers were observed in 40% of the females participating in sexual behaviors (of $n = 32$ cycling and well-habituated females) and in 53% of the males ($n = 35$).

Mating patterns

The majority of the mating behaviors (91% of $n = 876$ mating attempts) occurred when a female was in peak estrus, i.e., when a female's sexual swelling was at its maximum size. Males initiated most of the mating attempts (86%; Fig. 2). We observed 876 mating attempts between 32 females and 35 males (Fig. 3) of which 540 resulted in copulations. Males with genital ulcers performed fewer pelvic thrusts during copulations than non-ulcerated males (median of 5 and 8 pelvic thrusts, respectively; Mann-Whitney U test, $W = 63.948$; $P < 0.001$).

Among the 32 focal females (table S1), we observed an average of 2.94 cycles (range, 1 to 6) within the 18-month study period. During this period, each female had an average of 1.8 mating partners (range, 1 to 6; Fig. 3), with a median of 1 partner per 3 cycles. Females spent 95% of the maximum sexual swelling time in consortship with a male partner.

Contrary to our expectations, the number of mating attempts observed for each possible female-male dyad revealed no significant effect of the GHS of the male or the female (fig. S1), indicating a lack of support for the hypothesis that GHS status affects mating attempts. This result was obtained irrespective of whether the mating attempts were initiated by the males [model TA-1 (total attempt–1); Table 1] or by the females [model TA-2 (total attempt–1); Table 1]. However, as we predicted, acceptance of mating attempts was influenced by the GHS of both baboons in a dyad. Attempts initiated by males [model SA-1 (successful attempt–1); Table 2] were significantly less likely to result in copulations if either the male or the female was genitally ulcerated (male GHS, $P = 0.007$; female GHS, $P = 0.021$). The odds of a successful male-initiated copulation were 3.2 times higher if the male was non-ulcerated versus ulcerated and 3.1 times higher if the female was non-ulcerated versus ulcerated. In contrast, acceptance of mating attempts initiated by females [model SA-2 (successful attempt–2); Table 2] was not significantly influenced by either male or female GHS (male GHS, $P = 0.55$; female GHS, $P = 0.37$), despite the high number of mating avoidance events by males (Fig. 2).

DISCUSSION

In animal populations, mating is tightly linked to fitness maximization, and therefore, the selection of healthy partners is crucial to avoid fitness costs associated with STIs. We examined whether wild olive baboons avoided mating with individuals affected by conspicuous genital ulcers caused by *T. pallidum*. Our results demonstrate a significant effect of clinically apparent *T. pallidum* infection on the mating behavior of female baboons. Females were more likely to avoid copulation if approached by males with ulcerated genitals, indicating behavioral avoidance of diseased conspecifics. NHP females are often more susceptible to STI acquisition than males, as

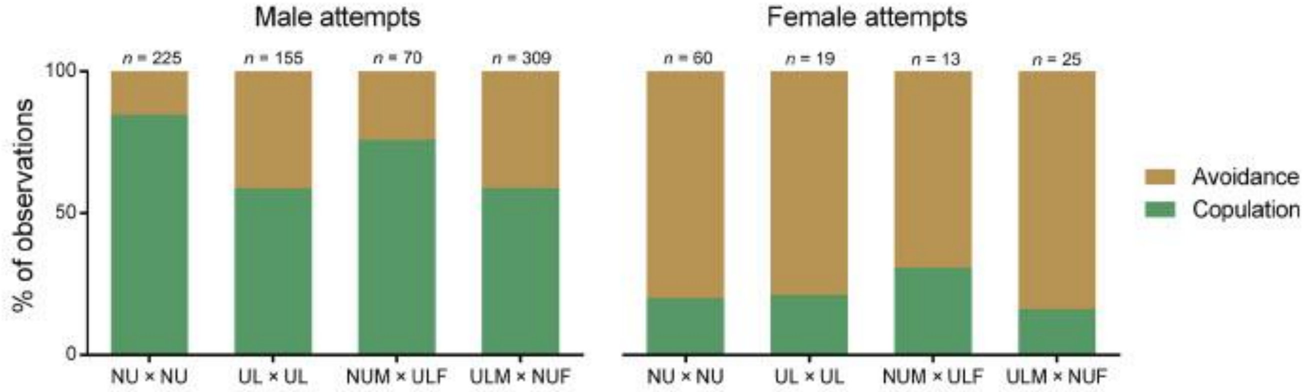

Fig. 2. Percentage of male and female mating attempts according to their GHS. Each attempt could result in either copulation (green bar) or avoidance (brown bar). The percentage of observations is shown on the *y* axis. The attempts between individuals according to their GHS are shown on the *x* axis. NU × NU (non-ulcerated × non-ulcerated), UL × UL (ulcerated × ulcerated), NUM × ULF (non-ulcerated male × ulcerated female), ULM × NUF (ulcerated male × non-ulcerated female). Sample sizes are shown at the top of each bar.

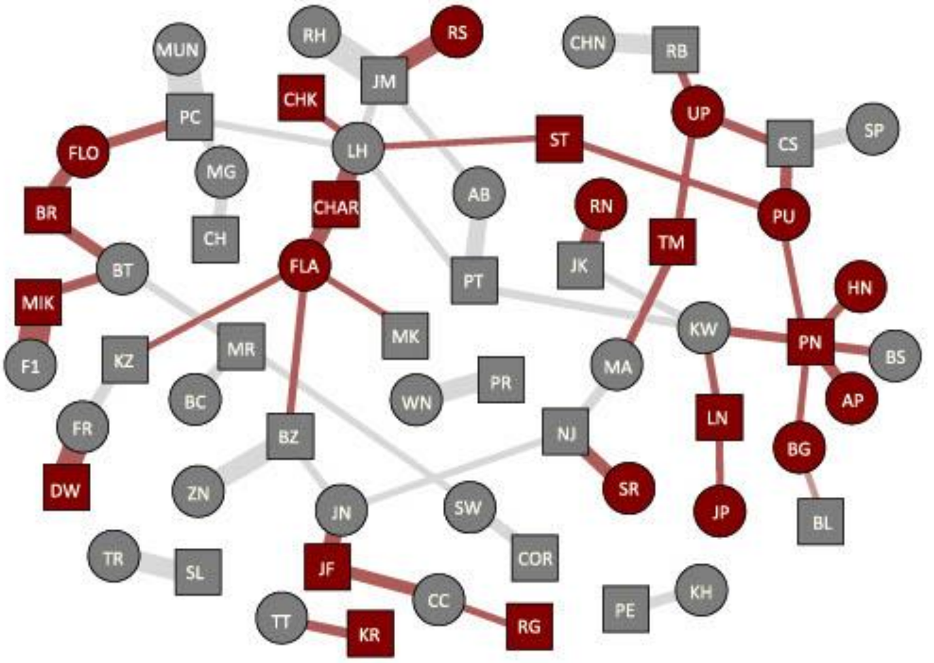

Fig. 3. Olive baboon mating network. Nodes represent individual baboons and are colored according to each baboon's GHS. Red nodes represent ulcerated individuals and gray non-ulcerated. Individuals who switched GHS are colored according to the status which had a higher number of copulations. Squares and circles represent males and females, respectively. Edges are weighted by the number of copulations among dyads and respective focal time. Edge colors correspond to the pairwise GHS of the nodes they connect, with red edges representing copulations where at least one of the individuals is ulcerated, while gray edges represent copulations between non-ulcerated individuals.

is observed in humans (*2*). Female-biased disease risk avoidance is widespread across species, and infections can significantly affect mate choice (*18*). In general, males that are infected with directly transmitted parasites (e.g., nematodes, protozoa, bacteria, and viruses) are less preferred mating partners by their conspecific females (*18*). As compared to men, women also exhibit a higher level of disgust toward potential disease threats (e.g., contaminated environment and spoiled food) and show a higher tendency to avoid infected sexual partners [e.g., individuals exhibiting genital lesions (*19*, *20*)]. The results of our study are in accordance with this generalized higher disgust reported in females since mating with STI-infected partners can entail greater costs to females due to obligatory investment in gestation, lactation, and infant rearing.

We also found that avoidance by females was more frequent if females themselves had ulcerated genitals. The progressive scarification of the genitalia due to infection can lead to a permanently open state of the vagina and anus, which increases urogenital infections (i.e., promoting miscarriages) and risk of dystocia. Thus, in addition to affecting the mate choice of non-ulcerated individuals, *T. pallidum* appears to affect mating behavior of ulcerated females, as genital

Table 1. Total attempt models. Weibull mixed-effects models evaluating whether the total number of mating attempts is influenced by the dyad's GHS of the male and/or the female. Mating attempts initiated by males and females are shown in TA-1 and TA-2, respectively. Given are posterior means, SDs, 2.5 and 97.5% confidence intervals (CIs), and effective sample sizes (*n*). Rhat = 1 (model convergence) for all parameters. Models were run using four chains, each with 2000 iterations, a burn-in of 1000, and thinning set to 1.

