Possible relationship between sexual dimorphism, sexual coercion, and consequential wounding in non-human primates.

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Abstract

Sexual coercion is an aggressive behaviour expressed by males in order to mate with females, which will additionally bring a cost to the female. The intensity of sexual coercion by males, and the physical consequences for the females, differs between species. The goal of this essay is to investigate whether there is a relationship between sexual dimorphism, sexual coercion, and wounding in non-human primates. Next to that the presence of counterstrategies by females are investigated. In this literature study a possible link has been found between having a small sexual dimorphism and a greater intensity of sexual coercion. Additionally, there also seems to be al link between a small sexual dimorphism and more severe wounding. However, this pattern of severe wounding is not found in the bonobos (Pan paniscus) even though their small sexual dimorphism. This is due to the fact that they do not exhibit sexual coercion. Regarding female counterstrategies, it seems that females use several different techniques to reduce the cost of sexual coercion, like hiding ovulation or emitting submissive vocalizations.

Introduction

Males and females have conflicting reproductive interests due to asymmetries in their levels of parental investment [1] and also due to different potential reproductive rates [2]. Both genders have different beneficial strategies for reproduction. In most species the female invests more time and energy in the offspring than the male does. The male's reproductive success is limited primarily by his access to fecund females. Males and females have equal reproductive success, however the productive success is more variable in males. This makes it beneficial for males to be more eager to mate than for females. Additionally, it can be beneficial for males to be less choosy about their mating partners which in turn will also improve their mating success [3]. As an result, reproductive strategies developed in which they need to minimize reproductive cost imposed by the opposite sex [4]–[6]. One reproductive strategy males use is sexual coercion. Sexual coercion is a form of aggressive behaviour of one sex to the other, of the male to the female. Which in turn is making it more likely that the female will mate with the male. Additionally, the aggressive behaviour also reduces the chance of mating with other males by for instance restricting a female's ability to solicit other males [7], [8]. Sexual coercion is a behaviour that comes with a cost to the female [9], for instance in the form of wounding. The aggressive behaviour expressed during sexual coercion and the cost induced on the females varies between species.

The main goal of this thesis is to investigate how the intensity of sexual coercion and the consequential wounding is distributed over the non-human primates in the great apes, baboons, and macaques. Additionally, the possible effects of sexual dimorphism on sexual coercion and wounding are investigated. This leads to the main question of this thesis: ***"Is there a relationship between sexual coercion, wounding, and sexual dimorphism in non-human primates?"***

The main question is divided into several sub-questions. The first sub-question is "*Is the degree of sexual dimorphism linked to the amount and intensity of sexual coercion in non-human primates?".* It has been predicted that male sexual coercion increases with sexual dimorphism [10], therefore it is hypothesized that a higher male-biased sexual dimorphism results in a greater intensity of sexual coercion. However, in a study done in male western gorillas *(Gorilla gorilla gorilla)* there seemed to be a significant correlation in the silverbacks between body length and aggression, in which smaller males were more aggressive towards females [11].

The second sub-question is "*Is there a link between the frequency of sexual coercion and the degree of wounding on the females in non-human primates?".* It is hypothesized that females that receive greater amounts of aggression by males will receive a more severe degree of wounding, due to higher exposure to the aggression.

The third sub-question is *"Is the degree of sexual dimorphism linked to the amount of wounding in non-human primates?".* It is hypothesized that a higher degree of sexual dimorphism is linked to more severe wounding.
Lastly, possible female counter strategies against male sexual coercion are investigated. Bringing the research question "*Are females able to reduce the cost of sexual coercion?"*. It has been stated that females are expected to evolve countermeasures to the male strategy to minimize the cost of male sexual coercion [10]. Therefore, it is hypothesized that females will be able to reduce the cost of coercion.
To answer these questions, comparative tables will comprise of several non-human primates. For this comparison the great apes, baboons and macaques are used to see whether there are differences between and within species. These tables include sexual dimorphism, sexual coercion, wounding and the social organisation of the different animals as categories of analysis.

Sexual coercion

Sexual coercion is an aggressive behaviour which makes aggressive males more likely to mate with the female. Additionally, it also reduces the chance of females of mating with other males [7], [8]. Sexual coercion comes with a cost to the female [9], [12], such as wounds.

There are two different types of sexual coercion: direct and indirect. With direct sexual coercion, males use force or intimidate females into mating with them. Meanwhile, in indirect coercion the use of force is to decrease the chance that the female will mate with other males [9], [12]. Sexual coercion can be expressed by low-ranking males (non-preferred males) and higher ranking males (preferred males). Both males have a different goal by exhibiting sexual coercion: In low-ranking the goal is to overcome female resistance, mainly via direct coercion. On the other hand, in high ranking males the goal is to constrain female promiscuity by reducing the females ability to solicit other males, which is indirect coercion [7], [13].

Definition of sexual coercion

Smuts and Smuts defined when male aggression can be interpreted as a form of sexual coercion. They stated that three specific conditions have to be present [9].

The first condition is that the male aggression towards the female should intensify in the context of reproduction. They stated that the most fecund females should receive the highest rates of aggression of the males [7], [9]. An example of this can be found in chimpanzees. The parous females which were maximally swollen received significantly higher rates of aggression than nulliparous females which were also maximally swollen. Additionally, parous females suffer significantly higher rates of male aggression when they are maximally swollen than in periods of lactational amenorrhea, tha tis from the birth of an infant until the resume of full sexual swellings [7].

The second condition is that male aggression against females should correlate with increased mating activity [7], [9]. They state that a male should have higher rates of copulation with a female that they were relatively more aggressive towards. For instance, male chimpanzees copulate at higher rates with females they were more aggressive towards, compared to females they were less aggressive towards [7].

The final condition is that there must be a cost of the male aggression towards females, such as wounding. It is stated that the females would be better off not experiencing these high levels of aggression [7], [9]. This has been confirmed in chimpanzees in which cycling parous females exhibited significantly higher levels of cortisol than cycling nulliparous females [7]. Additionally, parous females showed elevated levels of cortisol excretion during oestrous periods compared to

periods of lactational amenorrhea [7]. Next to the elevated stress levels, the sexual coercion can also lead to severe wounding from males towards females [3], [12], [14].

Forms of sexual coercion

There are three different types of direct sexual coercion, which are differentiated by the temporal proximity of their effects. Forced copulation grants immediate reproductive success, meanwhile intimidation and harassment give reproductive success in the long term. Additionally, the strength exhibited per strategy varies. Forced copulation involves violent restraint, which is accompanied by strong force. Harassment uses less force than forced copulation. And lastly intimidation, which required the least amount of force [3], [15].

The first form of direct sexual coercion is -'forced copulation'. This is seen as the most extreme form of sexual coercion. During forced copulation the male uses force to overcome female resistance to mating, which directly increases the males mating success [7]. The male uses superior speed or strength to catch and physically restrain a female while he copulates with her by force [16]. This form of sexual coercion results in immediate mating. In this way the male enhances his reproduction chance [7].
The second form of direct sexual coercion is 'harassment'. This involves repeated attempts to copulate that impose costs on females, which eventually results in female submission and immediate mating [7], [16].
And lastly, there is intimidation. This form of sexual coercion consists of physical punishment of females who refuse to mate. In turn this results in increasing the chance of accepting the male as a mate in the future [7], [16].
All the previously mentioned strategies are expected to involve males that are non-preferred, seeing mainly non-preferred males need to overcome female resistance [7]. Even though forced copulation, harassment and intimidation all likely evolved under different circumstances, they have similar consequences for the behaviour of females and, therefore, on the mating strategies of males [16].

There is also indirect sexual coercion. This behaviour is also referred to as coercive mate guarding [3], [9]. The goal of this directed aggression is to prevent females from mating with other males [3], [9], [17], [18]. Mate guarding consist of herding, punishment and sequestration [3]. Herding is a form of aggression directed towards females to induce immediate separation from rival males and to restore proximity to the guarding male [3]. During punishment, the female receives aggression when associating or copulating with other males, decreasing the likelihood of this behaviour in the future [3]. It is found that by repeatedly attacking females in the weeks preceding ovulation, males appear to increase their chances of monopolizing sexual access to females around ovulation, which in turn increases their probability of successful reproduction [19]. And lastly there is sequestration, in which the female is forcefully separated from the social group. This happens particularly during periods of maximal fecundity, which prevents the female from mating with other males [3], [20]. In contrast to direct sexual coercion, indirect sexual coercion is not only expressed by non-preferred males but also by preferred males.

Cost of sexual coercion.

It is found that repeated sexual coercion is likely to have some costs. These costs can include loss of feeding time, increased energy expenditure and increased risk of predation [16]. These costs can affect both males and females. However, males are substantially larger than females which makes these costs bigger for females. Next to that, multiple males court the same female simultaneously, which in turn increase the costs [16]. Additionally, males could benefit from raising these costs and, with that, they will increase their probability to mate with the female. However, the females will

benefit by behaviour or morphology that raises the costs for the male to continue his mating attempt [16].

In chimpanzees *(Pan troglodytes schweinfurthii),* male aggression results in a physiological cost for females, as parous chimpanzee females have increased levels of glucocorticoid secretion. However, it is hard to conclude that the increase in cortisol levels was caused by male aggression, seeing that cortisol can also increase due to increased travel or feeding competition. When comparing the parous and nulliparous females it is however suggested that it was likely due to aggression [7].

Sexual coercion in Chacma baboons *(Papio ursinus)* is costly and represents the main source of injuries for cycling females. Daily rates of female injury varied across the reproductive cycle and mirrored the rate of male aggression: swollen females received the most injuries [19]. Additionally the females that receive higher rates of aggression per hour from males suffered more injuries [19].

Relevance of sexual coercion in primates

Sexual coercion is widespread in primates and other mammals. Whenever females prefer promiscuity, there is the potential for conflicts between males and females because of their mating strategies [7]. This conflict in mating strategy can in turn result in sexual coercion, e.g., aggression. These findings highlight the importance of considering the influence of male aggression in studies of female choice [8]. Direct sexual coercion is primarily relevant for non-preferred males which in turn improve their reproduction chance. The preferred males mainly use indirect sexual coercion to discourage females to mate with other males, which in turn improves their reproduction chance.

A study by Baniel and colleagues presented new evidence supporting the use of sexual intimidation in wild Chacma baboons [19]. They stated that such behaviour was previously reported only in chimpanzees; however this finding indicated that it may occur in a wide range of primates. Additionally, they stated that the widespread use of sexual intimidation could help explain core aspects of the reproductive strategies with regards to mate choice, social structures and sexual dimorphism [19].

However, bonobos do not employ coercive aggression against females in immediate context of courtship [17], [21]. During a study of bonobo behaviour the researchers found that within this species there is no excessive use of force [22]. The males perform strong advances toward females during periods of high excitement, but they never use their physical strength to force females into sexual contact [17], [23]. This results in no wounding due to the sexual coercion [17]. Bonobos have high levels of sexual contact, which is called socio-sexual contact. This could be because there are physiological differences between the ovarian cycles in bonobos compared to other primates. Bonobos have a slightly longer maximum swelling duration than chimpanzees. The presence of this prolonged swelling could be related to the extended attractivity and hypersexuality of female bonobos [24].

Sexual coercion comparison

In this study the amount, intensity, and physical consequences of sexual coercion in different species are investigated. The primate families that are analysed are the great apes, the macaques, and the baboons. Gathered information is summarized into several tables, which are located after the conclusion (see page 17). Additionally, to the provided information and tables in this article there is more information available in the Appendix, see for social trades Appendix I and regarding sexual coercion Appendix II.

The great apes

For this study, the apes that have been researched are the western gorilla *(Gorilla beringei beringei)*, the mountain gorilla *(Gorilla gorilla gorilla)*, the Bornean orangutan *(pongo pygmaeus)*, the Sumatran orangutan *(pongo abelii)*, the bonobo (*pan paniscus),* and the chimpanzee *(pan troglodytes)*. Humans *(Homo sapiens)* have been excluded, due to wide variety of cultural influences. Within the great apes there are many differences, regarding group size, social communities and distribution of males and females. Orangutans, chimpanzees and bonobos for instance live in a dispersed social system [22], [25]. However, orangutans live in single male units meanwhile communities of bonobos are multimale-multifemale [26]. In these multimale-multifemale societies of bonobos there is absence of male dominance, instead there is co-dominance of males and females. This implies that some females have dominance over some males [17], [27], [28]. This female dominance may be due to strong group forming coalitions [29], [30]. Chimpanzees are another species that always lives in multimale-multifemale communities [31]. For gorillas it varies whether they live in a one-male group of in a multimale group. In these groups there is a dominant male, the silverback [31], [32]. An overview of the different social structures within the great ape family can be found in Table 4A. Western gorillas have the greatest male-biased sexual dimorphism in the great apes, with a ratio of 2.*4 (male body mass / female body mass)* [33]. Additionally, they also have the greatest male-biased sexual dimorphism of all the primate species mentioned here, see Table 1. Next up are both subspecies of orangutan, with a ratio of 2.2 *(m/f)*. The mountain gorilla has after the orangutan shows the greatest male-biased dimorphism. It has been mentioned that bonobos have similar sexual dimorphism as chimpanzees [30]. Bonobos have a male-biased sexual dimorphism value of 1.4*(m/f)*, which is a bit more than the 1.3 *(m/f) of chimpanzees* [33].