TA-1 model

Term	Mean	SD	CI lower	CI upper	*n* (effective)
Intercept *q*	−3.40	0.24	−3.89	−2.94	2799
Intercept β	−2.11	0.20	−2.53	−1.75	2550
Main effects:					
GHS females *q*	0.04	0.28	−0.52	0.59	4000
GHS females β	0.17	0.24	−0.31	0.64	4000
GHS males *q*	0.37	0.28	−0.18	0.92	2942
GHS males β	0.07	0.24	−0.40	0.56	3025
Random effects:					
Male ID *q*	0.24	0.17	0.01	0.63	1803
Male ID β	0.14	0.11	0.01	0.40	2027
Female ID *q*	0.17	0.13	0.01	0.47	2424
Female ID β	0.11	0.09	0.00	0.33	4000

TA-2 model

Term	Mean	SD	CI lower	CI upper	*n* (effective)
Intercept *q*	−3.56	0.28	−4.15	−3.05	4000
Intercept β	−1.32	0.25	−1.80	−0.83	4000
Main effects:					
GHS females *q*	0.12	0.32	−0.51	0.73	4000
GHS females β	0.50	0.34	−0.18	1.17	4000
GHS males *q*	−0.21	0.35	−0.92	0.44	4000
GHS males β	−0.27	0.35	−1.00	0.37	4000
Random effects:					
Male ID *q*	0.43	0.27	0.02	1.02	1222
Male ID β	0.19	0.16	0.01	0.59	1982
Female ID *q*	0.24	0.18	0.01	0.65	2192
Female ID β	0.32	0.22	0.01	0.83	1385

ulcers are likely painful and potentially cause afflicted females to refrain from mating.

While we found no evidence to support the hypothesis that males avoid mating opportunities based on their own or their partner's GHS, genitally ulcerated individuals performed significantly fewer pelvic thrusts during copulation than non-ulcerated males. Fewer pelvic thrusts might result in no or fewer ejaculation events. In addition, some symptomatic individuals were observed showing unusual body contractions with simultaneous vocalizations (e.g., kecking) during urination. As observed in females, genital ulcers seem to be equally painful for males, thus, to a certain extent, ulcerated males might also incur fitness costs.

STIs have been hypothesized to constitute a key selection pressure in shaping the evolution of mating strategies (*14*, *15*, *21*). A model based on a human hunter-gatherer population indicated that a high prevalence of STIs in large group sizes could foster the emergence of socially imposed monogamy (*22*). Cycling females of yellow and olive baboons have been reported to copulate with most of the males comprising their group (*23*, *24*). In contrast, in our study, female olive baboons only consorted and mated with few partners (average of 1.8), despite the large pool of males available ($n = 35$). While the reason for this low promiscuity is unclear, and studies reporting on olive baboon promiscuity are scarce, it would be important to investigate whether factors such as group size, pathogen incidence, pathogen virulence, and fitness consequences due to *T. pallidum* exert a selective pressure on our baboon population, which, in return, could lead to altered mating strategies.

A potential limitation of our study is that we were unable to collect data on male dominance rank; however, we think it is unlikely that including rank data in our models would significantly affect our findings. First, the vast majority of sexually mature males (83%) in our study group engaged in copulations and established consortships with peak-estrous females, indicating a lack of mating skew according to rank. Second, despite the fact that dominance rank has

Table 2. Successful attempt models. GLMMs evaluating whether the success of a mating attempt (i.e., likelihood of copulation) is influenced by the dyad's GHS of the male and/or the female. Mating attempts initiated by males and females are shown in SA-1 and SA-2, respectively. Estimates, SEs, df, and 2.5 and 97.5% confidence intervals are shown for fixed effects. Significant variables ($P < 0.05$) are shown in bold. Intercept with reference category for non-ulcerated individuals.

Term	Estimate	SE	CI lower	CI upper	X^2	df	P
SA-1 model							
Intercept	2.371	0.477	1.628	3.326	*	*	*
GHS females	−1.127	0.480	−1.962	−0.325	7.187	1	**0.007**
GHS males	−1.167	0.481	−2.151	−0.228	5.315	1	**0.021**
SA-2 model							
Intercept	−1.542	0.469	−2.782	−0.735	*	*	*
GHS females	0.577	0.647	−0.738	1.983	0.794	1	0.373
GHS males	−0.396	0.657	−1.727	1.055	0.348	1	0.555

*Not shown due to very limited interpretation

been considered a predictor of mating success in yellow and olive baboons, it is also a subject of high variation among groups and individuals, and it appears to depend on multiple factors (*25*, *26*). This highly contrasts with chacma baboons, where rank and access to estrous females are strongly connected (*27*). In addition, in yellow and olive baboons, group size and composition are important determinants of mating access among male baboons: High-ranking males tend to lose their monopoly over cycling females in large groups (*28*), and male dominance ranks are less pronounced in large groups with many cycling females (*29*). Given that olive baboon groups at LMNP are extraordinarily large (averaging approximately 150 individuals), we consider that rank does not play a major role regarding access to reproductive females in our study population. Instead, our results indicate that partner preference is crucially important at LMNP, as we observed cycling females maintaining a consistent male partner across consecutive estrus cycles.

Empirical studies on mating behavior in relation to STIs are scarce and mainly confined to arthropods. In these, no evidence of mating avoidance or discrimination between healthy and sick conspecifics has been found (*30*–*32*). Fitness disadvantages, disgust, and pain anticipation might be influencing the mating patterns of our group. Our study reporting on the ability of a long-lived vertebrate to discriminate among mating partners according to health status sheds light on how sexually transmitted pathogens can markedly shape mating dynamics in a group of NHPs. Last, given that *T. pallidum* is present in humans in overlapping areas with infected NHPs (*11*), the investigation of the underlying mechanisms affecting pathogen transmission is of the uttermost importance to mitigate health risks for both human and wildlife communities.

MATERIALS AND METHODS

Study site and subjects

Fieldwork was conducted at LMNP, Northern Tanzania (3°28′ S 35°46′E), during two field seasons (April to December) in 2015 and 2016. LMNP is a small protected area (approximately 580 km^2) with almost 220 km^2 of lake coverage. In 2016, we conducted a survey estimating the population size of the LMNP baboons in the park excluding the recently added area of the Marang forest (250 km^2). The population was estimated to consist of approximately 5200 olive baboons, and individuals with ulcerated genitals were observed in most groups within LMNP.

We habituated our study group ($n \approx 170$ baboons) over a 4-month period before data collection. To enhance location of the group, we radio-collared three adult females (Advanced Telemetry Systems Inc., Isanti, MN, USA). Proceedings on immobilization and anesthesia are described in (*13*). Our analyses focused on 26 adult and 11 subadult females (after excluding data of females observed <1.5 hours) and 28 adult and 7 subadult males. Age categories were defined as in (*33*). Adult males were identified by their large body size and fully developed secondary sexual traits; subadult males were larger than females but lacked secondary sexual characteristics (e.g., large shoulder mane and elongated canines). Adult females were identified as individuals that have reached full body size, whereas subadult females were smaller and lacked elongated nipples (but were already cycling).

Genital health status

Within our study group, baboons were categorized as either "genitally ulcerated" or "non-ulcerated," based on their GHS, using macroscopic visual cues [as in (*10*)]. In both males and females, genital ulcerations were observed ranging from small-medium ulcers to severe necrotizing dermatitis and mutilation of the outer genital structures (Fig. 1).

Behavioral data

We conducted focal follows (*34*) from dawn to dusk on subadult and adult females. We aimed for full-day focal follows, but if a focal individual was out of sight for more than 10 min, then another baboon was selected. We recorded 597 hours of observation data, with an average of 16.40 ± 10.02 hours (mean ± SD; range, 1.50 to 39.00 hours) per focal female. We prioritized following females in their peak estrus [denoted by maximal tumescence of the anogenital area and bright pink color (*35*)] to maximize the number of mating events observed. We collected data on the sexual behavior of focal females and their partners (table S1), recording when dyads participated in consortships in which a male maintained close proximity to a female and attempted to prevent other males from mating with her (*24*). In addition, we collected data on the frequency and success of mating attempts led by either males or females. Male-led mating attempts were identified as a male trying to mount a female with the performance of pelvic thrusts (*36*). Attempts led by females were documented when a female presented her perineum to a male while lifting her tail (*37*). Attempts by either sex were considered successful if they resulted in copulation. Because of the loss of the corpus penis or phimosis, some males were unable to engage in intromission and/or ejaculation, precluding our ability to use these behaviors to define successful mating attempts. An unsuccessful attempt was defined as a female rejecting a male's attempt to mount (e.g., by sitting or fleeing) or a male refraining from mounting a female after she presented to him. Behavioral data were recorded on a hand-held device (Samsung Galaxy Hand Note) in the field using Pendragon 5.1.2 software (Pendragon Software Corporation, USA) and transferred daily onto computers for error checking and data storage.