Sexual coercion – Great apes

The most common forms of sexual coercion used by different species of great apes are shown in Table 2A. Additionally, the most extreme forms of sexual coercion expressed by the species are indicated, next to the occurrence of that behaviour. The animals are organised according to the level of occurrence of the most extreme form of coercion. It has been stated that orangutans show some of the most extreme cases of sexual coercion in the animal kingdom [9]. The main form of sexual coercion in orangutans is forced copulation, which is a direct form of sexual coercion [22]. However, the high occurrence of forced copulation is mainly performed by unflanged males, which are unpreferred. The bigger flanged males perform consortship and mate guard of females [34]. Next to forced copulation, males also use harassment within the context of unwanted mating attempts, which is often done by a nonpreferred male [22]. The males chase, pull and physically restrain the females [35]. In some orangutan populations 50% of the matings are forced [12], [22]. Additionally, it is shown that dominant males used some form of aggression in 86% of the copulations. This suggests that female preference may result via intimidation [35]. Chimpanzees are marked as the second most sexual coercive animals in the great apes. Aggression from a male can include hits, kicks, slaps, pounding, dragging and biting [36], [37]. Male chimpanzees rarely use forced copulation [22]. This is because males are usually able to mate an unwilling female via aggressive display [9], [12], [38], [39], but also females rarely exhibit extreme resistance to male solicitation [12]. However sexual coercion is mainly indirect in chimpanzees, which is expressed via mate guarding, including sequestration, herding and punishment [22]. The males primarily mate guard oestrous females instead of non-oestrous females [7], [12], [40], [41]. Punishments might represent male intimidation over females, used to dissuade future resistance to the establishment of consortship [9], [12], [38]. Mate guarding is generally accompanied by male aggression against rival males, it is expected to involve primarily high-ranking males. On other hand it is expected that forced copulation involves primarily nonpreferred or low-ranking males [12]. The intensity of the aggression expressed varies. A

strong predictor of the received aggression was the female fecundity [12], [36]. It has been found that aggression is mainly directed towards females in oestrous [22], swollen females receive more aggression than not swollen females [42], noncycling and nulliparous females receive less male aggression than cycling mothers [12].
The next most sexually coercive species is the mountain gorilla, which has the greatest sexual dimorphism among the great apes [33]. Because of the sexual dimorphism, any aggressive behaviour by the male can be seen as an intimidating threat of force [31], [43]. Coercion is performed through display rather than physical aggression [31]. Males use aggression toward females either to discourage them from matings with other males within the group, or to advertise his own qualities to other females and males [31]. Male bodyguard can protect females from coercion by other males [44]. Therefore, the male' ability to protect females is one of the key factors influencing female choice [31].
In western gorillas, the most used forms of sexual coercion by males are harassment and intimidation. Additionally, they also display herding, which is more likely to occur when there are potentially migrant females. The aggressive behaviour shown by males towards females can include displacement, aggressive vocalizations, display and physical aggression [11].
And lastly, the bonobos, a species that use sexual behaviour to ease tension and defuse potential conflict [17], [23], [45]. This is done via genital rubbing [45], [46]. This behaviour is expressed by males (rump-rump rubbing), females (genitogenital-rubbing) and even immature individuals [24]. It has never been reported that male bonobos use coercive aggression against females [17], [21]. Females are not coerced into matings or consortship, which suggests a possible absence of male sexual coercion in bonobos [17], [30]. Males have been shown to approach towards females during periods of high excitement. However, they never use their physical strength to force females into sexual contact [17], [23]. Additionally, male bonobos do not use aggression to discourage females into mating with other males [17]. In general there is a low level of aggression within and between groups for both males and females [17].

Physical harm – Great apes

The physical harm inflicted during sexual coercion varies among species. In Table 3A the physical consequences of sexual coercion in the great apes are shown. For instance, the physical consequences for orangutans are relatively low even though sexual coercion is frequent, mainly in the form of forced copulation. Aggression during mating has not been reported to lead to physical wounding or sustained injuries as a result of rape [25], [35], [47]. The males use force to have successful copulations, they seldom wound females. Severe wounding has not been reported yet within orangutans [22].
In the case of chimpanzees, the physical harm inflicted by the males into females varies. Most cases of male to female aggression occurred without physical contact [12]. However, male chimpanzees attack and wound females more frequently than many other primate males do [12], [17], resulting in regular wounding [22]. The brutal aggression expressed by males toward females can lead to severe wounding and stress [3], [12], [14].
Next up are the gorillas. In mountain gorillas, bite wounds are extremely rare. However, there are reports of severe bite wounds on the heads of females. This is especially prevalent before a dominance turnover [31]. In the western gorilla sexual coercion creates costs to females physiology, energy expenditure and physical injuries [11], [48]. However, the aggressive behaviour often takes the form of display and physical aggression rarely results in wounding [11].
Last up are the bonobos. Because of the lack of sexual coercion, there is no wounding reported as a consequence of sexual coercion [17].

Macaques

The macaque species investigated in this study are the rhesus macaque *(Macaca mulatta),* the Japanese macaque *(Macaca fuscata)*, the stump-tailed macaque *(macaca arctoides),* the Sulawesi crested black macaque *(Macaca nigra)*, the Formosan rock macaques *(macaca cyclopsis)*, the Barbary macaque *(Macaca sylvanus)*, the long-tailed macaque *(Macaca fascicularis)* and the Tonkean macaques *(Macaca tonkeana)*. There are differences between these animal species in their lifestyle, aggression, and dominance amongst other things. Most macaques live in a multimale-multifemale group. It is also found that in some macaque species the males immigrate and enter new troops as subordinates. These males can attain a dominant position after several years, which is an inside takeover, this is found in rhesus macaques, Japanese macaques and stump-tailed macaques [10], [49], [50]. The preference for certain males also varies across species. In some species, the females mate promiscuous, for instance in the Barbary macaque or Japanese macaque [51], [52]. In these species, there is not necessarily a preference for dominant males [10], [53]. An overview of the different social structures within the macaque family can be found in Table 4B.
When looking at the sexual dimorphism in the macaques there is a great variety. The Sulawesi crested black macaque has the greatest male-biased sexual dimorphism with a value of 1.8, see Table 1B [33]. The other male-biased sexual dimorphisms in macaques are; Tonkean macaque (1.7), the long-tailed macaques (1.5), barbary macaque (1.5), stump-tailed macaque (1.5), Japanese macaque (1.4), rhesus macaque (1.3) and lastly the Formosan rock macaque (1.2) [33].

Sexual coercion - Macaques

The use of sexual coercion is different among the macaque species. Additionally, there seem to be differences in sexual coercion between low- and high-ranking macaques. The most common forms of sexual coercion used by specific macaque species are shown in Table 2B.

In Rhesus macaques, the females typically outnumber the males [54]. The females choose a dominant protective male that can protect them from harassment by subordinate males [55]. The males form relationships with particular females. Other males that threaten those particular females or offspring of that female will receive aggression [3], [56], [57]. It is found that female suffer higher rates of male attacks while in the proximity of low-ranking males than in proximity of high-ranking males [55], [58]. Nevertheless, females choose mates independently of male dominance rank even though they could minimize costs by consistently mating with high-ranking males [55]. Therefore there is not necessarily a preference for mating with dominant males [10], [53]. The rhesus macaques use mate guarding only when the females are in oestrus [20]. Additionally the males threat, chase and occasionally bite oestrus females [55], [58], [59].
For the Japanese macaques, the dominance rank also does not always predict mating success [60]. Males, especially the highest ranking male, can determine when females are nearing their ovulation and therefore have their highest probability of conception. The males concentrate their mating efforts during that period. This finding implies that in high ranking males the timing of ovulation is not concealed, in contrast to other males [61]. Resulting in dominant males having the highest paternity [53], [62]. Japanese macaques males have higher copulation rates with females they are relatively more aggressive towards [3], [60]. The forms of sexual coercion shown are punishment, chasing and herding [3], [60], [63], [64]. The males only express mate guarding when the female is in oestrus [20]. High ranking males will closely follow oestrous females from 1 to 7 days, which in turn prevents other males from approaching [60]. Females that attempt to mate with subordinate males are punished by the dominant male [10]. It is also shown that males use aggression to coerce reluctant females into mating [60], [65]. There are seasonally different patterns of aggressive behaviour [66]. The frequency of chasing increases during the mating season. The males that were chasing focused on oestrous and non-oestrous females [63].

In the stump-tailed macaques there is a clear-cut linear dominance hierarchy as expressed in teeth-baring display [67]. The stump-tailed macaques perform sneaky copulations [10]. The most prevalent form of sexual coercion is harassment in the form of threats, chases, and biting. It is shown that there is increased aggression during the breeding season [59].
Next up are the Sulawesi crested black macaques, which have the greatest sexual dimorphism [33]. They are a highly socially tolerant species, characterized by a low level of intense aggression and a high tendency to reconcile [68]. Males immigrate to other groups, in which they base their strategy on their relative fighting ability and thus potential rank in the new group. If a high rank is acquired, this could lead to potential reproductive benefits [69]. Adult females sexually solicited high-ranking males more often than low-ranking males. High-ranking males received more grooming from adult females, which indicates that high-ranking males are attractive social partners for females. Additionally, they copulated more frequently with receptive females than low-ranking males do [70]. Low ranking males have higher degree of harassment than higher ranking males [70]. Frequency and intensity of aggression towards females were greatest for mid-ranking males [70]. Males in all rank displayed significantly more aggression toward sexually receptive females than toward females in other oestrous states [70]. The high-ranking males are the least aggressive toward females [70].
The barbary macaque is a species that has a highly promiscuous mating system [51]. The reproductive success of the male is related to his rank [52]. Males are expected to compete for mates mainly via rank relations. There is an age dependent hierarchy within this species, in which a 7-year old male dominante a 6-year old male. Later on in life, the older males are often subordinate to young adults in dyadic fights and therefore depend on coalition partners during conflicts [71] In general there is little information known in regards to sexual coercion in barbary macaques.
In the Long-tailed macaques the female reproductive success depended on dominance rank and group size. There is a clear dominance hierarchy among females. A high-ranking female is significantly more likely than a low-ranking female to give birth again when they had a surviving offspring being born the previous year [50]. The reproductive success of males is related to their rank [52]. Lower ranking group members get a more peripheral spatial position which in turn reduced reproductive success [50]. There is also a maternal dominance affects the reproductive success of offspring. A high born male is more likely to become dominant in another group [50]. Daughters achieve a dominance rank position similar to their mother, a close correlation between the lifetime reproductive success of mother and daughter [50]. The sexual coercion that is expressed by Long-tailed macaques is that they mate guard when the females are in oestrus [20]. Male direct aggression as frequently or even more frequent towards females than towards other males [3].
Last up are the Tonkean macaques. In the Tonkean macaques, the females advertise the timing of their ovulation. This female sexual advertising promotes indirect mate choice via competition among males [72]. Females mainly mated with dominant males [72]. Dominant males exerted mate guarding to coerce swollen females. In a study by Rebout et al., they found that the top-ranking male had fathered two-third of all the offspring [72]. Within this species, the males only mate guarding when the females are in oestrus [20]. Dominant males mate guard females to monopolise sexual access to parous females that were in the fertile stage of their reproductive cycle. Mate-guarding males successfully prevented fertile females from expressing direct mate choice in Tonkean macaques. Higher ranking males may use threats and attacks to prevent females from expressing a possible preference for rival males, thereby reinforcing their reproductive success [72]. Mate-guarding males use mild coercive behaviours to prevent females from mating with other males during conception time [72].
Even though some information has been collected on sexual coercion in macaques, there is still a lot more research needed. In some species information on sexual coercion is still lacking, for instance in the Barbary macaques and the Formosan rock macaques.

Physical harm – Macaques

The physical harm inflicted by the different macaque species varies. In Table 3B the induced physical harm by different species is ranked on severity. The species that has been ranked as the most harmful is the rhesus macaques. Within this species, the most wounding is reported during the birth and mating season [66]. These incidents involve punctures, slashes and/or cuts. The slashes and cuts are significantly more prevalent than punctures [59]. In Japanese macaques, there are numerous reports of severe sexual aggression which could result in wounding on the female [10], [63]. Many females in oestrus or pre-oestrus are attacked and get wounds [65]. Next up are the stump-tailed macaques, whose incidents of wounding has involvements of punctures, slashes and/or cuts [59]. In the long-tailed macaques the biting between members of a stabilised group was never seen to result in deep wounds, whereas biting between stranger caused extensive and deep wounds on a few occasions [73]. For the Sulawesi crested black macaque it is known that low ranking males are more aggressive towards females than high ranking males are [70]. Next up is the Tonkean macaque. In this species the females did not suffer any physical costs, nor did males use aggression to force reluctant females into copulation [72], and no injuries or violent attacks have been reported towards females [72].

Even though there is some information known about the wounding in macaques, there is still information missing for some species. For the Formosan rock macaques and the Sulawesi crested black macaques more information is necessary to investigate the macaque species better.

Baboons

Six species of baboons are studied here, the chacma baboon *(papio ursinus)*, the Kinda baboon *(papio kindae)*, the yellow baboon *(papio cynocephalus)*, the olive baboon *(papio anubis)*, hamadryas baboon *(papio hamadryas)* and the Guinea baboon *(papio papio)*. In the baboon species there is one sexually active leader [74], [75]. However, there are differences regarding the social structure. The chacma baboon, Kinda baboon, yellow baboon and the olive baboon live in a uni-level: male dispersal system. These species live in multimale-multifemale groups and have polygynous mating systems [74], [75]. In these societies the males leave their group and join another, often when in adolescence or fully grown [74], [76]–[80]. On the other hand, the Guinea baboon and hamadryas baboon live in a multi-level system, which is based on one-male units [75]. In hamadryas baboons, the males are the main protector and the main aggressor of the females [20]. In these communities, there is female-biased dispersal [74]. These females do not disperse voluntarily, but are rather coerced by males to change one-male-unit member ship [74], [81]–[83]. In the Guinea baboon on the other hand the females freely transfer between units, parties and gangs [74], [81]–[83]. An overview of the different social trades within the baboon family can be found in Table 4C. When looking at the sexual dimorphism rates in the baboons the chacma baboons have the greatest male-biased sexual dimorphism with a value of 2.0, see Table 1C [33]. The other male-biased sexual dimorphism in baboons are; the Olive baboon (1.9), Guinea baboon (1.9), Hamadryas baboons (1.8), Yellow baboons (1.8) and lastly the kinda baboon (1.8) [33].