Statistical analyses

Total attempt model

We first investigated whether the number of mating attempts was affected by the GHS of a dyad. To examine this, we developed a dataset that indicated the corresponding number of attempts made by the male and female of every possible dyad in the study group, along with their respective GHSs. Including every possible dyad allowed us to consider all potential mating attempts, as mating could theoretically occur between any cycling female and any male in the group. This dataset included a high proportion (96.3%) of zero attempt data, with data for nonzero attempts showing extremely high variance ($\sigma^2 = 149.9$). Distributions commonly used in instances of zero inflation [e.g., zero-inflated Poisson or negative binomial distributions (*38*)] were a poor fit for our data; however, the discrete Weibull distribution (*39*) proved to be a good fit (fig. S2). In particular, the discrete Weibull distribution is highly flexible in modeling under- and overdispersed data relative to the Poisson distribution (*40*). The discrete Weibull probability mass function is defined as

$$P(X = x) = q^{x^{\beta}} - q^{(x+1)^{\beta}}$$

with positive shape parameter β and parameter q satisfying $0 < q < 1$. As no current R packages offered the functionality to fit mixed-effects models with a discrete Weibull distribution, we used the Bayesian programming language "Stan" to develop discrete Weibull mixed-effects models (*41*). We built two models: one predicting the number of attempts led by males (model TA-1; Table 1) and a second for attempts led by females (model TA-2; Table 1). Each model assumed that q and β were a linear combination of the male GHS and the female GHS (fig. S2). Both linear predictors also included male and female identities as crossed random effect variables affecting model intercepts. We used uninformative or weakly informative priors. Fixed effect coefficients had normally distributed priors and SDs equal to 100. Random effects were assumed to be normally distributed with SDs sampled from Cauchy prior distributions with location parameters equal to zero and scale parameters equal to 25. All models were fitted using R v 3.4.4 (*42*) with the "Rstan" package (*43*).

Successful attempt model

Here, we examined whether the success of a mating attempt is affected by the GHS of the dyad. Our dataset included the success (1/0) of each mating attempt observed, along with the GHS of the male and female involved in the mating attempt. We built two generalized linear mixed models (GLMMs) (*44*): one model for attempts led by males (model SA-1; Table 2) and a second model for attempts led by females (model SA-2; Table 2). Each model assumed that the probability of a successful mating event depended on the GHS of the male and GHS of the female. Both models had a binomial error structure with a logit link function and included the individual and pair identities as random effects. In addition, we included the focal observation time as an offset term to account for variation in observation effort among cycling females. The interactions between male and female GHS were nonsignificant and were excluded from the final models. Models were run in R v 3.4.4 (*42*) with the lme4 package v 1.1-15 (*45*), and *P* values are shown based on likelihood ratio tests of individual fixed effects [function drop1 with argument *test* set to "Chisq", (*46*)].

Network visualization

We constructed a mating network (Fig. 3) using a force-directed (Fruchterman-Reingold) layout in R v 3.4.4 (*42*) with the igraph package v 1.2.2. Connections between nodes (edges) were weighted according to each dyad's copulation rate (i.e., the number of copulations after controlling for the female's observation time). To aid in visualizing connections among nodes, we made minor adjustments to the final network graphic (e.g., preventing overlapping nodes).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/5/12/eaaw9724/DC1

Fig. S1. Posterior probabilities with q and β estimation parameters.

Fig. S2. Observed and predicted values using a discrete Weibull distribution.

Table S1. Focal females and their respective mating partners.

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Supplementary Materials for

Mating avoidance in female olive baboons (*Papio anubis*) infected by *Treponema pallidum*

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This PDF file includes:

Supplementary Materials

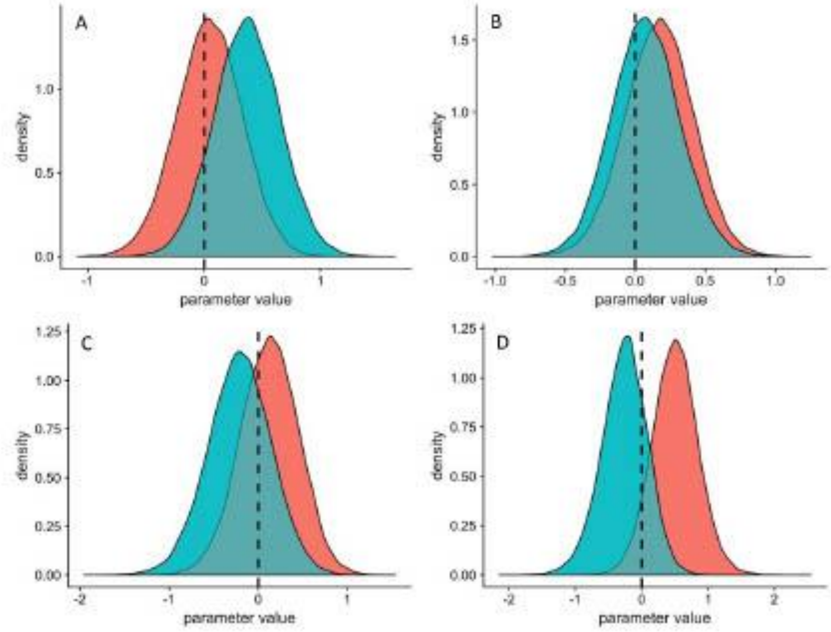


Fig. S1. Posterior probabilities with *q* and β estimation parameters. Posterior probability plots estimating the discrete Weibull distribution shape parameters, q (**A**, **C**) and β (**B**, **D**), in relation to the male attempts model (**A**, **B**) and female attempts model (**C, D**). Male genital health status (GHS) and female GHS fixed effects are displayed as blue and red, respectively. The posterior probabilities for both male and female GHS fixed effects cross the zero threshold in each panel, showing no support for the hypothesis that GHS affects the number of mating attempts.

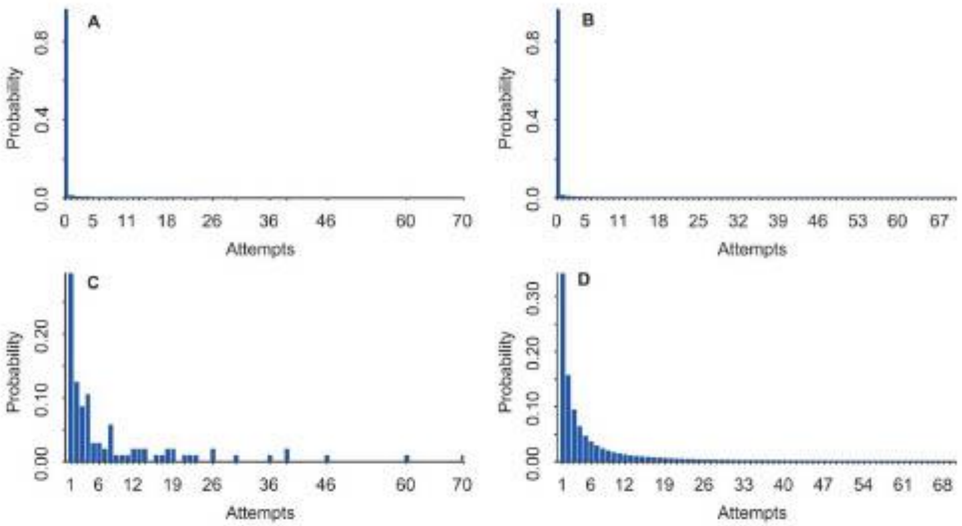
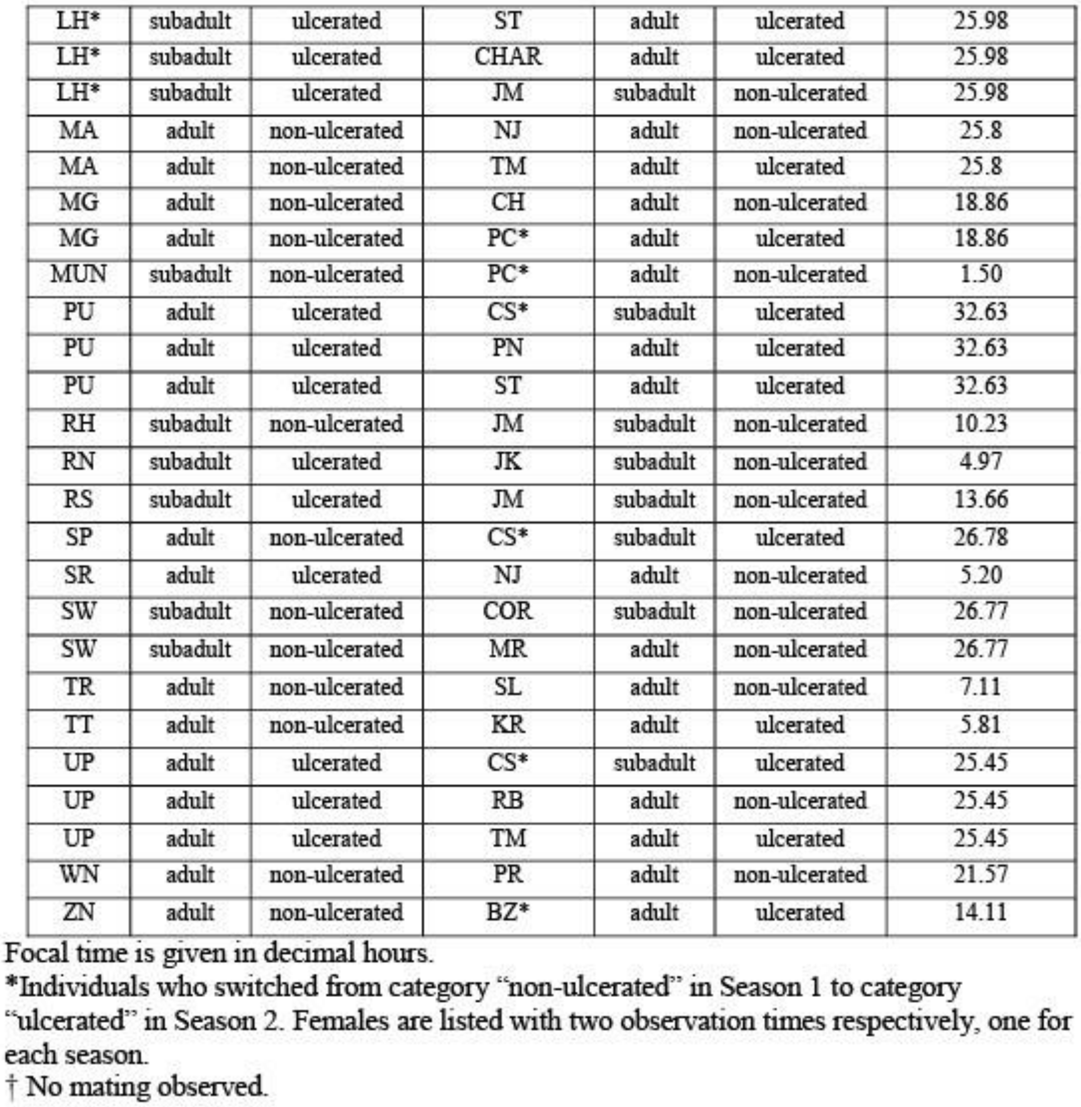


Fig. S2. Observed and predicted values using a discrete Weibull distribution. Observed data (left) as compared to the model predicted values (right) with only q and β (shape and scale) parameters. **A**, **B** shows the full dataset and demonstrates the model's ability to predict the zero-attempt data. **C**, **D** excludes zero-attempt data (values > 1) and demonstrates the model's ability to predict the non-zero attempt data.

Table S1. Focal females and their respective mating partners.

female	age class	female GHS	male mating partner	age class	male GHS	focal time (h)
AB	subadult	non-ulcerated	JM	subadult	non-ulcerated	19.39
AB	subadult	non-ulcerated	PT	adult	non-ulcerated	19.39
AP	adult	ulcerated	PN	adult	ulcerated	4.96
BC	subadult	non-ulcerated	MR	adult	non-ulcerated	10.5
BG	adult	ulcerated	BL	adult	non-ulcerated	24.64
BG	adult	ulcerated	PN	adult	ulcerated	24.64
BS	adult	non-ulcerated	PN	adult	ulcerated	15.32
BS	adult	non-ulcerated	RD	adult	ulcerated	15.32
BT	adult	non-ulcerated	BR	adult	ulcerated	5.79
BT	adult	non-ulcerated	MIK	adult	ulcerated	5.79
BT	adult	non-ulcerated	MR	adult	non-ulcerated	5.79
CC	adult	non-ulcerated	JF	subadult	ulcerated	16.70
CC	adult	non-ulcerated	RG	subadult	ulcerated	16.7
DH	adult	non-ulcerated	FE	adult	non-ulcerated	1.64
CHN	adult	non-ulcerated	RB	adult	non-ulcerated	8.05
F1	adult	non-ulcerated	MIK	adult	ulcerated	5.86
FLA	adult	ulcerated	BZ*	adult	ulcerated	20.28
FLA	adult	ulcerated	CHAR	adult	ulcerated	20.28
FLA	adult	ulcerated	KZ	adult	non-ulcerated	20.28
FLA	adult	ulcerated	MK	adult	non-ulcerated	20.28
FLO	adult	ulcerated	BR	adult	ulcerated	14.42
FLO	adult	ulcerated	PC*	adult	ulcerated	14.42
FR*	adult	non-ulcerated	DW	adult	ulcerated	11.02
FR*	adult	ulcerated	KZ	adult	non-ulcerated	18.37
HN	adult	ulcerated	PN	adult	ulcerated	27.02
IN	adult	ulcerated	†	†	†	11.31
JN	subadult	non-ulcerated	BZ*	adult	ulcerated	28.95
JN	subadult	non-ulcerated	JF	subadult	ulcerated	28.95
JN	subadult	non-ulcerated	NJ	adult	non-ulcerated	28.95
JD	adult	ulcerated	RB	adult	non-ulcerated	10.33
JP*	adult	non-ulcerated	†	†	†	5.50
JP*	adult	ulcerated	LN	adult	ulcerated	23.06
KH	subadult	non-ulcerated	PE	subadult	non-ulcerated	9.72
KN	subadult	non-ulcerated	†	†	†	2.43
KW	adult	non-ulcerated	JK	subadult	non-ulcerated	22.35
KW	adult	non-ulcerated	LN	adult	ulcerated	22.35
KW	adult	non-ulcerated	PN	adult	ulcerated	22.35
KW	adult	non-ulcerated	PT	adult	non-ulcerated	22.35
LH*	subadult	non-ulcerated	CHAR	adult	ulcerated	13.03
LH*	subadult	non-ulcerated	CHK	adult	ulcerated	13.03
LH*	subadult	non-ulcerated	JM	subadult	non-ulcerated	13.03
LH*	subadult	non-ulcerated	PC*	adult	ulcerated	13.03
LH*	subadult	non-ulcerated	PT	adult	non-ulcerated	13.03



LH*	subadult	ulcerated	ST	adult	ulcerated	25.98
LH*	subadult	ulcerated	CHAR	adult	ulcerated	25.98
LH*	subadult	ulcerated	JM	subadult	non-ulcerated	25.98
MA	adult	non-ulcerated	NJ	adult	non-ulcerated	25.8
MA	adult	non-ulcerated	TM	adult	ulcerated	25.8
MG	adult	non-ulcerated	CH	adult	non-ulcerated	18.86
MG	adult	non-ulcerated	PC*	adult	ulcerated	18.86
MUN	subadult	non-ulcerated	PC*	adult	non-ulcerated	1.50
PU	adult	ulcerated	CS*	subadult	ulcerated	32.63
PU	adult	ulcerated	PN	adult	ulcerated	32.63
PU	adult	ulcerated	ST	adult	ulcerated	32.63
RH	subadult	non-ulcerated	JM	subadult	non-ulcerated	10.23
RN	subadult	ulcerated	JK	subadult	non-ulcerated	4.97
RS	subadult	ulcerated	JM	subadult	non-ulcerated	13.66
SP	adult	non-ulcerated	CS*	subadult	ulcerated	26.78
SR	adult	ulcerated	NJ	adult	non-ulcerated	5.20
SW	subadult	non-ulcerated	COR	subadult	non-ulcerated	26.77
SW	subadult	non-ulcerated	MR	adult	non-ulcerated	26.77
TR	adult	non-ulcerated	SL	adult	non-ulcerated	7.11
TT	adult	non-ulcerated	KR	adult	ulcerated	5.81
UP	adult	ulcerated	CS*	subadult	ulcerated	25.45
UP	adult	ulcerated	RB	adult	non-ulcerated	25.45
UP	adult	ulcerated	TM	adult	ulcerated	25.45
WN	adult	non-ulcerated	PR	adult	non-ulcerated	21.57
ZN	adult	non-ulcerated	BZ*	adult	ulcerated	14.11

Focal time is given in decimal hours.

*Individuals who switched from category "non-ulcerated" in Season 1 to category "ulcerated" in Season 2. Females are listed with two observation times respectively, one for each season.

† No mating observed.

CHAPTER 3: FEMALE POST-COPULATORY BEHAVIOR IN A GROUP OF OLIVE BABOONS (*PAPIO ANUBIS*) INFECTED BY *TREPONEMA PALLIDUM*

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Author contributions: FMDP, SK, and DZ designed the study. FMDP, ISC, IFL and SK performed field work. FMDP collected the data in the field. FMDP performed the data analyses. FMDP, SK and DZ wrote the paper.

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ABSTRACT

In nonhuman primates pathogens are known to exert a profound and pervasive cost on various aspects of their sociality and reproduction. In olive baboons (*Papio anubis*) at Lake Manyara National Park, genital skin ulcers caused by *Treponema pallidum* subsp. *pertenue* lead to mating avoidance in females and altered mating patterns at a pre-copulatory and copulatory level. Beyond this level, sexual behavior comprises also post-copulatory interactions among the sexual partners. To investigate whether the presence of genital skin ulcers has an impact at the post-copulatory level, we analyzed 517 copulation events of 32 cycling females and 29 males. The occurrence of post-copulatory behaviors (i.e., copulation calls, darting [female rapid withdraw from the male] and post-copulatory grooming) was not altered by the presence of genital skin ulcerations. Similarly to other baboon populations, females of our group were more likely to utter copulation calls after ejaculatory copulation. The likelihood of darting was higher after ejaculatory copulations and with the presence of copulation calls. Post-copulatory grooming was rarely observed but when it occurred, males groomed females for longer periods when females uttered copulation calls during, or preceding mating. Our results indicate that despite the presence of conspicuous genital skin ulcers, the post-copulatory behavior was not affected by the genital health status of the dyad. This suggests that infection cues play a major role before and during mating but do not affect post-copulatory behavior.