Sexual coercion - Baboons

In Table 2C the most common form of sexual coercion used by baboon species is shown. The most sexual coercive animal within the baboon species is the hamadryas baboon. Hamadryas baboon males mainly do coercive mate guarding, via herding, punishment, and sequestration. With this behaviour males increase their chance of copulation and conception, meanwhile decreasing the female's chance of conception and copulation with other males [20]. Compared to other baboons the hamadryas are more extreme mate guarders, because males always mate guard their females [20]. The males are vigorous mate guarders [84]. Females likely benefit from this association with a protective male because it increases the survival prospect of their offspring[20], [31], [85]. The

relationship between male leader and female can be described as permanent consortship [20], [85]. During a takeover, the levels of directed aggression towards females are far higher. In most cases, this aggression is expressed by the takeover male towards the female he is attempting to take over There has been aggression only within the context of takeovers, e.g. biting on back, possession grip and pushing [20]. In this context the aggression functions to control female sexuality. Next to that, it is also found that females receive more aggression when they are more fecund [3], [20].
Other baboon species also do mate guarding, but only during oestrus [20]. Male Chacma baboons are also vigorous mate guarders [84]. Chacma baboon females who receive more aggression throughout their cycle by a certain male are more likely to be mate-guarded by him during the ovulatory window, resulting in a higher mating success in the long term for the male aggressor [19]. Male chacma baboons also perform threats, chases, sexual intimidation and attacks [19], [86]. It is found that males preferentially targeted cycling females. The males direct violent aggression at females at times when the females are relatively likely to conceive [19]. Additionally, it is found that high ranking males are more likely to chase females than low-ranking males [86]. The aggression is used against females to both compete with other males and coerce females into mating with them[20], [86].
In the Olive baboon the females are frequently assaulted during feeding competition or when a male defended a third-party female; many attacks occurred during male-male competitive context (26%) or were seemingly unprovoked (32%) [86]. It is found that direct female coercion increases the mating success of the males [86]. The Olive baboon performs harassment in the form of biting. The areas bitten during aggressive interactions are the neck, back and tail [59].
The Guinea baboons show a more relaxed relationship between males and females than in other species, such as hamadryas baboons [87]. Male form relatively stable relationships with one or several females, but these relationships appear to be much looser than in hamadryas baboons. Where Hamadryas baboons permanently mate guard the female, the Guinea baboon are more than half of the time not found within 5 m of the female. It was found that male Guinea baboons are generally less aggressive than male chacma baboons, against males and females [87]. It was found that male-female interactions patterns were not strongly affected by female reproductive state., neither did the grooming nor aggression patterns changed with changes in the female reproductive state [87].
Regarding the sexual coercion in the Kinda baboon and yellow baboon there is still a lot of information to gain. It is known that males are mate guarders during oestrus [20]. However, there is little known about aggressive behaviour next to mate guarding. It is found that in the yellow baboons the alpha males achieved higher conception rates than expected apparently because they exercised mate choice more effectively than lower-ranking males [88].

Physical harm - Baboons

The information about wounding due to sexual coercion can be found in Table 3C. Within this table, the physical consequences of sexual coercion are collected and ranked per species within the baboon family. Unfortunately, there is no information known yet regarding wounding due to sexual coercion in every baboon's species.
The species that is seen as the most harmful is the hamadryas baboons, in which the males always mate guard. This causes the females to be exposed to a lot of potential harassment. The males bite in the neck of the females, which rarely breaks the skin or produce blood. This neck biting does not seem to harm the females in most cases. However, if a female is often the victim of neck-biting she will become hairless and covered in wounds [20]. Hamadryas females appear to live in constant fear of aggression by males [20].
Next up are the Chacma baboons. Male aggression is a major source of injuries for fertile females.

The females that received the highest rates of aggression by males also suffer the most injuries [19]. However, there is no strong evidence found that male attacks have substantial fitness costs to females [86]. It was found that females rarely have obvious injuries following an assault [86]. Injuries inflicted by males can consist of open cuts, punctures of the skin, swelling or limping [19]. Due to the great sexual dimorphism in Chacma baboons, males can do great damage with their canines and relative size difference. However, it does seem that males restrain themselves in their attacks. They avoid inflicting injuries that could harm a female's reproductive potential [86]. Even though males avoid injuring females, an attack can result in serious wounding. These injuries can in turn compromise the survival of females, due to reduced foraging/travelling efficiency and increased risk of infection [19], [86].
In the Olive baboons females are bitten in the neck, back and tail during aggressive interactions [59]. Due to the high impact of direct female coercion, there is a high severity of male-female attacks in olive baboon populations [86].
Unfortunately, there was no information found on the physical consequences of sexual coercion in the Kinda baboon and the Yellow baboon.

Female counter strategies

As been stated previously, sexual coercion comes with a cost to the female [9], [12]. Therefore, it would be beneficial for the females to have counter strategies in response to sexual coercion to reduce its cost.

The great apes

One of the main risks for females is infanticide. Bornean female orangutans alter their behaviour according to their conception risk. Additionally, females can conceal their ovulation. Near ovulation, females mate with prime flanged males, improving the conception chance by a preferred male. When the conception risk is low the females' willingness for association and mating with non-prime males increases[35]. Sumatran orangutan females lower their rates of harassment by maintaining spatial association with adult males; this is a social tactic that females employ to have protective service of a male. This is done via either consortship or by non-mating temporary parties [34].
Another tactic to reduce sexual coercion is done by showing submissive behaviour. In female gorillas, the submissive behaviour is expressed in the form of non-aggressive vocalization. This suggests that females seek to minimize aggressive behaviour [31]. In Mountain gorillas, females are protected by the silverback for potential infanticidal outsider males. Additionally, it also has been reported that females will mate with multiple partners, also during the time of conception, which also can reduce the chance of infanticide [32]. On the other hand, female Western gorillas mate exclusively with the same male before and after conception. This appears to be a strategy to minimize male interest in other females together with reinforcing her status. Potentially this could delay conception in other females [89]. Additionally, it is thought that a counterstrategy against sexual coercion is female dispersal. This strategy can reduce the risk of infanticide through the female choice of better protective males [90].
For female chimpanzees, highly promiscuous mating has the beneficial effect of paternity confusion. Seeing female chimpanzees frequently travel alone or in small groups, they regularly encounter males which are potential infanticidal in the absence of the alpha male. Therefore high-ranking males may not be able to offer reliable protection from infanticide, which emphasize the importance of promiscuous mating [12]. Additionally, the females also show submission in 96% of the cases. This was done by fleeing, emitting sound of distress or submissive vocalisations. In 5% of the cases, the females were described to retaliate. The females then showed chasing or attacking behaviour. The behaviour of females never involved more than a quick hit or slap which was usually accompanied by submissive behaviour [12].

A species in which it has been suggested that sexual coercion is absent is the bonobo. Interestingly, female bonobos can mask their timing of ovulation. This eventually caused the relaxed social conditions that allowed the evolution of "communication sex" [28]. Females do direct aggression against approaches by unwanted males. On the other hand, the males who have a friendly relationship with do not receive any aggression [21].

Macaque

A tactic of the females of Japanese macaque to minimize their sexual coercion is to not signal their probability of conception via proceptive behaviour during the fertile phase of the ovarian cycle [61]. Female is also able to reject mounting attempts by dominant and subordinate males [60]. She does that by making the male unable to assume a mounting position or by walking away from him [60], [64].

In the Sulawesi crested black macaques, females try to be near high ranking males. The presence of a high-ranking male in the surrounding has several benefits, namely high-ranking males may deter low-ranking and subadult males from harassing the female. Additionally, females may suffer less feeding competition from other males when they are near a high-ranking male. Lastly, high-ranking males are usually preferred sexual partners [70].

It is found that in Tonkean macaque sexual presentations indicated that females accepted different types of partners, supporting the weak-selectivity hypothesis regarding direct mate choice [72].In direct mate choice, the females show a preference for a certain partner. ON the other hand there is indirect mate choice, in which females select partners by displaying sexual attractive traits. This in turn promotes competition between males. This resulted in the outcome that indirect mate choice appears to be more important than direct mate choice in Tonkean macaque females [72]

Unfortunately, there is still little information known about female counterstrategies against sexual coercion. No information was obtained regarding the Rhesus macaque, Stump-tailed macaque, Long-tailed macaque, Formosan rock macaque and the Barbary macaque.

Baboons

With regards to the counterstrategies in baboons is there still little information known. During this literature study, only information regarding counterstrategies in Guinea baboons was found. In the Guinea baboons it has been observed that in 20% of the cases of male-directed aggression towards females there was counter aggression [87]. Next to that, females transfer to other males both between and within their parties. These changes occur irrespective of their reproductive state. There seemed to be no clear pattern in predicting female transfer and no obvious fighting of males over females [87].

Conclusion

In this study, different primate species were compared within their family. The goal was to investigate whether there is a relationship between sexual coercion, wounding and sexual dimorphism in non-human primates. To answer these questions regarding the obtained tables are used.

The first sub-question is whether sexual dimorphism is linked to the intensity of sexual coercion in non-human primates. When looking at the great apes, the animal with the greatest sexual dimorphism, the mountain gorilla, is ranked as the one showing the lowest sexual coercion intensity among the great ape family. Gorillas use the display as their main form of sexual coercion rather than physical aggression. In this species, it seems that the greater sexual dimorphism results in more display behaviour and less physically aggressive behaviour. The animal with the second greatest sexual dimorphism in the great apes is the Bornean orangutan and Sumatran orangutan. These

primates have been qualified as one of the most sexual coercive animals in the animal kingdom. Within this species, sexual harassment is very common as well as forced copulation. However, it is important to point out that the high occurrence of forced copulation is mainly done by unflanged males, which are smaller than the flanged males and therefore have a smaller sexual dimorphism. The bigger flanged males perform consortship and mate guard females. After the orangutans, the most extreme form of sexual coercion is conducted by the chimpanzees, which have the lowest sexual dimorphism in the great ape family. Within the chimpanzee species there is rarely forced copulation, but that is because males are usually able to mate females via aggressive display. When looking at chimpanzees there seems to be a relationship between a smaller sexual coercion with a more extreme form of sexual coercion. However, another species within the great ape family with a similar sexual dimorphism to chimpanzee is the bonobo. The bonobos are a remarkable species that do not express sexual coercion, meanwhile having a similar sexual dimorphism as chimpanzees. It is difficult to conclude whether there is a relationship between sexual dimorphism and intensity of sexual coercion in the great apes. However, there does seem to be a relationship between a small sexual dimorphism and a greater intensity of sexual coercion.
When looking at sexual coercion and dimorphism in macaques the Sulawesi crested black macaque has the largest male-biased sexual dimorphism. Unfortunately, little information about the sexual coercion in this animal species is known, apart from harassment. The second largest male-biased sexual dimorphism is found in the Tonkean macaque, which Is also one of the most sexually coercive macaque species. The most common form of sexual coercion in Tonkean macaques is mate guarding, but they also attack and make threats towards females. The most sexually coercive macaque is the rhesus macaque which has a low sexual dimorphism Within this species the males frequently harass females. Future research is needed to investigate sexual dimorphism more, seeing there is little to no information available about Formosan rock macaques and Barbary macaques regarding this topic.
Within the baboons the most sexually dimorphic animal is the chacma baboon, which is also one of the most sexual coercive baboons. The most sexually coercive baboons are the hamadryas baboons, which have a smaller sexual dimorphism. The hamadryas baboons are the most vigorous mate guarders in the baboon family. They always mate guard the female. Within this species the males are the main protectors and main aggressors of the female. Unfortunately, there is still a lot of data on sexual coercion in baboons missing. For the Kinda baboon and the yellow baboon there is only known that they mate guard during oestrus.
To conclude, there is a lot of variation between the sexual dimorphism and the amount of sexual coercion expressed by that animal. Within the baboons and macaques there is a lot of information missing regarding sexual coercion. Within the baboons the greatest sexual coercion is expressed by the hamadryas baboon. The Hamadryas baboon has a similar sexual dimorphism to yellow baboons and Kinda baboons, which are the lowest sexual dimorphic baboons. It seems that in some species that have a low sexual dimorphism, they express a greater amount of sexual coercion, for instance seen in chimpanzees and rhesus macaques. On the other hand, the bonobos, that have similar sexual dimorphism as chimpanzees, does not seem to use sexual coercion at all. However, the lack of sexual coercion expressed by the bonobos is not found in other species. Based on the information gathered in this essay there does seem to be a relationship between sexual dimorphism and the intensity of sexual coercion, in which a small sexual dimorphism is linked to a greater intensity of sexual coercion.