Keywords: sexually-transmitted infection, genital skin ulcers, copulation call, darting, post-copulatory grooming, diseases

1 INTRODUCTION

Mating is intrinsically associated with sexual selection, which occurs through competition over mates or mate choice (Darwin, 1871; Anderson, 1994). Mate choice might confer both direct and indirect fitness benefits to the choosy individual. Such benefits might be a higher level of parental care or the accumulation of "good genes" in the offspring (Andersson, 1994, Kokko et al., 2003). One important fitness criterion in the mating context is the health status of the potential partner. Thus, individuals should choose healthy partners, since mating with a sick individual may not only have negative effects on the offspring (i.e. a poor health status can be an indication of a poor immune system which would then passed on to the offspring), but also on the health of the choosy individual itself, if the disease can be transmitted (Hillgarth, 1996; Martinez-Padilla et al., 2012). The latter becomes particularly obvious if the disease is sexually transmitted. A poor health status can alter both the individual´s attractiveness as a sexual partner, and its competitive ability and performance in the mating context (Beltran-Bech et al., 2014). This is particularly true when courtship and mating are energetically demanding phases (Key & Ross 1999).

In some primate species, males follow females for hours and days, maintain close proximity, increase their grooming bouts and try to monopolize mating (e.g., Smuts, 1987; Dixson, 2013). Such an investment comes along with time and energy costs, which diseased males might not be able to cover. Likewise, females might not engage with males during copulation, e.g., not showing proceptive and receptive behavior, not permit subsequent matings or not showing interest in post-copulatory grooming.

In baboons, copulations are usually defined by male mounting with intromission and pelvic thrusts upon the female, which can culminate with ejaculation (Saayman, 1970, Ransom, 1981). Yet, the number of mounts and pelvic thrusts per mount may vary. An ejaculatory mount is usually identified by an ejaculation pause, where the male remains rigid upon the female for a few seconds (Saayman, 1970). During or after copulation, females might utter copulation calls which are typically low-frequency rhythmic vocalizations (Bouquet et al., 2018). In addition, female baboons often exhibit a characteristic post-coital sprint over several meters away from the male, a post-copulatory withdraw-behavior that is known as ‘darting’ (Hall & DeVore 1965; Saayman, 1970; Ransom, 1981; Smuts, 1985; Bercovitch, 1995; Collins, 1981; O’Connell & Cowlishaw 1995). Finally, pairs may engage in post-copulatory grooming (PCG), which can be initiated either by the male or the female (Saayman, 1970).

At Lake Manyara National Park (LMNP), olive baboons (*Papio anubis*) are infected with a putative sexually transmitted infection caused by the bacterium *Treponema pallidum* subsp. *pertenue* (*TPE*, Knauf et al., 2012, 2018; Harper et al., 2012; Chuma et al., 2016). Clinical symptoms are characterized by genital skin ulcers (in the following referred to as genital ulcers), a moderate to severe ulceration of the anogenital skin in both males and females (Figure 1). Progressive scarification of the tissue can lead to a permanently open state of the vagina and anus in females; while in males it cause phimosis or loss of the corpus penis (Knauf et al., 2012). At LMNP, genital ulcers in baboons have been linked with mating avoidance by females and altered copulatory patterns by males, i.e., ulcerated individuals exhibit fewer pelvic thrusts (Paciência et al., 2019). Since *TPE* infection has been associated with pre-copulatory mate choice, we aimed to investigate whether the post-copulatory behavior is altered by the genital health status (i.e. presence of genital ulcers) of the mating pairs.

FIGURE 1 Genital skin ulcerations caused by *Treponema pallidum* subsp. *pertenue* in an adult female (top) and a subadult male (bottom) olive baboon at Lake Manyara National Park, Tanzania.

2 MATERIALS AND METHODS

This research adhered to the rules and regulations of the Tanzanian and German laws. The Animal Welfare and Ethics Committee of the German Primate Center approved the entire study.

2.1 Study site and subjects

Fieldwork was conducted at LMNP, Northern Tanzania, during two field seasons (April to December) in 2015 and 2016. Our baboon group was habituated during four months before the data collection phase of the study to facilitate behavioral observations from a distance of fewer than five meters.

The group consisted of approximately 170 individuals, of which 53 were adult and subadult females, 35 adult and subadult males and more than 70 immature individuals. In our analyses, we included 32 cycling females and their 29 male partners which could all be individually identified. The genital health status (GHS) was visually assessed and all adult and subadult individuals were classified as either genitally “ulcerated” or “non-ulcerated” using macroscopic visual cues (Knauf et al., 2012). Genital ulcerations could range from small-medium ulcers to a severe mutilation of the outer genitalia (Figure 1).

2.2 Behavioral data

We conducted full-day focal follows (Altmann, 1974) from dawn to dusk on 32 cycling females. To maximize the number of observed mating events, we focused on females in their peak estrus, denoted by maximal tumescence and bright pink color of their anogenital skin (Zinner et al., 2004). We collected 597 hours of observation data, with an average of 16.40 ± 10.02 hours (mean ± SD, range 1.50 – 39.00 hours) per focal female. We collected data on the number of mating events, type of copulation, and the presence of copulation calls, darting behavior and PCG (Table 1). Behavioral data were recorded in the field on a hand-held Samsung Galaxy using Pendragon 5.1.2 software (Pendragon Software Corporation, USA).

TABLE 1 Definition of variables

	Definition
Copulation/mating event	male mounting an estrous female and performing pelvic thrusts (with intromission*) and with or without ejaculation
Type of copulation	ejaculatory or non-ejaculatory: indicated by visible fresh sperm on the male's penis or by the sperm plug on the female's genitalia after copulation
Pelvic thrusts	number of male pelvic thrusts during copulation
Copulation call	context-specific calls female utter during, or at the end of a copulation
Darting	rapid withdraw in which a female can run away several meters from the male after copulation
Post-copulatory grooming (PCG)	male/female grooms the mating partner 15 seconds after copulation occurred

*Except for severely ulcerated males that lack the corpus penis as intromission cannot occur

2.3 Statistical analysis

We run generalized linear mixed models (GLMM, Baayen, 2008) to examine the post-copulatory behavior of our baboon population. All models were performed in R v3.4.4 (R Core Team 2018) with the lme4 package v 1.1-15 (Bates et al., 2015) and collinearity of the variables was checked using the package car (Fox & Weisberg 2011). Maximum likelihood ratio tests were used to test the full model with fixed factors against the null model (Faraway, 2006). Since interactions between the fixed predictors did not significantly improve any model fit, we excluded them from all models for parsimony and a more reliable interpretation of the main effects. In all models, female, male and pair identities were included as random factors.

2.5 Model description

Model 1: Copulation calls

The first model analyzed whether the occurrence of copulation calls was affected by the male or female GHS, the type of copulation, or the number of pelvic thrusts. The response variable was the presence or absence of copulation calls per mating event (1/0) with a binomial error structure and a logit link function.

Model 2: Darting behavior

With the second model, we examined whether post-copulatory darting was affected by the male or female GHS, type of copulation and the occurrence of copulation calls. The response variable was the presence or absence of darting per mating event (1/0) with a binomial error structure and a logit link function.

Model 3: Occurrence of post-copulatory grooming (PCG)

With the third model we investigated whether the occurrence of PCG is affected by the GHS of the male and female, respectively, presence of copulation calls and the type of copulation. Here the response variable was the presence or absence of PCG per mating event (1/0) with a binomial error structure and a logit link function.

Model 4: Duration post-copulatory grooming (PCG)

With this model, we examined whether the duration of PCG (in seconds) was affected by the presence of copulation calls and the type of copulation. Here we generated two GLMMs; one model for PCG performed by males (PCG-M) and another for PCG performed by females (PCG-F). Each model assumed that the duration of PCG depended on the presence of copulation calls and type of copulation. Both models were fitted using the glmmADMB package (Fournier et al., 2012) with a negative binomial error structure and a logit link function.

3 RESULTS

The prevalence of 'genital ulcerated' individuals in our study group (determined visually) remained relatively stable throughout the 18-months study period. Only three adult females and three adult males switched from 'non-ulcerated' to 'ulcerated' between field seasons. Therefore, at the end of the study, 44% (N=23) of the 53 adult and subadult females and 47% (N=17) of the 35 adult and subadult males displayed genital ulcers (Figure 1). Genital ulcers were observed in 40% (N=32) of the females participating in sexual interactions and in 53% (N=35) of the males. In total, we have observed 517 copulations among 32 females and 29 males. Evidence for ejaculation was found in 31.5% (N=163) of the copulations. Females uttered copulation calls in 25.5% (N=132), darting occurred in 41.7% (N=216) and PCG in 27.2% (N=141). The frequency of copulations calls and darting differed slightly between ejaculatory to non-ejaculatory copulations (Figure 2). But the likelihood of uttering copulation calls increased with ejaculatory mating (p<0.001, Table 2). Males who lacked the corpus penis were observed ejaculating towards the ground or against their legs as there was no way to direct the sperm into the female´s genital tract. Nevertheless, two females in our study group uttered copulation calls even when mating with males lacking the corpus penis, where intromission was not observed (i.e., males solely performed pelvic thrusts).