The second sub-question was whether the amount of received sexual coercion and the degree of wounding on the female is linked in non-human primates. When looking at the great apes there is a lot of variation in the physical harm that is inflicted due to sexual coercion.
The chimpanzee is seen as the animal with the most physical consequences for the female as a consequence of sexual coercion, even though chimpanzees do not express the greatest intensity of

sexual coercion. Orangutans are concluded to have the greatest intensity of sexual coercion, in which females are intimidated and harassed, but this does not lead to physical wounding. It is found that in the orangutans there are no sustained injuries due to the forced copulation. Next is the gorilla, females rarely have any physical consequences due to sexual coercion from males. And lastly, there is no wounding reported in bonobos related to sexual coercion, seeing that is absent in this species. When looking at the great apes there does not seem to be a clear relationship between the intensity of sexual coercion and the wounding.
When looking at the macaques the most sexually coercive animal is the rhesus macaque. This animal also seems to be having the highest incidence of wounding reported. Within this species the degree of sexual coercion seems to be related to the greatest amount of wounding. The next most sexually coercive macaque is the Tonkean macaque. In this species, the females did not suffer any physical harm. There are no injuries or violent attacks reported from males towards females, which contradicts the idea that sexual coercion and wounding seem to be related. After that is the Japanese macaque the most sexually coercive. As in the rhesus macaques, there are numerous reports of sexual aggression which resulted in damage to the females. Unfortunately, there is still a lot of information mission in the macaque family, regarding sexual coercion and physical wounding missing.
And finally, when looking at sexual coercion and wounding in baboons there is still a lot of information unknown. All the baboons do mate guarding, but the intensity varies among species. It seems that the hamadryas baboons is the most vigorous mate guarder of all baboons. Even though the skin of females is rarely broken by neck-biting, frequent biting in a short time can result in hairlessness and being covered in wounds. Female hamadryas baboons appear to be in constant fear of being aggressed by males. In this species it seems that the amount of sexual coercion received is positively correlated to the amount of wounding. After the hamadryas baboons, the chacma baboons are the most sexually coercive and inflict the most injuries. There are rarely females seen that exhibit obvious injuries after an assault, however there are reports of open wounds, punctures of the skin, swelling and limping. After that are the olive baboons and then the Guinea baboons. In the olive baboons, the females are bitten in the neck, back and tail. However, no mentions of severe injuries were found during this literature study. As mentioned earlier there is still a lot of data on sexual coercion and wounding in baboons missing, which therefore could be interesting to investigate further in future research
All in all the degree of wounding as a result of sexual coercion seems to vary between species. There does not seem to be a clear relationship between the amount of sexual coercion and the degree of wounding in all species. In some species the high amount of sexual coercion is linked to a high degree of wounding, for instance in the chimpanzee or rhesus macaque. In others the high amount of sexual coercion is not linked to a high degree of wounding, for instance in the orangutan species or Tonkean macaques. However, for the baboons there does seem to be a relationship between the received sexual coercion and the degree of wounding, however more research is needed within this family seeing there is a lot of information missing. There could be an effect of the group structure or the male-female ratio.

The third sub-question was whether the degree of sexual dimorphism was linked to wounding in non-human primates. Within the great ape family, the western gorilla shows the largest male-biased sexual dimorphism. However, it is found that aggression resulting in wounds is extremely rare within this species. Another species with a large sexual dimorphism is the Bornean orangutan. Intimidation and harassment did not lead to physical wounding in the Bornean orangutan even though the males are at least twice the as big as the females. On the other hand, the most severe wounding was done by the chimpanzee, the great ape with the smallest sexual dimorphism. Within this species brutal

aggression can lead to severe wounds and stress. The bonobos are a species with a sexual dimorphism similar to chimpanzees, yet no wounding due to sexual coercion has been reported, due to the absence of sexual coercion within this species.
The macaque species with the most severe wounding reported is the rhesus macaque, which also has one of the smallest sexual dimorphism. The only animal that has a smaller sexual dimorphism is the Formosan rock macaque, however little information is known about the degree of wounding due to sexual coercion in this species. The Japanese macaque has a slightly larger sexual dimorphism than the rhesus macaque. They are after the rhesus macaque the most wounding macaque. There are numerous reports of severe sexual aggression that eventually resulted in damage on the females.

The stump-tailed macaque is slightly more sexual dimorphic, but causes less physical consequences on the female, see Table 3B. In line with these findings, in a great sexually dimorphic monkey, the Tonkean macaque, the females did not suffer any physical costs. No reports of injuries or violent attacks on females have been found. The greatest sexual dimorphic macaque is the Sulawesi crested black macaque; however, no wounding information was found.
Within the baboon family there is less variation in the sexual dimorphism than in the great apes or the macaques. Due to the lack of variation in sexual dimorphism it is difficult to conclude an effect of sexual dimorphism on the severity of wounding in baboons. The most sexual dimorphic baboon is the chacma baboon. Within this species, injuries from aggression are rarely found, although there are reports of open cuts, skin punctures, swelling and limping. The hamadryas baboons, which has one of the smallest sexual dimorphism ratios, is seen as the most wounding of all baboons. The males bite the females, which does not seem to physically harm the females. However, frequent biting can lead to wounds. No information of the yellow baboon and the Kinda baboon regarding wounds was found.
In conclusion, the collected data on severity of wounding and sexual dimorphism in these primate species does give some insight into the relationship between the two. In the macaques, the animals with the smallest sexual dimorphism are inflicting the most severe wounding. On the other hand, the animals with the greatest sexual dimorphism rarely inflict wounds. However, it is important to note that there is still a lot of information missing on the topic of wounding in the macaques. Information regarding the macaques with the greatest and smallest sexual dimorphism is yet to be collected. The relationship between a small sexual dimorphism and a high degree of wounding can also be found in the great apes, when excluding the bonobos. Chimpanzees have the smallest sexual dimorphism in this family, and also inflict the most severe wounding. With regards to the baboons, there is wounding information missing in the species with small sexual dimorphism ratios.

There is wounding information known for the Hamadryas baboon meanwhile having one of the smallest male-biased sexual dimorphism ratios. The male hamadryas baboons are seen as inflicting the most severe wounding on the females of all baboon species. The females are bitten, which could when inflicted frequently lead to hairlessness and being covered in wounds. After the hamadryas baboons the chacma baboons are most severely wounding. They are the most sexual dimorphic baboon species. Within this species there are rarely obvious injuries found. It seems that the males restrain themselves during their assaults. Nevertheless, there are reports of open cuts, skin punctures, swelling and limping. Overall, there does seem to be a relationship between a small sexual dimorphism and a higher degree of wounding on the females.

With regards to the fourth sub-question, whether females can reduce the cost of sexual coercion, there is still a lot of information unknown. It seems that some females can reduce the cost the males put on them. This is mainly reducing the cost of infanticide. Additionally, in some species, for instance, in the Bornean orangutan, the female can hide their ovulation. This causes the males not to

be able to know when the conception chance is high. Other strategies in which the females try to reduce the cost of sexual coercion is via the use of submissive behaviour, in the form of non-aggressive vocalizations. Although there has been some information regarding this topic provided in this paper, there is still a lot more research needed to investigate female counter strategies against sexual coercion.

Finally, to conclude how sexual coercion, wounding and sexual dimorphism is related in non-human primates. Regarding the answered sub-questions there seem to be a trend in having a small sexual dimorphism, high sexual coercion and or a high degree in wounding, which has been expressed in the great apes, macaques, and baboons. However, a remarkable exception is seen in the bonobos, which do not seem to exhibit sexual coercion. The bonobo is a species that has a remarkable social structure, which perhaps leads to this lack of coercion. They exhibit socio-sexuality, in which they use sexual behaviour as a means to ease tension and defuse potential conflict. The link between small sexual dimorphism and a high sexual coercion could perhaps be linked to the dominance of the males over the females. It could be possible that when males have less physical advantage over the female, they will compensate by being more aggressive to maintain their dominance over the female. While this study does not offer a conclusive answer to the question of which affects sexual coercion is specifically, it does give insight into the possible relationship between sexual dimorphism and the related degree of wounding. Additionally, it also points out the importance of more research, seeing there is still a lot of information missing especially regarding wounding information in the macaque and baboon species. Lastly, this study gives more insight into the possible importance of the dominance relationship between male and female. This can be possibly seen in the bonobos, in which a lack of sexual coercion possibly due to the unique social structure of co-dominance. On the other hand, this lack of sexual coercion could also be due to socio-sexuality. For future research it would also be interesting to compare the bonobo with the chimpanzee, seeing they have similar sexual dimorphisms, and they are both living in multimale-multifemale groups. Additionally, it would be interesting to investigate whether there is an effect female to male ratio on sexual coercion and wounding severity. Lastly, there is more research needed into the female use of counterstrategies against sexual coercion.

Tables

Table 1A: Great apes

Name	*Male body mass kg*	*Female body mass kg*	*Ratio male/female*
1. Western gorilla *(Gorilla beringei beringei)*	170.4 [33]	71.5 [33]	2.38
2. Bornean orangutan *(Pongo pygmaeus)*	78.5 [33][33]	35.8 [33]	2.19
3. Sumatran orangutans (Pongo abelii)	77.9 [33]	35.6 [33]	2.19
4. Mountain Gorilla *(Gorilla gorilla gorilla*	162.5 [33]	97.5 [33]	1.67
5. Bonobos *(pan paniscus)*	45 [33][33]	33.2 [33]	1.36
6. Chimpanzee *(pan troglodytes)*	59.7 [33]	45.8 [33]	1.30

Table 1B: Macaques

Name	*Male body mass kg*	*Female body mass kg*	*Ratio male/female*
1. Sulawesi crested black macaque *(Macaca nigra)*	9.89 [33]	5.47 [33]	1.81
2. Tonkean macaques *(Macaca tonkeana)*	14.9 [33]	9 [33]	1.66
3. Long-tailed macaques *(macaca fascicularis)*	5.36 [33]	3,59 [33]	1.49
4. Barbary macaques (Macaca sylvanus)	16 [33]	11 [33]	1.45
5. Stump-tailed macaques *(macaca arctoides*)	12,2 [33]	8,4 [33]	1.45
6. Japanese macaques *(macaca fuscata)*	11 [33]	8.03 [33]	1.37
7. Rhesus macaques *(Macaca mulatta)*	*Site 1:* 11 [33] *Site 2:* 7.71 [33]	*Site 1:* 8.80 [33] *Site 2:* 5.37 [33]	*Site 1:* 1.25 *Site 2:* 1.43 *Gem*: 1.34
8. Formosan rock macaque *(Macaca cyclopsis)*	6 [33]	4,94 [33]	1.21

Table 1C: Baboons

Name	*Male body mass kg*	*Female body mass kg*	*Ratio male/female*
1. Chacma baboon *(Papio ursinus)*	29.8 [33]	14.8 [33]	2.01
2. Olive baboon *(Papio anubis)*	25.1 [33]	13.3 [33]	1.92
3. Guinea baboon *(Papio papio)*	*Range:* 25-27 [91] *Gem:* 26	*Range:* 7-21 [91] *Gem:* 14	1.86 [91]
4. Hamadryas baboons *(Papio hamadryas)*	*Site 1:* 16.9 [33] *Site 2:* 21 [33]	*Site 1:* 9.9 [33] *Site 2:* 11.4 [33]	*Site 1:* 1.71 *Site 2:* 1.84 *Gem:* 1.78
5. Yellow baboon *(Papio cynocephalus)*	21.8 [33]	12.3 [33]	1.77
6. Kinda baboon *(Papio kindae)*	17.2 [33]	9.75 [33]	1.76

Table 1: *Sexual dimorphism in several species. Calculated by male body mass / female body mass. Animals are ranked by their sexual dimorphism, starting with the greatest sexual dimorphism. The table is separated into 3 different families; A: Great apes, B: Macaques and C: Baboons.*

Table 2A: Great apes

Species	*Most common form sexual coercion*	*Most extreme form sexual coercion*	*Occurrence most extreme form*
Bornean orangutan *(Pongo pygmaeus)*	Sexual harassment – chasing, pulling and restraining the female[35]. Next to that mate guarding[92].	Forced copulation [35].	High *High occurrence forced copulation – unflanged males* [35].
Sumatran orangutans *(Pongo abelii)*	Sexual harassment [34] and mate guarding [92].	Forced copulation [34].	High *High occurrence forced copulation – unflanged males*[34].
Chimpanzee *(pan troglodytes)*	Mainly indirect; sequestration, herding and punishment [7], [9], [12], [38], [40], [41]. Aggression includes; hits, kicks, slaps, pounding, dragging and biting [36], [37].	Forced copulation [22].	Rarely *Primarily because females rarely exhibit extreme resistance* [12]
Western gorilla *(Gorilla gorilla gorilla*	Harassment and intimidation [11].	High level of sexual coercion via agonistic behaviour – displacement, physical aggression [11].	Low *Result in wounds is rare* [11].
Mountain Gorilla *(Gorilla beringei beringei)*	Display – threat [31].	High aggression; hits, bites, kicks and attacks [31], [93].	Low *Bite wounding extremely rare* [31].
Bonobos *(pan paniscus)*	Possible absence of sexual coercion [17], [21].	Possible absence of sexual coercion [17], [21].	Never *Males never force females into sexual contact* [17], [23].

Table 2B: Macaques

Species	*Most common form sexual coercion*	*Most extreme form sexual coercion*	*Occurrence most extreme form*
Rhesus macaques *(Macaca mulatta)*	Harassment - Chase and bite [55], [58]. Mate guard – female oestrus [20]	Threats, chases and biting – with an high level of aggression [59].	*Frequent d*uring reproductive period females [55], [58].
Tonkean macaques *(Macaca tonkeana)*	Mate guarding when female oestrus [20] and threats and attacks which prevent expressing preference for rival males [72]	Threats and attacks [72]	Aggression ore often towards females than towards other males [3]
Japanese macaques *(Macaca fuscata)*	Harassment - Punishment, chasing, herding [3], [60], [63], [64].	Coerce reluctant females into mating [60], [65].	*Frequency of chasing increased mating season* [59].