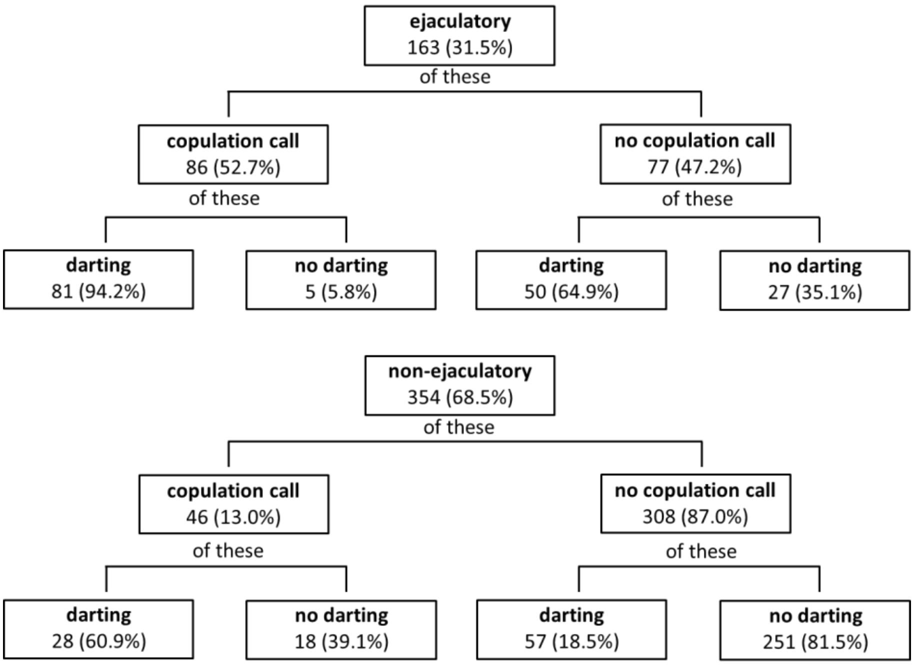

FIGURE 2 Frequency of copulation calls and darting after ejaculatory copulations (top; n = 163) and non-ejaculatory copulations (bottom; n = 354). Total number of copulations = 517.

TABLE 2 Copulation call model. Binary GLMM evaluating if the likelihood of uttering a copulation call is affected by the male and female genital health status (GHS), the number of pelvic thrusts and the type of copulation. Estimates, standard errors (SE), z-values, and 2.5% and 97.5% confidence intervals (CI) are shown for fixed effects. Intercept with a reference category for ulcerated individuals and ejaculatory events.

Term	Estimate	SE	CI lower	CI upper	z value	P
Intercept	-3.725	0.830	-5.639	-2.245	-4.490	-
Male GHS	0.057	0.803	-1.518	1.758	0.071	0.944
Female GHS	1.482	0.945	-0.347	3.553	1.569	0.117
Type of copulation	2.800	0.430	2.005	3.706	5.759	<0.001

Darting was observed in 80% (N=131) of the copulations with ejaculation, in contrast to only 24% (N=85) of the non-ejaculatory copulations. Darting was also more frequent when females uttered copulation calls (94%, N= 81). These observations were corroborated by our second model. The likelihood of darting was higher when females gave copulation calls and when the male ejaculated (p<0.001, Table 3). Darting never led to the termination of a consortship as males kept track of the females, even if the female covered distances of more than 10 meters. Moreover, consort take-overs were rarely observed in our group (n=7 over the 18-months study period).

TABLE 3 Post-copulatory darting model. Binomial GLMM evaluating if the likelihood of darting is influenced by the male and female genital health status (GHS), presence of copulation calls and type of copulation. Estimates, standard errors (SE), z-values, and 2.5% and 97.5% confidence intervals (CI) are shown for fixed effects. Intercept with reference category for ulcerated individuals, presence of copulation calls and ejaculatory events.

Term	Estimate	SE	CI lower	CI upper	z value	P
Intercept	-1.468	0.503	-2.537	-0.497	-2.919	-
Male GHS	-0.525	0.621	-1.714	0.770	-0.844	0.118
Female GHS	0.883	0.565	-0.242	2.092	1.563	0.398
Copulation call	2.408	0.480	1.502	3.402	5.017	<0.001
Type of copulation	2.500	0.380	1.781	3.277	6.586	<0.001

In most cases (72.8%, N= 376), no PCG occurred. When it occurred, males initiated PCG more often than females regardless of the type of copulation (Table 4). The occurrence of PCG was neither affected by the occurrence of copulation calls nor by the type of copulation (Table 5). However, the duration of PCG performed by males was longer when females uttered copulation calls (p=0.019). No effect was found for PCG initiated by females (Table 6).

TABLE 4 Frequency of post-copulatory grooming (PCG) initiation in relation to copulation type (number of cases in parentheses).

	Copulations (512)*	Ejaculatory 30.6 % (159)	Non-ejaculatory 68.2 (353)
No PCG	72.7% (376)	77.3 % (123)	71.46% (253)
Male initiated	17.7% (92)	15 % (24)	19.2 % (68)
Female initiated	8.5% (44)	4.5 % (12)	9 % (32)

*Five copulations excluded from the total (n= 517) as PCG could not be assessed properly

TABLE 5 Post-copulatory grooming (PCG)-presence model. Binomial GLMM evaluating if the likelihood of PCG is affected by the male and female genital health status (GHS), presence of copulation calls and type of copulation. Estimates, standard errors (SE), z-values, and 2.5% and 97.5% confidence intervals (CI) are shown for fixed effects. Intercept with reference category for ulcerated individuals, presence of copulation calls and ejaculatory events.

Term	Estimate	SE	CI lower	CI upper	z value	P
Intercept	-1.278	0.257	-1.819	-0.770	-4.978	-
Male GHS	0.520	0.307	-0.125	1.130	1.695	0.090
Female GHS	0.017	0.377	-0.828	0.681	-0.045	0.964
Copulation call	-0.070	0.319	-0.707	0.561	-0.220	0.826
Type of copulation	-0.178	0.278	-0.739	0.362	-0.641	0.521

TABLE 6 PCG duration model. GLMMs evaluating if the duration of PCG is affected by the presence of copulation calls and type of copulation. Estimates, standard errors (SE), z-values, and 2.5% and 97.5% confidence intervals (CI) are shown for fixed effects. PCG performed by males and females is shown in PCG-M and PCG-F respectively. Intercept with reference category for ulcerated individuals, presence of copulation calls and ejaculatory events (GHS = genital health status).

Term	Estimate	SE	CI lower	CI upper	z value	P
	PCG-M					
Intercept	5.213	0.185	4.851	5.575	28.24	-
Male GHS	0.106	0.191	-0.268	0.480	0.555	0.579
Female GHS	-0.197	0.180	-0.550	0.156	-1.091	0.275
Copulation call	0.472	0.201	0.078	0.864	2.352	**0.019**
Type of copulation	0.029	0.198	-0.359	0.417	0.147	0.883
	PCG-F					
Intercept	5.229	0.229	4.780	5.677	22.84	-
Male GHS	0.337	0.327	-0.304	0.978	1.029	0.304
Female GHS	-0.124	0.331	-0.773	0.525	-0.375	0.708
Copulation call	-0.147	0.456	-0.485	0.780	0.456	0.648
Type of copulation	0.164	0.588	-0.381	0.709	0.588	0.556

4 DISCUSSION

The impact of sexually transmitted infections on the mating behavior of nonhuman primates is still poorly understood. Our data from the LMNP baboons suggest that genital ulcers have an impact on female mate choice and male mating performance (Paciência et al., 2019), whereas the post-copulatory behavior seems to remain unaffected by the presence of genital ulcers.

Female olive baboons at LMNP produce copulation calls less often than other baboon species (yellow baboons: 80%, Collins, 1981; 96.9%, Semple, 1998; chacma baboons: 83%, Saayman, 1970; O'Connell & Cowlishaw 1994; Guinea baboons: 39%, Boese, 1973; olive baboons: 19%, Ransom, 1981; 62%, Bercovitch. 1985, 25% this study; but not hamadryas baboons: 18%, Swedell & Saunders 2006; 26.1% Nitsch et al., 2011). Moreover, female olive baboons at LMNP uttered copulation calls more likely when mating was followed by ejaculation. Similar findings were observed in previous studies, where copulation calls occurred more frequently, or had a longer duration after ejaculatory copulations (Saayman, 1970; Deputte & Goustard 1980; Collins, 1981; Todt et al., 1995; O'Connell & Cowlishaw 1994; Walz, 2016, but see Semple et al., 2002). Copulation calls have been suggested to constitute a mechanism to incite male-male competition in chacma baboons (O'Connell & Cowlishaw 1994; Crockford et al., 2007). In olive baboons, however, due to the long-term consortships (i.e. during the estrous periods) and even "friendships" (i.e., outside the estrus period (Smuts, 1985)), it was proposed that copulation calls function to reassure consortship formation and/or continuation with mating partners (Walz, 2016). According to the female choice hypothesis, calls can be directed to the current partner to encourage mate-guarding or to continue copulating (Todt et al., 1995). This can lead to a reduction of the likelihood of copulating with other partners and an increase in paternity certainty in males preferred by the female (Maestripieri & Roney 2005).

The occurrence and frequency of darting behavior is highly variable among olive baboons (25%, Ransom, 1981; 92%, Bercovitch, 1985; 76%, Walz, 2016, 41.7%, this study) as well as in chacma baboons (78%, Hall, 1962; 75%, Hall & DeVore 1965; 86–89%, Saayman, 1970; 78%, O'Connell & Cowlishaw 1995). In our study group, females darted more often after an ejaculatory mating and when the female uttered copulation calls. Similar observations were reported in another population of olive baboons, where females darted longer distances after ejaculatory copulations (Walz, 2016). While darting distance in chacma baboons was not affected by the occurrence of ejaculation, it was positively correlated with the duration of copulation calls (O'Connell & Cowlishaw 1995). In olive baboons, females have been described to run immediately after the copulation from the mating male towards another male (Hall & DeVore 1965), leading to consort take-overs (Smuts, 1985). Such behavior was not observed at LMNP as the darting female was usually followed by the consorting male, and consort take-overs were seldom observed. This might be due to the long term bonds observed between males and females in estrus, as females would frequently mate with the same male during different cycling periods (Paciência et al., 2019).

The function of post-copulatory grooming (PCG) is still unclear. Males might use PCG to prevent females from mating with other males and reduce sperm competition

(Berenstain & Wade 1983; Kuester & Paul 1992; Nurnberg et al., 1994; Sonnweber et al., 2015). On the other hand, females might employ PCG as a means to either stimulate or avoid mating with the same male (Slob et al., 1986; Bancroft, 2005; Gumert, 2007) or decrease the risk of harassment by males (Smuts, 1985). Quantitative studies on PCG in baboons are scarce. In olive baboons, PCG presence has been related to the quality of the social bonds between the mating partners (Smuts, 1985). Yet, in chacma baboons, it is more frequently performed by females than males, except for females in their "swollen phase", (i.e. maximum turgescent phase), where the grooming frequency by the male partners is higher (Saayman, 1970). In Barbary macaques, where PCG has been studied extensively, this behavior is known to occur in half of the mating events (Taub, 1980; Small 1990; Kuester & Paul 1992; Sonnweber et al., 2015). In this species, males are more likely to groom females after ejaculatory copulations, while females groom more often males after non-ejaculatory events (Sonnweber et al., 2015). This stands in contrast to our data from olive baboons at LMNP, where PCG did not take place in the majority of the cases and was neither affected by the type of copulation nor the presence of copulation calls. However, PCG duration performed by males was affected by female copulation calls irrespective of the type of copulation. Because copulation calls give hints to all males in the group that copulation just occurred, it might lead to male-male competition, and thus, males might be willing to increase their grooming bouts to prevent females from searching subsequent copulations with other males, which could aid in reducing sperm competition.

The clear comprehension of the possible functions of post-copulatory behaviors in nonhuman primates is still missing. In order to fill this gap, it is essential to collect and share quantitative data on sexual behavior and mating patterns of nonhuman primates. This is particularly important when group living species are affected by a sexually transmitted infection that has an impact on both sociality and reproduction leading to altered group dynamics.

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AUTHOR CONTRIBUTIONS

F.M.D.P, S.K and D.Z designed the study. F.M.D.P, I.S.C, I.F.L and S.K performed field work. F.M.D.P collected the data in the field. Data analysis was done by F.M.D.P. The paper was written by F.M.D.P, S.K and D.Z.

COMPETING INTERESTS

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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CHAPTER 4: GENERAL DISCUSSION

4.1. Pre-copulatory behaviour

Reports on pathogens causing STIs in the wild are rare and mainly confined to arthropods with no indication of mating avoidance towards diseased partners (milkweed leaf beetles [Abbot & Dill 2011]; two-spot ladybirds [Webberley *et al.* 2002]; decorated crickets [Luong & Kaya 2005]). In my thesis, I first addressed whether disease cues such as the presence of genital ulcerations, affect the pre-copulatory behaviour, more specifically if there is an impact on the mating decisions of both males and female olive baboons and their copulatory patterns. Mate choice for mate quality is widely accepted as a mechanism by which individuals can maximize their fitness and/or offspring quality (Darwin 1871; Andersson 1994; Paul 2002; Dillen *et al.* 2010; Peretti & Cordobon-Aguilar 2007). I found evidence of mating avoidance by females in situations where the mating partner displayed genital ulcerations. In addition, the likelihood of copulation also decreased for ulcerated females, giving hints to potential pain avoidance.

Contrary to females, males did not avoid mating irrespective of their own or their partner's sexual genital health status. This, however, does not mean that males are not able to identify disease cues shown by females. Quite often, at a pre-copulatory level, male baboons perform a visual, tactual and olfactory inspection of the perineal region of the females (Saayman 1970). In our group, when males inspected sick females, it was often the case that individuals would in addition to smell, inspect in detail the genital ulcers of the female, by touching or plucking necrotic tissue from the ulcers. Interestingly, after this thorough inspection, males often cleaned their hand on the ground, rubbing the fingers on the sand. This "hand-cleaning behaviour" was never observed when males touched the perianal area of non-ulcerated females.

A pre-requisite for a successful copulation is the presence of ejaculation, but mating does not always lead to ejaculation (Dixson 1998, Nitsch *et al.* 2011). This could also be the case in ulcerated males, as they performed fewer pelvic thrusts in comparison to non-ulcerated, which might lead to a decreased number of ejaculatory copulations.

In my study group, adult males initiated more often sexual mounts than did their female partners, as is the case in chacma baboons (Saayman 1970). However, mounting initiations by females were rarely avoided by males, while attempts by males evoked a variety of responses from females. This stands in contrast with Saayman (1970), where female chacma baboons seldom rejected mating attempts from males. Females from my group were observed rejecting male mounting attempts either by running away or sitting down. Cases where male harassment resulted in mating were rarely observed. It has been suggested that in mammals, rejection of mating partners by females might be too costly due to a highly male biased operational sex ratio or the risk of harassment, due to males' larger body sizes (Clutton-Brock & Parker 1995; Eberle & Kappeler 2004). Repeated male aggression (i.e. coercion) has been linked to mating benefits in chacma baboons (Baniel *et al.* 2017). However, in olive baboons, males are characterized by a higher tolerance with low rates of aggression towards females (Bercovitch 1995; Walz 2016) and females are able to reject mating attempts by males (Ransom 1981; Smuts 1985; Stumpf & Boesch 2005; Bailey *et al.* 2015, Chapter 2). This is in accordance with my study, as agonism towards cycling females or coercive mating was seldom observed. In cases where the male displayed solely mild threats (staring, eyebrow rising, short chases), only very few cases escalated into physical aggression (i.e. biting and injury infliction). Additionally, in my study, females often counter attacked male harassment by chasing the male back, either alone or with the support of other females as observed in other species such as the Guinea baboons (Goffe *et al.* 2016).

4.2. Infection avoidance at a copulatory level

Animals (including humans) evolved means and mechanisms to detect potential pathogen threats via tactile, olfactory and visual cues indicating pathogen presence (Guilford & Dawkins 1991, Oaten *et al.* 2009, Kavaliers *et al.* 2004, Tybur *et al.* 2009). This ability to recognize and avoid individuals in situations presenting actual/potential pathogen threats is crucial for host defence and pathogen avoidance. Therefore, the assessment of the health status of potential sexual partners is crucial to mitigate potential disease impacts. In my study group, with exception of one anecdotal event, post-copulatory counterstrategies, such as male genital self-grooming or urination were not observed, which is in accordance with Nunn (2003), where a metanalysis revealed no support for behavioural counterstrategies to STIs in different NHPs.

In many species, females actively choose their mates, despite the potential costs of being choosy (Andersson 1994). The higher prevalence of STIs in females (NHPs: Nunn & Altizer 2004 and Koalas [*Phascolarctos cinereus]* Jackson *et al.* 1999) indicates that females are exposed to a higher pathogen load than males. Although studies demonstrated some cases of male mate choice (Edward & Chapman 2011; Lawrence 1986) or even mutual mate choice (Lihoreau *et al.* 2008), across species, disease risk avoidance is more female biased (Beltran-Bech & Richard 2014). In group-living species, females may choose smaller social groups despite increased predation risks (Côté & Poulin 1995) as living in a larger social group might increase the risk of disease transmission (Freeland 1976; Loehle 1995). In a recent study, it was found that disease avoidance due to an infectious skin disease might drive the dispersal decisions of female western lowland gorillas (*Gorilla gorilla gorilla*), as adult females avoided breeding groups with a high prevalence of this skin disease (Baudouin *et al.* 2019). In humans, women also respond more sensitively to disease threats (e.g. potentially contaminated objects, body fluids, genital ulcerations) than males (Haidt *et al.* 1994; Fessler & Navarette 2003; Curtis *et al.* 2004). Additionally, aversion to diseased individuals has been proposed to shape many aspects of the human sociality, such as sexual attitudes and xenophobia (Schaller *et al.* 2015). Therefore, the intricate host-pathogen relation have not only driven the evolution of defence mechanisms (see chapter 1.2) but also potentially influenced the evolution of the human social systems. This shared “disgust pattern” among humans and NHPs, seems to be an outcome of the female’s enhanced evolutionary role in protecting themselves (and potential offspring) due to fitness costs associated with gestation, lactation and infant rearing.