Stump-tailed macaques *(Macaca arctoides*)	Harassment - Threats, chases, and biting	Higher level of aggression in harassment [59].	*Increased aggression during breeding season* [59].
Long-tailed macaques *(Macaca fascicularis)*	Mate guarding – female oestrus [20]	Heavy physical assault: biting [73].	*Light physical assault: more often* *Heavy physical assault: rarely* [73].
Sulawesi crested black macaque *(Macaca nigra)*	Harassment [70].	N.A.	*N.A.*
Formosan rock macaque *(Macaca cyclopsis)*	N.A.	N.A.	*N.A.*
Barbary macaques (Macaca sylvanus)	N.A.	N.A.	*N.A.*

Table 2C: Baboons

Species	***Most common form sexual coercion***	***Most extreme form sexual coercion***	***Occurrence most extreme form***
Hamadryas baboons *(Papio hamadryas)*	Mate guarding – always [20].	Harassment - Threating, chasing, hairpulling, biting, grabbing (neck biting most common) [20].	High rates during take overs [20].
Chacma baboon *(Papio ursinus)*	Mate guarder – oestrus [20].	Harassment – threat, chase, sexual intimidation and attacks [19], [86]	*Swollen females- more injuries* [19], [86].
Olive baboon *(Papio anubis)*	mate guarding – oestrus [20].	Harassment – biting [59].	Frequently assault during feeding competition [86].
Guinea baboon *(Papio papio)*	Mate guarding – oestrus [20].	Aggressive interactions Fischer et al., 2017)	Not often [87]
Kinda baboon *(Papio kindae)*	Mate guarding – oestrus [20].	N.A.	*N.A.*
Yellow baboon *(Papio cynocephalus)*	mate guarding – oestrus [20].	N.A.	*N.A.*

Table 2: *Most prevalent form of sexual coercion used by different species. Also, the most extreme form of sexual coercion is noted down. This is sexual coercion which is linked to high aggression or physical harm. Animals are ranked from most sexually coercive towards least sexual coercive within a family. Some data was not available. The table is separated into 3 different families; A: Great apes, B: Macaques and C: Baboons.*

Table 3A: Great apes

Species	*Physical consequences*
Chimpanzee *(pan troglodytes)*	Attack and wounding female more frequent than other primate males [12], [17]. Brutal aggression can lead to severe wounds and stress [3], [12], [14].
Sumatran orangutans *(Pongo abelii)*	Direct cost of harassment and forced copulation is in the reduced foraging efficiency and time spend on unsolicited social interactions. additionally there is increased risk of disease transmission from mating with multiple partners [34]..
Bornean orangutan *(Pongo pygmaeus)*	Females are intimidated and harassed. However it does not lead to physical wounding[35].
Mountain Gorilla *(Gorilla beringei beringei)*	Bite wounding extremely rare [31].
Western gorilla *(Gorilla gorilla gorilla*	Aggression resulting in wounds is extremely rare [11].
Bonobos *(pan paniscus)*	Low level of aggression. No wounding reported due to sexual coercion [17]. There is a suspected absence of sexual coercion.

Table 3B: Macaques

Species	*Physical consequences*
Rhesus macaques *(Macaca mulatta)*	Incidents of wounding were involving punctures and/or cuts [59]. Wounds on the head. Females received most wounding during birth and mating season [66].
Japanese macaques *(Macaca fuscata)*	Numerous reports of severe sexual aggression, which can result in damage on the female. Many females in oestrus and pre-oestrus get wounds [10], [63].
Stump-tailed macaques *(Macaca arctoides*)	Incidents of wounding classified involving punctures and/or cuts [59]. Significantly more wounds on the head [59]. *Lower incidence of violence than rhesus monkeys* [67].
Long-tailed macaques *(Macaca fascicularis)*	Biting between member of an stabilised group was never seen to result in deep wounds, whereas biting between stranger caused extensive and deep wounds on a few occasions [73]. Females suffered 1,35 wounds per animal per period during heavy assault, compared to male receiving 1,56 and juveniles 0,29 wounds per animal. Indicating that males suffer greater wounding by other males than females [73]..
Sulawesi crested black macaque *(Macaca nigra)*	N.A. Low ranking males more aggressive towards females than high ranking males [70].
Tonkean macaques *(Macaca tonkeana)*	Females did not suffer any physical costs, nor did males use aggression to force reluctant females into copulation. No injuries or violent attacks reported to females [72].
Formosan rock macaque *(Macaca cyclopsis)*	N.A.
Barbary macaques (Macaca sylvanus)	N.A.

Table 3C: Baboons

Species	*Physical consequences*
Hamadryas baboons *(Papio hamadryas)*	Neck-biting rarely breaks the skin or produce blood. It does not seem to physically harm females in most cases. However, victims of frequent neck-biting in short time will become hairless and covered in wounds [20].

	Females appear to live in constant fear of aggression by males (Swedell & Schreier, 2009.
Chacma baboon ***(Papio ursinus)***	Females receive higher rates of aggression from males suffered more injuries [19]. No strong evidence that male attacks had substantial fitness costs to females [86]. Females rarely exhibit obvious injuries following an assault. Males seem to restrain themselves [86].. Although there have been reported: open cuts, punctures of skin, swelling and limping [19].
Olive baboon ***(Papio anubis)***	Direct female coercion high impact on mating success. This could explain the severity of male-female attacks in olive baboon population [86]. Females are bitten in neck, back and tail during aggressive interactions [59].
Guinea baboon ***(Papio papio)***	Male guinea baboons generally less aggressive than male chacma baboons towards males and females [87].
Kinda baboon ***(Papio kindae)***	*N.A.*
Yellow baboon ***(Papio cynocephalus)***	*N.A.*

Table 3*: Physical consequences of sexual coercion in different species. Animals are ranked from most physical harm to least. Some data was not available. The table is separated into 3 different families; A: Great apes, B: Macaques and C: Baboons.*

Table 4A: Great apes

Species	Average group size	Groups	Transfer
Bornean orangutan *(Pongo pygmaeus)*		Single male units [26]. Dispersed society [25]. Flanged males living solitary and subordinate unflanged males travel in small bands [22].	
Sumatran orangutans *(Pongo abelii)*		Dispersed society. Flanged males living solitary and subordinate unflanged males travel in small bands [22].	
Mountain Gorilla *(Gorilla beringei beringei)*	14-16 individuals [31]. Dispersal- Egalitarian [94].	One-male groups and multimale groups [31], [32].	Females travel between social groups, giving them the opportunity to choose among different males [31].
Western gorilla *(Gorilla gorilla gorilla*		One-male groups and multimale groups [31].	Females always disperse out of their natal group [90]. Male dispersal likely to be influenced by the distribution of females in social groups and by the extent of mating opportunities within their natal group [31].
Chimpanzee *(pan troglodytes)*	Up to 140[17] Dispersal- Egalitarian[94].	Multimale-multifemale communities [31].	Females frequently travel alone or small groups [12]. Immigrating males entering troop start as subordinates [10].
Bonobos *(pan paniscus)*	Up to 140, which form parties [17]. Dispersal- Egalitarian[94].	Multimale-multifemale communities [31]. Dispersed social system (like orangutans) [22]. *Strong female-female bonds* *Weaker male-male bonds* [17].	Immigrating males entering troops as subordinate, after several years dominant [10]. Great female relationships, therefore reduced tendency to travel alone [17].

Table 4B: Macaques

Species	Average group size	Groups	Transfer
Rhesus macaques *(Macaca mulatta)*	Resident-Nepotistic [94].	Multimale- multifemale groups [54]. Adult females typically outnumber adult males [54].	Immigrating males entering troops as subordinates. After several years attain dominant position (inside takeover) [10], [49], [50].
Japanese macaques *(macaca fuscata)*	Resident-Nepotistic [94].	Multimale- multifemale groups [52], [61].	Immigrating males entering troops as subordinates. After several years attain dominant position (inside takeover) [10], [49], [50].

		Exhibit social relationships that are intolerant or despotic [95].	
Stump-tailed macaques *(macaca arctoides*)	Resident-Nepostistic-Tolerant [94].	*Compared to rhesus monkeys they have more relaxed style* [67]. *Place greater emphasis on social cohesion* [67].	Immigrating males entering troops as subordinates. After several years attain dominant position (inside takeover) [10], [49], [50].
Sulawesi crested black macaque *(Macaca nigra)*	Resident-Nepostistic-Tolerant [94].	Large multimale-multifemale group [68]. *Highly socially tolerant* *Low level aggression + high tendency to reconcile* [68].	Males immigrate to new groups. They base immigration on relative fighting ability for potential higher rank [69].
Formosan rock macaque *(Macaca cyclopsis*	Resident-Nepotistic [94].		
Barbary macaques (Macaca sylvanus)	Around 30 animals [51]. Resident-Nepotistic [94].	Multimale-multifemale groups. With an balanced adult sex ratio [51]. Highly promiscuous mating system [51]. Males form coalitions [71].	Males 4-5 years old: are satellite males which sneak copulations [71]. Males 6-7 years: are peripheral males stay at edge of group during mating season [71]. Males 7>: established group member [71].
Long-tailed macaques *(macaca fascicularis)*	Group size variable. Between 10 – 34 individuals [50]. Resident-Nepotistic [94].	Group living primate [50].	
Tonkean macaques *(Macaca tonkeana)*	Resident-Nepostistic-Tolerant [94].		

Table 4C: Baboons

Species	***Average group size***	***Groups***	***Transfer***
Chacma baboon (Papio ursinus)	From dozen to roughly one hundred animals [74], [91]. Dispersal- Egalitarian [94].	Uni level: male dispersal. One sexually active leader [74]. Multimale-multifemale groups [74], [77]–[79]. polygynous mating system [75]. *Females form strong bonds, and are core of the group* [74], [77]–[79].	Males leave the group after they are fully grown[74], [76]. They will join another group [74], [77]–[79].
Kinda baboon *(Papio kindae)*	Resident-Nepotistic [94].	Uni level: male dispersal. One sexually active leader.	Males leave the group and join another [74], [77]–[79].

		Multimale-multifemale groups [74]. polygynous mating system [75]. *Females form strong bonds, and are core of the group* [74], [77]–[79].	
Yellow baboon *(Papio cynocephalus)*	From dozen to roughly one hundred animals [74], [91], [96]. Resident-Nepotistic [94].	Uni level: male dispersal. One sexually active leader. Multimale-multifemale groups [74]. polygynous mating system [75].	Males often immigrate during adolescence [74], [80].
Olive baboon *(Papio anubis)*	From dozen to roughly one hundred animals [74], [91], [96]. Resident-Nepotistic [94].	Uni level: male dispersal [74]. One sexually active leader. Multimale-multifemale groups [74], [77]–[79]. polygynous mating system [75].	Males often immigrate during adolescence [74], [80].
Hamadryas baboons *(Papio hamadryas)*	Temporarily aggregate into groups of several hundreds of individuals. size varies from 30-400 [74], [91], [97], [98]. Dispersal- Egalitarian [94].	Multi-level: based on one-male units [75]. Males are both main protector and main aggressor of their females [20].	Female-biased dispersal [74]. Females do not disperse voluntarily, but are rather coerced by males to change one-male-unit membership [74], [81]–[83].
Guinea baboon *(Papio papio)*	temporarily aggregate into groups of 100 – 300 individuals or even more [74], [97]. Resident-Nepotistic[94].	Multi-level: on one-male units [75]. Males strong bonds with high degree of male-male cooperation and high degree of spatial tolerance [74], [87]	Female-biased dispersal. Females freely transfer between units, parties and gangs [74], [81]–[83]. Male philopatry [74], [81]–[83].

Table 4: *Social trades in different species. The average group size, living community and male or female transfer is pointed out. The table is separated into 3 different families; A: Great apes, B: Macaques and C: Baboons.*

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Appendix I: Social trades

Group size / male:female ratio / social structure	Sexual dimorphism	Dominance establishment / Relative dominance	Mating
Wild Orangutan *(Pongo spp.) (Pongo)*			
Orangutans live in dispersed society [25]. Flanged males live solitary. Subordinate unflanged males, travel in small bands [22]. Adult sex ratio varies with the availability of fecund females, which is related to the female energetic status. This is affected by food availability [22]. The ratio of males to females is significant predictor of the degree of female resistance for both flanged and unflanged males ($p<0.01$). As the amount of males increases the amount of forced copulations seen by both flanged and unflanged males increases [22]. Significant correlation between forced copulations by flanged males vs. forced matings by unflanged males ($p<0.005$)[22]. Orangutans are divided into two species. These species are able to	There are two adult, sexually mature morphs: flanged and unflanged males[22], [92], [99]. Distribution of flanged and unflanged males depends on the locality[92] Flanged males very large (>80 kg) and secondary sexual characteristics [22], [100]. Flanged males have prominent fatty cheek, and a throat sac facilitating the long call vocalization [99]. Unflanged males smaller. They are comparable to females in their size and facial morphology. Unflanged males have lower \testosterone than flanged males. Unflanged males divided into 3 categories (small, medium and large) [22], [100].	Residential status and male rank within a given male 'type' is an important determinant of female choice[22]. Little interaction between females and males. When there is interaction it is in consortship and mating context [22].	Unflanged males: forced copulation Flanged males: consensual Females may benefit by resisting occasional matings (reduce cost multiple matings + reduction total mating duration) [22] Flanged males sire more offspring than unflanged males [101] Unflanged males only father offspring during periods of rank instability[100]. Females preferentially mate with unflanged males when conception risk is low, as an anti-infanticide tactic Unflanged males more commonly fathering offspring with nulliparous females, who receive less interest form dominant flanged males [41], [92], [100].

interbreed in captivity and produce fertile offspring[25].			
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Bornean orangutan *(Pongo pygmaeus)*			
Single male units [26] Non-gregarious species [34]. If they cannot maintain long consortship, other flanged males could sire offspring as well at any given time at a particular site, whereas unflanged males will be virtually excluded [92].	Body mass male / body mass female gives a sexual dimorphism of 2.2 [33]. Two flanged males for one unflanged male [92]. There are more flanged males in Bornean than Sumatran populations[92], [100]. Males divided into two morphological groups: subadult (unflanged) and adult (flanged). Adult males attain twice the size of sub adult males and are distinguished by pronounced secondary sexual characterises [34].	Adult males are almost invariably dominant to subadult males [34], [102].	Near ovulation females mated cooperatively only with prime flanged males who they encountered at higher rates. [35]. Females cooperate in majority of copulation attempts. Cooperative matings are significant more likely with flanged males than with unflanged males [92]. In general females mated most frequently with unflanged males than flanged males, but they did so exclusively when conception risk was low [35]. In Bornean orangutans females do resist a higher proportion of mating attempts by flanged males than Sumatran orangutans [92]. Female orangutan directs most preceptive mating behaviour toward the flanged males that are resident within her home range. Meanwhile unflanged males usually obtain mating by force [34], [102].

			Whether female resists depends not only on status and morph of the male, but also on factors such as female parity and the relationship between the partners [92]. Rate of fruit availability varies dramatically, therefore the rate of copulations may be explicitly tied to varying fruit production and thus study periods may show pronounced variation in the number of copulations [22].
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Sumatran orangutans (Pongo abelii)			
Obtaining a male bodyguard could protect females from coercion from other males [44]. Flanged males can afford to maintain longer consortship[92]. Nearly all adult female – male consortship occurred during periods of high fruit abundance [34].	Body mass male / body mass female gives a sexual dimorphism of 2.2 [33]. There are in the groups two unflanged males for one flanged male [92]	Flanged males are seen as adult males. The unflanged males are seen as subadult males [34]. Also referred to as Prime males for the flanged males and non-prime for the unflanged males [35].	Females cooperate in majority of copulation attempts. Cooperative matings are significant more likely with flanged males than with unflanged males[92]. Lower refusal rate of flanged males than in Bornean orangutans[92]. Non-dominant flange males are at a disadvantage compared to more agile unflanged males in acquiring matings [92]. Rates of copulation initiated by subadult males increased during months of high fruit abundance, and

			most mating attempts were directed toward females with weaned infants [34].
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Mountain Gorilla *(Gorilla beringei beringei)*			
Although they are classified as having a one-male mating system, approximately 50% of the groups contain two or more silverbacks. [31], [32]. The occurrence of both one-male groups and multimale groups leads to differences in behavioural strategies for both sexes [31] . Size group: 14-16 individuals – Kyugurilo group between 2000-2005 (2 silverbacks, 5 females + some juveniles and infants) [31] Females transfer between social groups multiple times in live, giving them the opportunity to choose among different males [31]. Males may either queue dominance position in multimale group or disperse upon themselves and try to attract females for own social unit. [31].	Body mass male / body mass female gives a sexual dimorphism of 1.7 [33]. Great sexual dimorphism: males weight 200 kg which is roughly twice the size of adult females [31]. Males ability to protect females one of key factors influencing female choice [31]. Obtaining a male bodyguard could protect females from coercion by other males [44].	Greater size males enables them to easily dominate females, therefore likely candidate sexual coercion [31]. Males can be viewed as aggressors and protectors of females. It indicates an opposing male's fighting ability that a female wishes to avoid, but at the same time measures the protective abilities of the male. [31]	Use aggression to discourage mating with other males within the group or to advertise his own qualities to other females and males [31]. Subordinate males more likely than dominant males to mate with subordinate females [32]. Mating harassment terminated copulations by subordinate males, but not those by dominant males [32].

Dispersal- Egalitarian [94]			
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Western gorilla *(Gorilla gorilla gorilla)*			
Nearly all Western gorilla groups contain one male [31] Male dispersal likely to be influenced by the distribution of females in social groups and by the extent of mating opportunities within their natal group [31]. Females dispersed out of their natal group before their first offspring, even if the dominant male is not their father [90]. Females have very weak social relationships with one another [103]. Females choice for high-quality males may be influenced due to the formation of their relatively rare social system, smaller group size may be more important for females than previously thought, which runs counter to the males' interest of having a high number of females [90].	Body mass male / body mass female gives a sexual dimorphism of 2.4 [33]. Extreme sexual dimorphism. It is the greatest sexual dimorphism in the great apes. In which males are a lot bigger and stronger than females [90].	In a multimale group males will either queue for dominance position or disperse upon maturity and attempt to attract females for a new social unit [31]. One of benefits of high dominance status is exclusive or high reproductive success through the monopolization of females [32]	Dominant males mate significantly more than subordinate males [32]. Dominant males sire approximately 85% of offspring in multimale groups [31], [104]. Increased male-male aggression during female oestrus [31]. Dominant males mate more with cycling adult and pregnant females [32].

Group size / male:female ratio / social structure	Sexual dimorphism	Dominance establishment / Relative dominance	Mating
Chimpanzee *(pan troglodytes)*			
Multimale-multifemale communities [31]. Immigrating males entering troops as subordinates and then attaining dominance only after several years (inside takeover). This is by necessity the mating system of male philopatric species such as chimpanzees bonobos and spider monkeys [10]. Communities up to 140 individuals which form temporary subgroups ('parties'). These parties fluctuate in size, composition and duration[17] Females frequently travel alone or in small groups [12]. Female chimpanzees mated more frequently with males that groomed them more. During oestrus females were groomed more frequently by males than at other times [42], [105]. Males groomed swollen females less as the availability of swollen females in the group increased [105], [106].	Body mass male / body mass female gives a sexual dimorphism of 1.3 [33]. Sex difference in age specific fertility. Males take longer to reach maximum fertility rate,. Additionally males attained a higher maximum fertility than females, followed by a steeper decline with age [41].	Every adult male is dominant to every female and the ability to dominate females is unrelated to his status in the male hierarchy [12]. Aggression amongst males prominent feature in chimpanzee's social life. Additionally females are as likely as males to be victims of male aggression [12]. Male rank was correlated with copulation rate, probably due to mate guarding by high-ranking males [107].	Females mate highly promiscuous with males [13], [41]. Males have higher copulation rate with females towards they are relatively more aggressive[3]. There is a preference for mating with dominant male [10], [13]. It is suggested that the females prefer high ranking males during periovulatory period. However, this could also be due to: that high ranking males were guarding females more closely to ovulation. Additionally, almost all female solicitations of adult males failed when higher-ranked males were nearby. An additional complication is that females may be resistant to male solicitations because they are wary of approaching a potential aggressor [12]. Females frequently travel alone or in small groups and regularly encounter potential infanticidal males in absence of the alpha. Thus even high-ranking males may not be able to offer reliable protection

High ranking males groomed swollen females less than lower ranking males [106]. Dispersal- Egalitarian[94]			from infanticide. Under these circumstances, the benefit of paternity confusion may be paramount. If that is the case there is only potential benefit of mating with high ranking males for good genes. [12]. Adolescent male appear to focus their reproductive efforts on young females. They were more likely to conceive with nulliparous or primiparous females [41]. Older males may rely on coalition to lengthen their reproductive career [41]. Promiscuous opportunistic mating typically occurs early in the female's cycle before her swelling reaches maximum tumescence, and is unlikely to result in fertilization. As she nears ovulation she will typically either participate in a possessive mating relationship (involved with alpha male) or form a consortship [9].
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Bonobos *(pan paniscus)*			

Multimale-multifemale communities [26]. Dispersed social system (such as orangutans) [22]. Immigrating males entering troops as subordinates and then attaining dominance only after several years (inside takeover. This is by necessity the mating system of male philopatric species such as chimpanzees bonobos and spider monkeys [10]. Many intergroup encounters (including sexual interactions between communities) [17]. Communities up to 140 individuals which form temporary subgroups ('parties'). These parties fluctuate in size, composition and duration[17]. Exhibit more frequent male-female and female-female associations. Least frequent male-male associations [17], [108]. Females have greater social interactions with each other. Therefore there is a reduced tendency for females to travel alone	Body mass male / body mass female gives a sexual dimorphism of 1.4 [33]. Females are on average 82,5% of the size of males.[30]. (similar to chimpanzees) Maximal sexual swelling not linked to highest chance of copulation [17]	Absence of male dominance, instead there is co-dominance. Meaning that some females have dominance over some males[17], [27], [28]. This alliance allows females to control access to food There is a strong tendency for females to maintain feeding priority [17], [28]. Female co-dominance increases due to core interactions between the sexes and as a consequence of all factors that increase the development of the hierarchy [27] The unusual level of female dominance may (at least partly) be due to the strong cohesiveness in grouping forming coalitions [29], [30] .	Sex occurs in a nonreproductive context. It is a social interaction, which can calm tensions [17], [28], [46]. Well-known genital-genital rubbing [45], [46].

and less disparity in male and female ranging behaviour[17]. There are weaker male-male bonds. Indicating that there are less male-male associations and therefore reduced importance of male coalitions for establishing and maintaining rank and defending territories[17]. Novel use of socio-sexuality. They use sexual behaviour to ease tension and defuse potential conflict [17], [23], [45]. Sexual interactions can involve individuals of all sex and age classes: it occurs between. Males (rump-rump rubbing), females (genitogenital-rubbing) and between immature individuals and adults [17], [45]. Genitogenital-rubbing appears to be characteristic of female *Pan paniscus* (bonobos) [17]. Dispersal- Egalitarian[94]			

2

3 **Other primate families:**

Group size / male:female ratio / social structure	Sexual dimorphism	Dominance establishment / Relative dominance	Mating

Rhesus macaques *(Macaca mulatta)*			
Multimale-multifemale groups. Adults females typically outnumber adult males [54]. Females will choose dominant protective males that can protect them from harassment by subordinate males [55] Males form special relationships ("friendships") with particular females, and males direct aggression toward females who threaten their friends or their friends' offspring [3], [56], [57]. Immigrating males entering troops as subordinates and then attaining dominant position after several years (inside takeover) is often seen [10], [49], [50]. Conciliatory tendencies more elevated within kin [109]. Resident-Nepotistic [94]	Adult males larger than adult females. Body mass male / body mass female gives a sexual dimorphism of 1.3 [33]. The intermediate degree of sexual dimorphism could provide females with greater freedom to exercise any preference they might have for mating with several mates [110].	Male dominance hierarchies [55]. Clear-cut linear formal dominance hierarchy as expressed in teeth-baring displays [67]. Female friends crucially help males achieve and maintain high rank [9], [57]. Females suffer higher rates of male attacks while in proximity to low-ranking males than while in proximity to high-ranking males [55]. Male rank is reportedly related to reproductive success [52]. Males suffer wounding significantly more often than females [59].	Unlikely that male attacks are ritualized displays enabling females to evaluate male quality. Rather **females choose mates independently of male dominance rank**, even though they could minimize costs by consistently choosing high-ranking males [55]. Not necessarily preference for dominant males in macaques for mating and number of copulations [10], [53].
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Japanese macaques *(macaca fuscata)*			
Multi-male/multi-female group structure [52], [61].	Adult males larger than adult females. Body mass male / body	Dominance rank not always significantly predict male mating success [60]. However, highest	Promiscuous mating pattern [52].

Immigrating males entering troops as subordinates and then attaining dominant position after several years (inside takeover) is often seen [10], [49], [50]. Exhibit social relationships that are intolerant or despotic [95]. Resident-Nepotistic [94]	mass female gives a sexual dimorphism of 1.4 [33].	ranking male was able to discriminate females nearing ovulation and to concentrate their mating effort, implying that the timing of ovulation was not concealed from them (in contrast to other males) [61] Male dominance rank did not always significantly predict male amating success or, when paternity was known, male reproductive success[60]. Number of copulation with ejaculation was positively correlated with male dominance rank, it was not correlated with number of offspring. Males could not choose ovulatory females as mating partners: the number of copulations with ejaculations with females during ovulatory weeks was not related to male's rank [52].	Paternity highest in dominant Japanese macaque males; here, male competitive efforts prove more successful than female mating preference [53], [62]. The alpha male seemed able to monopolize most female matings [61] Both female proximity maintenance towards males and male aggression were correlated with increase in fertile matings. Most aggression appear to be by-product of increased time spent in proximity of female. But some aggression is sexual coercion. Males have higher copulation rate with females towards they are relatively more aggressive [3], [60]. Not necessarily preference for dominant males in macaques[10], [53]. It has been reported that the highest ranking males have long, and in some cases exclusive consortship, while lower ranking males tend to have shorter, sometimes covert consortship.

			These longer consortship increase the probability of insemination [64]. Females can reject the mounting attempts of both dominant and subordinate males[60]. They cannot assume the proper mounting position or by walking away [60], [64]. Females showed some indications of preference for mates likely to retain or attain high rank in the future [111]
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Stump-tailed macaques *(macaca arctoides*)			
Immigrating males entering troops as subordinates and then attaining dominance only after several years (inside takeover) is often seen in number of macaques [10], [49], [50]. Compared to rhesus monkeys the stumptails have a more relaxed style. They place great emphasis on social cohesion than the rhesus monkeys [67]. Resident-Nepostistic-Tolerant [94]	Adult males larger than adult females. Body mass male / body mass female gives a sexual dimorphism of 1.5 [33].	Clear-cut linear formal dominance hierarchy as expressed I teeth-baring displays [67]. Increased wounding in the birth season under captive conditions suggests that the pattern of increased wounding reported during the breeding season under free ranging conditions may reflect xenophobic responses to immigrating males, rather than direct male-male competition for estrous females [59]. Males suffer wounding significantly more often than females [59].	They perform sneaky copulations, they do not exhibit many of the potentially more costly traits [10].