4.3 Post-copulatory behaviour

To gain some deeper insight into the impact of genital health status on the mating behaviour of my study group, I investigated whether the presence of genital ulcers had an effect on the post-copulatory behaviour. Females due to their higher costs of reproduction should be particularly choosy with respect to conspicuous signs of disease. Thus, behavioural avoidance should not only be observed at a pre-copulatory level, but also at a post-copulatory level. Females should decrease the likelihood of their proceptive behavior, such as uttering copulation calls, perform darting and post-copulatory grooming, as these behaviours have been linked to an increase of subsequent matings in baboons (O'Connell & Cowlishaw 1994; Walz 2016). Increasing the likelihood of mating events, would be translated in our group, to an increased pathogen exposure for females, and therefore, higher disease transmission. However, despite this fact, my results show that at a post-copulatory level, female olive baboons did not show any behavioural modifications in relation to conspicuous genital ulcers (Chapter 3). The post-copulatory behaviour such as copulation calls and darting behaviour fell within the range reported for other baboon populations (e.g. Hall & DeVore 1965; Saayman 1970, Collins 1981; Ransom 1981; Smuts 1985; Bercovitch 1995; Bouquet *et al.* 2018, Chapter 3). In comparison with other nonhuman primate populations, only the occurrence and duration of post-copulatory grooming (PCG) seem to differ. In baboons there is a scarcity of studies on post-copulatory grooming, but in Barbary macaques, PCG occurs in half of the mating events (Taub 1980; Small 1990; Kuester and Paul 1992; Sonnweber *et al.* 2015). This contrasts to the results of my study, as baboons did not perform PCG in the majority of cases. However, when PCG occurred, males did groom females for a longer period of time after females uttered copulation calls. Taking into account my results, it seems that in my group, individuals might use the post-copulatory behaviour as a mean to strengthen the bonds with the mating partners (see Chapter 3), and that diseases do not play a major role after mating as observed before mating. Importantly, the detailed quantitative description of the behaviours that characterize the post-copulatory phase provides important comparative data and adds variability to the existent records on baboon sexual patterns.

4.2. STIs a selection pressure for monogamy?

Sexually transmitted infections are ubiquitous in animal populations with more than 200 sexually transmitted pathogens among 27 orders of hosts being known (Lockhart *et al*. 1996). In NHPs, STIs appear to be more frequent in promiscuous species (Nunn & Altizer 2006) and more prevalent amongst adult females (Nunn & Altizer 2004). Transmission of sexual infections relies heavily on the number of sexual partners and mating frequency (Thrall *et al.* 1997, 2000). Therefore, in the presence of an STI, a monogamous mating strategy can be advantageous if infection risk can be reduced by this strategy. However, there are reproductive fitness consequences by doing so, since by limiting the number of potential mates an individual might miss out on reproductive opportunities.

STIs have been hypothesized as a key driving force for the emergence of monogamy in animal populations (Sheldon 1993; Loehle 1995; Lockhart *et al.* 1996; Lombardo 1998; Poiani & Wilks 2000) and in humans (Immerman 1986; Immerman & Mackey 1997, Bauch & McElreath 2016). Other factors leading to social monogamy such as infanticide risk (if females concentrate paternity towards a protective male), and the spatial and temporal distribution of oestrous females (low vs high population density in a group) have been explored, (Lukas & Clutton-Brock 2013; Opie *et al.* 2013). Whether STIs fostered the evolution of monogamy, is debatable. Several authors tried to investigate this relation by using modelling based on data of both human and nonhuman populations. Such simulations are generally based on variables such as (i) disease prevalence, (ii) transmission rates, (iii) disease virulence, (iv) associated fitness costs (e.g. sterility, mortality), (v) types of mating structure (e.g. monogamy, harem polygyny), (vi) presence of mating seasons and (vii) presence of disease cues (i.e. conspicuousness). Thrall *et al.* (1997) presented one of the first formal models where STIs have been found to reduce promiscuity, although the model outcome revealed that strict monogamy was not expected to evolve either. Other models provided similar results (Graves & Duvall 1995; Thrall *et al.* 2000; Kokko *et al.* 2002; Ashby & Gupta 2013). McLeod & Day (2014) reported that monogamy is more likely to evolve in case pathogens cause mortality rather than sterility, while promiscuity should be more advantageous in cases where transmission rates are either high or low (in opposition to intermediate). The same authors reported that cryptic STIs causing host mortality are more conducive to the evolution of serial monogamy (contrary to Loehle 1995). Other authors reported that STIs could even lead to a coexistence of monogamy and promiscuity in the same population (Kokko *et al.* 2002; Boots & Knell 2002). In more recent modelling approaches, it was shown that accounting for infection avoidance (a parameter that was not included in previous models), significantly alters host population dynamics, and that promiscuity rather than monogamy may be promoted in denser host populations (Theuer & Berec 2018).

At Lake Manyara National Park, the unique combination of high *TPE* infection (Knauf *et al.* 2012, Chuma *et al.* 2018) with the relatively low degree of female promiscuity in my study group (see chapter 2) turns it into an ideal scenario to test some of the model predictions mentioned above. Whether *TPE* acted as an evolutionary force towards a reduction of female promiscuity in my study group is unknown, but on the long-run, by combining both behavioural and epidemiological data, one could contribute to fill in the blanks of this complex system of STIs and the evolution of mating systems.

4.3. One Health approach

Around 61% of all human pathogens and 75% of emerging infectious diseases are of zoonotic origin (Taylor *et al.* 2001). The recognition of the shared susceptibility of humans and animals to many pathogens has led to the concept of the multidisciplinary approach of One Health (Horby *et al.* 2014). The events that result in the successful species cross–over are frequently not well described and understood, but it is often triggered by changes in ecological or biological systems (Wilcox & Colwell 2005). Among others, such changes include (i) altered contact patterns between wild and domestic animals (e.g. Nipah virus, Horby *et al*. 2014), (ii) direct contact between humans and wild animals, e.g. bush meat has been implicated in the spill over of monkey pox, Nipah and Ebola virus (Brashares *et al.* 2011) and (iii) changes in species abundance (e.g. Hantavirus outbreaks in the Southwestern U.S.

have been attributed to fluctuations in the abundance of infected rodents, Horby *et al*. 2014).

Additionally, knowledge of a community's social system and contact structure can provide critical information for predicting infectious disease outbreaks (e.g. Nunn *et al.* 2008; Drewe 2010; Griffin & Nunn 2012, Rushmore *et al*. 2013). The contact structure of a population depends greatly on the specie's ecology, which drives social interactions, animal movement patterns, migration, dispersal, social systems and territoriality (Wey *et al.* 2008, Krause *et al.* 2007, Craft 2015). Therefore, creating realistic epidemiological models together with real-time data (e.g. Hamede *et al.* 2012, Rushmore *et al.* 2013) is essential for developing strategies to reduce the risk and impact of infectious diseases. This will enable to design better approaches (i.e. pathogen modelling) to prevent or create control measures (e.g., treatment, vaccination) for potential pathogen spill-overs. This is of major importance for example in situations of endangered wild populations that experienced disease outbreaks (e.g. Ebola and respiratory viruses in wild great apes) making infectious disease a major threat to their survival (Caillaud *et al.* 2006; Ryan & Walsh 2011). An important aspect in studying disease transmission is the role of the environment in pathogen transmission and the mechanisms that permit pathogens to be maintained in reservoirs (Brown *et al.* 2013). As an example, the non-reproducing *Leptospira* spirochetes can persist for several months in soils in the absence of a mammalian host (Bharti *et al.* 2003). Moreover, knowledge of the biology of the pathogen is essential to properly define a sequence and functional similarity threshold for a particular reservoir system as well as getting proofs of feasible transmission routes (Hallmaier-Wacker *et al.* 2017). In addition, one should be careful when creating disease models with the intent to generalize at a large scale. This is because each host species and groups within the same species have a particular set of characteristics (e.g. mating and social systems, dispersal patterns, lifespan etc.) that will influence the outcome of the model, and thus, influence the strategies applied at a broad scale (i.e. conservation efforts, treatment options).

Because *Treponema pallidum* is shared both by humans and NHPs understanding the social/sexual contacts and disease pathways on wild NHP populations might aid on developing efficient pathogen control strategies, and in the long-run, help understanding the relationship between human and nonhuman treponemes. The high prevalence of nonhuman primate infection in areas of tropical Africa where yaws is common in humans suggests that cross-species infection may occur (Knauf *et al.* 2013). Therefore, to be able to eradicate any kind of disease, all host species and potential reservoirs should be taken into account in the One Health triad linking humans, environment and humans.

5. CONCLUSION & FUTURE DIRECTIONS

I investigated the mating behaviour of a wild olive baboon population infected by *Treponema pallidum* (*TP*). At the pre-copulatory level, I found evidence that genital ulcers caused by *TP* induce behavioural changes in both females and males in the form of mate avoidance by females and altered mating patterns in males, respectively. In addition, despite the large group size of my study group, females had a surprisingly low number of male mating partners (i.e. low promiscuity), in particular when taking the large number of available male mating partners into account. At a post-copulatory level, there was no effect of the genital health status on the individual's behaviour. The post-copulatory behaviour of the olive baboons at LMNP did not differ largely from the behaviour of other baboon populations. And diseases do not seem to play a major role after copulating in contrast to what was found before copulation. Descriptive data on the mating behaviour of wild baboon populations has been missing from recent studies. My work addresses this gap and increases the diversity of data on baboon behaviour in different contexts. Finally, behavioural studies that involve Treponemes are of great importance to devise strategies for the safeguard of both humans and wildlife populations, as these bacteria affect not only humans, but a large number of nonhuman primate species across the African continent.

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DECLARATION

I hereby, declare that the work contained in the thesis "Mating behaviour of a wild olive baboon population (*Papio anubis*) infected by *Treponema pallidum"* was written by myself. Assistance of third parties was only accepted if scientifically justifiable and acceptable in regards to the examination regulations. Contributions to the individual chapters are indicated and all sources have been quoted.

Göttingen, 1st of October 2019

Filipa da Maia Domingues Paciência