Group size / male:female ratio / social structure	Sexual dimorphism	Dominance establishment / Relative dominance	Mating
Sulawesi crested black macaque *(Macaca nigra)*			
It is a large multimale, multifemale group, and are highly socially tolerant. Characterized of low level of intense aggression and high tendency to reconcile [68]. Exhibit social relationships that are more tolerant or egalitarian [95]. Organization similar to multimale groups in other macaque species, rather than the egalitarian social organization described for female Sulawesi macaques [70] There are individual differences in activity budgets of adult males and females in time spent moving, resting, feeding and socializing that may reflect differences in reproductive strategies of males versus females [112]. Males immigrate to new groups. They base their immigration strategy on relative fighting ability and thus potential rank in the new group, which lead to potential reproductive benefits [69].	Adult males larger than adult females. Body mass male / body mass female gives a sexual dimorphism of 1.8 [33].	Linear and transitive dominance hierarchy. High-ranking males are socially attractive [70]. The dominance rank correlated strongly with percentage of time near more than four neighbours, frequency of grooming received from adult females and percentage of time with an adult female as nearest neighbour [70]. Aggressive interactions between males involved closely ranked opponents significantly more often than males with large rank distances [70].	Adult females sexually solicited high-ranking males more often than low-ranking males [70]. High-ranking males received more grooming from adult females, which indicates that high-ranking males are attractive social partners for females. Additionally they copulated more frequently with receptive females than low-ranking males do [70]. Female primates often mate at times when they are not ovulating, males that mate more frequently, but at the wrong times will not necessarily sire more offspring [70].

Resident-Nepostistic-Tolerant [94]			
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Formosan rock macaque *(Macaca cyclopsis)*			
	Adult males larger than adult females. Body mass male / body mass female gives a sexual dimorphism of 1.2 [33].		
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Barbary macaques (Macaca sylvanus)			
Around 30 animals living in a highly promiscuous mating system [51]. Multimale-multifemale groups. With an balanced adult sex ratio [51]. Male intervened more often in dyadic conflicts in which related opponents were involved and supported related opponents more than unrelated opponent. Close kin supported each other more often than distant kin [71]. Some evidence for reciprocal support was found. However, reciprocity was probably by-product of targeting the same individual for dominance [71].	Adult males larger than adult females. Body mass male / body mass female gives a sexual dimorphism of 1.5 [33].	First there is an age dependent hierarchy, due to physical differences a 7 year old male dominates a 6 year old male. Later on older males are often subordinate to young adults in dyadic fights and therefore depend on coalition partners during conflicts [71]. Males preferably initiated interactions with males that were dominant to them. Males also initiated more interactions with males close in rank to themselves than distantly ranked males [114]. Male barbary macaques seem to intervene more often to stabilize and less often to improve their rank. Although data has revealed that kin	Male rank is related to reproductive success [52]. Males are expected to compete for mates mainly via rank relations [71]. Barbary macaques have a promiscuous mating system [71]. Between 4-5 years of age, males sneak copulations or disturb matings by others (satellite males), at 6-7 years of age males pursue a low risk strategy by staying at the edge of the group during mating season (peripheral males) [71]. Results been found that males use grooming as payment for mating, broadly assessing grooming-mating patterns cannot be solely explained

Coalition formation among nonkin is best interpreted as cooperation, based on self-interest [71]. Around 7 years old the males become established group members [71]. Males form coalitions [71]. Males groom females with whom they are mating more frequently and for longer periods than other females. And the relationship between grooming and mating remains significant in both sexual and nonsexual context. Additionally, females groomed males with whom they were mating more frequently and for longer periods than other males [113]. Resident-Nepotistic [94]		support, reciprocal support and cooperative support were all involved in coalition formation among male Barbary macaques [71].	by a male-driven grooming-for-mating exchange [113].
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Long-tailed macaques *(macaca fascicularis)*			
Group-living primate [50]. Group size variable. Between 10 – 34 individuals [50]	Adult males larger than adult females. Body mass male / body mass female gives a sexual dimorphism of 1.5 [33].	Male dominance is never contested by a female unless a male accidently frightens and infant or female with an infant [73].	Male rank is related to reproductive success [52].

Group-living primates tend to compete for access to food and for spatial positions affording enhanced safety from predation [50]. Female lifetime reproductive success depended on dominance rank and group size. High-ranking females significantly more likely than low-ranking females to give birth again when they did have a surviving offspring born the year before [50]. Resident-Nepotistic [94]		Lower ranking group members will get a more peripheral spatial position [50]. Maternal dominance affect their reproductive success. High-born male were more likely to become top-dominant (in another group) [50] There is a clear dominance hierarchy among females [50]. Daughters achieve dominance rank positions similar to their mother, a close correlation between the lifetime reproductive success of mother and daughter [50].	
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Tonkean macaques *(Macaca tonkeana)*			
Female advertise the timing of their ovulation. This female sexual advertising promotes indirect mate choice via competition between males [72]. Conciliatory tendencies similar for related and unrelated partners [109]. Resident-Nepostistic-Tolerant [94]	One of the greatest sexual dimorphism in macacas. Adult males larger than adult females. Body mass male / body mass female gives a sexual dimorphism of 1.7 [33].	Males very dominant over females.	Females mainly mated with dominant males [72]. Dominant males exerted mate guarding to coerce swollen females, and the top-ranking male fathered two-thirds of total offspring [72]
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**

Chacma baboon *(Papio ursinus)*			
Uni-level; male dispersal. One sexually active leader male and a variable number of females. Sometimes a follower male [74]. Mating system is polygynous [75]. Multi-male-multi-female groups. In these groups the females form the core. Related females form strong bonds. Meanwhile males leave the group and join another [74], [77]–[79]. Males leave natal group until after they are fully grown [74], [76]. In females, related individuals(matrilines) typically occupy adjacent ranks. For the females their female kin constitute the most important social partner [74], [77]–[79]. Females that form strong social bonds with other females live significantly longer than females who form weaker and less stable relationships [78]. Male alliances absent [74]. Group size: ranges from dozen to roughly one hundred animals [74], [91].	Males bigger than females [74], [91] . There is a huge sexual size dimorphism [86]. Body mass male / body mass female gives a sexual dimorphism of 2.1 [115]. Obtaining a male bodyguard could protect females from coercion from other males [44]. Female develops sexual swelling of the anogenital region when fertile. Max swelling typically coincides with ovulation [74], [116].	Clear hierarchies among males and females can be discerned based on aggressive interactions (threats, chases and physical aggression, as well as signals of submission) [74], [77]–[79] . High rank baboons monopolize access to conceiving females [79]. All males outrank all females. Sometimes after a male loses he could target a female either to relieve stress or to focus attention away from himself [86], [117]. Steep dominance hierarchies (despotic) [74]. Males form linear dominance hierarchies that are stable over the short-term, but rank reversals are common [86]. Females maintain close bonds with matrilineal kin, forming stable dominance hierarchies based on matrilineality [78], [86].	Loud copulation calls by females, this is to promote sperm competition, which in turn incite male-male competition (enables paternity uncertainty + high quality sperm) [74], [118]. Females interact and mate with several males in the group [75]. High-ranking males generally experience higher mating success than lower-ranking ones. [19], [74]. High-ranking males generally experience higher mating success than lower-ranking ones. Alpha male obtained 34% of all conceptions [119]. *This is more pronounced in chacma baboons (48%) than in olive baboons (25%) or yellow baboons(34%)*[74], [84], [88], [119]. Copulation calls by females and males [75].

Dispersal- Egalitarian [94]			
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Kinda baboon *(Papio kindae)*			
Uni-level; male dispersal. One sexually active male leader and a variable number of females. Sometimes a follower male [74]. Mating system is polygynous [75]. Multi-male-multi-female groups. In which related females form the core, while males leave the group and join another [74], [77]–[79] Males most significant grooming partner for females [74], [75]. Grooming is mainly driven by male partner occurs at all stages of female's reproductive cycle [120] Resident-Nepotistic [94].	Males bigger than females [74]. Body mass male / body mass female gives a sexual dimorphism of 1.8 [33]. They have relative to their size large testis volume compared to other baboon species [74], [120]. Female develops sexual swelling of the anogenital region when fertile. Max swelling typically coincides with ovulation [74], [116]. Kinda females exhibit small sexual swelling	Clear rank hierarchies among males and females can be discerned based on aggressive interactions (threats, chases and physical aggression, as well as signals of submission) [74], [77]–[79].	Females give inconspicuous calls during mating [74], [75]. Interact and mate with several males in the group [75]. High-ranking males generally experience higher mating success than lower-ranking ones. [19], [74]. High-ranking males generally experience higher mating success than lower-ranking ones *This is more pronounced in chacma baboons than in olive or yellow baboons* [74], [84]. Copulation calls by females and males [75].
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Yellow baboon *(Papio cynocephalus)*			
Uni-level; male dispersal. One sexually active leader male and a variable number of females. Sometimes a follower male [74].	Males bigger than females [74], [91] Body mass male / body mass female gives a sexual dimorphism of 1.8 [33].	Clear hierarchies among males and females can be discerned based on aggressive interactions (threats, chases and physical aggression, as	Females interact and mate with several males in the group [75]. High-ranking males generally experience higher mating success than lower-ranking ones. [19], [74].

Mating system is polygynous [75]. Multi-male-multi-female groups. In which related females form the core, while males leave the group and join another [74], [77]–[79]. The males often immigrate during adolescence [74], [80] In females, related individuals (matrilines) typically occupy adjacent hierarchical ranks. For the females their female kin constitute the most important social partner [74], [77]–[79]. Male alliances common [74], [121], [122] Group size: ranges from dozen to roughly one hundred animals [74], [91], [96]. Low reproductive skew, with alpha males siring around 1/3 of offspring [41], [88] Resident-Nepotistic [94]	Female develops sexual swelling of the anogenital region when fertile. Max swelling typically coincides with ovulation [74], [116]	well as signals of submission) [74], [77]–[79]	High-ranking males generally experience higher mating success than lower-ranking ones. Alpha male obtained 34% of all conceptions [88]. *This is more pronounced in chacma baboons (48%) than in olive baboons (25%) or yellow baboons(34%)*[74], [84], [88], [119] Male coalitions may be able to take the female away from a dominant male, in order to mate with them [74], [121] Growing evidence from genetic analyses of paternity in primates indicate that high-ranking males do indeed often experience higher paternity success than low-ranking males [88]. Copulation calls only by females [75].
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Olive baboon *(Papio anubis)*			
Uni-level; male dispersal. One sexually active leader male and a	Males are bigger than females [74], [91]. Body mass male / body mass	Clear hierarchies among males and females can be discerned based on aggressive interactions (threats,	Females interact and mate with several males in the group [75]. High-ranking males generally

variable number of females. Sometimes a follower male [74]. Mating system is polygynous [75]. Multi-male-multi-female groups. In which related females form the core, while males leave the group and join another [74], [77]–[79]. The males often immigrate during adolescence[74], [80] Females preferentially mate with their 'friends', and male-female bonds may thus function as a form of mating effort [119]. It is common in savannah baboons that recently immigrant males can acquire the alpha position (outside takeover) [10] In females, related individuals(matrilines) typically occupy adjacent ranks. For the females their female kin constitute the most important social partner [74], [77]–[79]. Male alliances common [74], [121], [122]	female gives a sexual dimorphism of 1.9 [33]. Female develops sexual swelling of the anogenital region when fertile. Max swelling typically coincides with ovulation [74], [116] Olive baboons exhibit large sexual swelling[74]	chases and physical aggression, as well as signals of submission) [74], [77]–[79] However the hierarchies are less clear than in chacma or yellow baboons. Additionally, the reproductive activity is less closely tied to male dominance ranks[79] Females remain in their natal groups throughout their lives and form matrilineal dominance hierarchies [79]	experience higher mating success than lower-ranking ones. Alpha male obtained 25% of all conceptions [119]. *This is more pronounced in chacma baboons(48%) than in olive or yellow baboons(34%)* [74], [84], [88], [119] Male coalitions may be able to take the female away from a dominant male, in order to mate with them [74], [121]. Copulation calls by females and males of some populations [75].

Group size: ranges from dozen to roughly one hundred animals [74], [91]			
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Hamadryas baboons *(Papio hamadryas)*			
Multi-level; female-biased dispersal [74]. Leader and follower males tend to be maternally related, which is in line with low dispersal rate. [74], [123]. Mating system is multi-level, based on one-male-units [75]. It is a multi-layered organization, ie. Smaller social units are nested within a larger one [97], [98]. Hamadryas females do not disperse voluntarily, but are rather coerced by males to change one-male-unit membership [81], [91]. Males show intense interest in adult females regardless of latter's reproductive state [85]. Females also more likely to be related within the population than expected by chance[74], [123].	Males bigger than females [74], [91]. Body mass male / body mass female gives a sexual dimorphism of 1.8 [33]. Female develops sexual swelling of the anogenital region when fertile. Max swelling typically coincides with ovulation [74], [116].	Perhaps the most male-dominated society across the primate order [20].	Males have a higher copulation rate with females towards they are relatively more aggressive than with females they are less aggressive towards. [3], [20]. Copulation calls by females and males [75].

Male hamadryas baboons are both the main protectors and the main aggressors of their females [20]. Females likely benefit from this association with a protective male because it increases the survival prospect of their offspring[20], [31], [85]. The relationship between male leader and female can be described as permanent consortship [20], [85]. Temporarily aggregate into groups of several hundreds of individuals. Sizes groups can vary from 30 to over 400 [74], [91], [97], [98]. Females-biased dispersal. Females do not disperse voluntary but rather are coerced by males to change one-male-unit membership, usually several times in their lifetime [74], [81]–[83]. This could contribute to weaker bonds the bonds among females [20], [124]. Dispersal- Egalitarian [94]			
Group size / male:female ratio / social structure	**Sexual dimorphism**	**Dominance establishment / Relative dominance**	**Mating**
Guinea baboon *(Papio papio)*			

Multi-level; female-biased dispersal [74]. Several units, three to five, (comprising a primary male, with occasional secondary males) form 'parties' with females. 2-3 parties constitute a 'gang' within a larger community [74], [87]. Some but not all males are highly related. *Suggestion kin promotes male tolerance* [74], [125] Mating system is multi-level, based on one-male-units [75]. Males maintain strong bonds with high-degree of male-male cooperation and a high degree of spatial tolerance [74], [87] Temporarily aggregate into groups of several hundreds of individuals, up to 300 or even more individuals in a multi-layered organization [74], [97]. It is suspected to be characterized by male philopatry and female dispersal [74], [81]–[83]. Females freely transfer between units, parties and gangs[74], [126]. There is female-biaed dispersal [81], [83] .	Males are bigger than females [74], [91] . Body mass male / body mass female gives a sexual dimorphism of 1.9 [33], [91]. Female develops sexual swelling of the anogenital region when fertile. Max swelling typically coincides with ovulation [74], [116]	Aggression between males rare. Therefore not possible to discern a dominance hierarchy with certainty [74], [128]. High degree of male-male cooperation and tolerance [87]. Do not form linear dominance hierarcies. The dominance relationships are generally less consistent [87]	Copulation calls by females and males [75]. Females mate with multiple males, though there is considerable skew in favor of the high ranking males [87] Each female was mainly found in close proximity (<2 m) of one specific male. Grooming between females and males was mostly confined to the primary male [87]. Of all the copulations observed, 98.6% occurred between females and their respective primary male [87]. Primary males more inclined to initate interactions than females were, as they initated 60% of all interactions [87]. Females maitnan rather exclusive relationships with a specific male during any point in time, while any given male may be affiliated with a varying number of females [87].

Females don't have inherent motivation to emigrate, they are 'transferred' through the use of physical aggression between males [20], [127] Some but nog all strongly socially bonded male are highly related, and populatin genetic and behavioural evidence indicate femle-biased dispersal [87] Resident-Nepotistic[94]			

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6 Appendix II: Sexual Coercion

Forms of Sexual coercion	Degree of sexual coercion	Forms of aggression	Intensity aggression	Physical and physiological consequences	Female counter strategy
Wild orangutan *(pongo spp.)*					
Mainly Direct: forced copulation[22]. - Females mate cooperatively with the flanged males[92], [102] Rarely harassment - within context unwanted mating attempts*(nonpreferred males)* [22] Infanticide not yet observed in wild orangutangs[101]	Most extreme cases of sexual coercion in the animal kingdom [9], [22]. Only force for direct coercion in the form of forced copulation [22]. In some orangutang populations more than 50% copulation are forced [12], [22].	During mating: Hitting and biting[22].	Can be very high. Aggression highly correlated with female resistance to mate [22]. No aggression outside mating context [22].	Extremely low. Relatively low intensity of struggles characterized by forces consort copulation. Females did not gain sustain injuries or wounds as a result of rape, despite the high rates of forced copulation [25], [47]. Males use force as a way to accomplish copulation but do not intentionally wound females. Severe wounding was never reported [22].	*Bornean:* Female orangutans modify their behaviour in accordance with conception risk [35]. Near ovulation females mate with prime flanged males. When conception risk was low, willingness to associate and mate with non-prime males increased [35]. This helps with reducing infanticide risk. *Sumatran*: Females that maintain spatial association with adult males, either via consortship or by non-mating temporary parties, received lower rates of harassment [34].

Forms of Sexual coercion	Degree of sexual coercion	Forms of aggression	Intensity aggression	Physical and physiological consequences	Female counter strategy
Bornean orangutan *(Pongo pygmaeus)*					
Mate guarding. Flanged males less successful at mate guarding[92]. Unflanged males perform forced copulations [35]. Females receive aggression, intimidation, harassment and infanticide [35]. Mating conflict may be defined as a male's attempt to increase the probability of a copulation while a female simultaneously attempts to reduce that probability [34]. Females receive aggression frequently, even from males with whom they mate preferentially [35]..	High level of forced copulations [35].	Aggression and physical restraint. This were in the form of chasing, pulling and restraining the female [35]. This were more often performed by prima males than non-prima males.	More aggression or physical restraint in their mating interactions by prima males. This suggest that female preference could instead be the result of intimidation [35]. Females even receive aggression from males that they preferentially mate with [35]. Prime males used some form of aggression n 86% of their copulations, including matings with no resistance and even with proceptive female initiations [35].	Aggression in mating context has not been reported to lead to physical wounding of females [35].	Female orangutans modify their behaviour in accordance with conception risk [35]. Near ovulation females mate with prime flanged males. When conception risk was low, willingness to associate and mate with non-prime males increased [35]. Females concealed ovulation. Additionally females resist matings, which reduced copulation time. This can also function as mechanism for mate selection [35]. These techniques function as an infanticide avoidance mechanism [35].

Forms of Sexual coercion	Degree of sexual coercion	Forms of aggression	Intensity aggression	Physical and physiological consequences	Female counter strategy
Sumatran orangutans *(Pongo abelii)*					
Mate guarding Flanged males may be more effective at mate guarding than their Bornean counterparts because they can afford to maintain longer consortship[92], [129]. Different tactics between flanged and unflanged males[34]. Flanged males form consortship and mate guard the female [34]. Unflanged males force copulation [34]. Sexual harassment is the predominant feature of the mating strategy that subadult males pursue [34]. Harassment increased during months of high fruit abundance. Females also incur	High sexual coercion by unflanged males via forced copulation [34].	Forced copulation is seen as harassment. It also contains coercive consortship under which the forced copulation occurs.	Females that have weaned infants receive the most frequent harassment [34].	Direct cost of harassment may include reduced foraging efficiency due to time spend on unsolicited social interactions, poor condition resulting from proximity to male-male competitive interactions and increased risk of disease transmission from mating with multiple partners [34]. Consortship with flanged males presumably also exact cost due t the effect of body size differences on foraging behaviour; and feeding competition is the primary explanation for solitariness in the large-bodied frugivores species [34].	Females that maintain spatial association with adult males, either via consortship or by non-mating temporary parties, received lower rates of harassment [34]. Female initiation of protective services by adult males is one social tactic that females employ to reduce sexual harassment [34]. Females with weaned infants maintained consortship with resident and non-resident adult males nearly exclusively during months of high fruit abundance [34]. Significant more copulation attempts by unflanged males failed

increased harassment as infants mature and the probability of resumed ovarian cycling rises[34].					when females consorted with flanged males, resident or non-resident [34]. Consorting females were presumably fertile, which implies that they would have been subject to higher rates of harassment [34].
Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Mountain Gorilla *(Gorilla beringei beringei)*					
Coercive behaviour through **display** rather than physical aggression, possibly due to great sexual dimorphism[31]. Display behaviour demonstrate male's health, which would facilitate female choice rather than coercive behaviour [31], [86]. Mating harassment was initiated and	Great sexual dimorphism. Therefore any aggressive behaviour can be seen as intimidating threat of force [31], [43]. The harassment usually consisted of mild aggression [32].	Males may express aggressive behaviour that may include: strutting displays and chest-beating. Estimate 60-78% linked to male mating tactics [31], [130] No association between male aggressive display and copulation, suggesting that male display are not a form of courtship aggression aimed at influencing mating in	Majority aggression is moderate – **showing displays** [31]. Mild aggression: grunting screaming Moderate aggression: chest-beating strut-walking as well as lunges toward the recipient High aggression: physical contact; hits, bites, kicks and attacks[31], [93].	Bite wounding is extremely rare. However, severe bite wounds found on the head of female before dominance turnover [31]. Increased levels of cortisol measured in females which are sexually receptive[7].	Females often show submissive behaviour, non-aggressive vocalizations, toward silverbacks, which suggests that females seek to minimize aggressive behaviour [31], [43], [131]. It has been reported that females will mate with multiple mates. This is also observed during the probable time of conception [32].

received by both dominant and subordinate males [32]. Mating harassment occurred infrequently (between 22%-30% of the matings) [32]. In multimale groups, silverbacks might use aggression towards females to discourage them from mating with other males within the group [3], [31] or to advertise his own qualities to other females and males [31], [86].		the short term [43]	In one-male and multimale groups recent female immigrants received higher rates of aggression than long-term residents [31], [43], [131]. One-male group: Lower frequency of aggression by males towards oestrous females (they have no choice to mate) compared to multi male groups [31], [103]. In multi male groups the males are not significantly more aggressive towards the females. However, the females do receive a higher overall rates of aggression due to the increased amount of males [31]. Lactating females receive the least amount of aggression		The harem-type grouping pattern of mountain gorillas is hypothesized to provide protection for females against potentially infanticidal outsider males. Additionally it represent a form of long-term mate guarding of females by males [32].

			by males [20], [31]		
Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Western gorilla *(Gorilla gorilla gorilla*					
Harassment and intimidation [11]. Herding was significantly more likely to occur when the group contained a potential migrant female [11] Males use sexual coercion to prevent females to transfer, primarily by herding them away from opposing group and/or exhibiting higher rates of aggression towards those females [11], [90] 64% of the male agonistic behaviours towards females were considered potential evidence of sexual	Higher degrees of sexual coercion when females approach opposing groups [11], [90].	Agonistic behaviour can include displacements, aggressive vocalizations, displays and physical aggression [11]	Migrant females received agonistic behaviour at a statistically significantly higher rate than other adult females[11]. Females receive significant higher rate during intergroup encounters than at other times [11]. Females in larger groups received less aggression from the silverbacks than those in smaller groups [11], [90]. Rate of aggression performed by silverbacks was significantly correlated with body length, which suggests that	The costs of sexual coercion can include physiological and energetic costs, physical injuries, or in extreme cases infanticide [11], [48]. Agonistic behaviour often takes the form of display and physical aggression resulting in wound is rare [11]. There are some reports of females being wounded, but it was impossible to measure exact impact or to assess level of stress in females [11].	Females mate exclusively with the same male before and after conception. OF this it can be concluded that it appears to be a strategy by which high—ranking pregnant females attempt to minimize male interest in other females, while reinforcing her own status and potentially delaying conception in others [89]. Additionally it is thought that female dispersal is a counter strategy against sexual coercion. It will counter the risk of infanticide through female choice for better protector males. Additionally it will also reduce the

coercion and/or courtship [11] Male-to-female agonistic behaviour is consistent with **sexual coercion and/or courtship** as an explanation, but **unable to distinguish** between these two male mating strategies [11].			smaller males were more aggressive [11].		impact of feeding competition or to avoid predators or outsider males [90].
Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Chimpanzee *(pan troglodytes)*					
Mainly: indirect *(sequestration, herding and punishment)* Rarely forced copulation (direct)[22]. Males can usually force an unwilling female to consort with him through the effort of aggressive displays to induce her to follow him, he will eventually attack her[9], [12], [38], [39].	Direct coercion: Forced copulation rarely occurs in chimpanzees.. primarily because females rarely exhibit extreme resistance to male solicitation[12] Conditioning aggression (hypothesis): 'fearful respect' will cause females to comply with male demands in future mating	Aggression includes: hits, kicks, slaps, pounding, dragging and biting[36], [37]. Females suffer charges, chases or physical attacks from individual males at a mean rate of 0.017 times per hour [7]. Most episodes of male-female aggression occurred without physical contact	Intensity of aggression varies dramatically. The female fecundity was a strong predictor of received aggression [12], [36]. Aggression was mainly directed towards oestrous females [22]. Swollen females received more aggression than not swollen females [42].	Most cases of male-female aggression occurred without physical contact [12]. Male chimpanzees attack and wound females more frequently than many other primate males do [12], [17]. Female chimpanzees experience relatively brutal aggression that can lead to severe wounding and stress	Females showed submission in 96% of the cases (fleeing, emitting sounds of distress or submissive vocalisation Females were described retaliating against adult males 5% of the time (chasing or attacking), in contrast to male aggression female reprisals never involved more than a quick hit or slap and were usually

Herding: Males regularly practice coercive mate guarding to oestrous females [7], [12], [40], [41] Punishment: Regular, apparently unprovoked attacks on anoestrous cycling females might represent male intimidation and might specifically function to dissuade future resistance to the establishment of consortship [9], [12], [38] Males intent not to overcome female mating reluctance, but to limit female promiscuity. **Because herding an punishment are generally accompanied by male aggression against rival males, they are expected to involve primarily high-ranking males** [12]	situations. Supported by the fact that females initiated periovulatory copulations most frequently with the males who had been most aggressive toward them throughout their cycles [12]. The aggression will make females more likely to mate with them and/or less likely to mate with other males [7], [12].	Direct charges – 65% Attacks 35% [12].	Noncycling and nulliparous females receive less male aggression than cycling mothers do[12] Some attacks did little harm (some kicks and slaps). Other attacks more vicious, incorporating extended episodes of hitting, kicking, biting, dragging female, lifting female and slamming her into the ground, jumping up and down of female's back and often a combination of two or more of these behaviours [12]. 9% of the observations more than one male simultaneously directed aggression at a single female. [12].	[3], [12], [14]. Wounding regularly occurs [22]. Soft tissue damage most common result of male attack, but skeletal wounding appears to occur at remarkably high rates in some populations [12], [14]. Occasionally takes severe forms, such as prolonged beating with fists, feet or branches. [12] Females can be hurt or occasionally killed by extra community males, such aggression is rare [12] There is elevated female cortisol excretion measured in reproductive context. Such increase was correlated with fecundity [7], [12]. Cycling parous females	accompanied by female submissive behaviour [12].

Direct coercion, forced copulation, involves force to overcome female resistance to mating. **It is expected to involve primarily nonpreferred or low-ranking males** [12]. Repeated aggression, sexual intimidation, toward cycling females makes them more likely to mate with them around ovulation. It is shown that aggression by high-ranking males toward females during their non-swollen periods was positively associated with likelihood of paternity. [8], [19], [107].				have higher levels of urinary cortisol than cycling nulliparous females. There were elevate levels cortisol during oestrous period, compared to periods of lactational amenorrhea. Nulli parous females showed no difference on oestrus versus non-oestrus days [7], [12].	
Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Bonobos *(pan paniscus)*					
Males have not been reported to employ coercive aggression	No excessive use of force[22]	No physical strength use to force sexual contact[17].	Low level of aggression within and between groups for both males	No wounding due to sexual coercion, due to lack sexual coercion	The reduction of the pressure from sexual coercion in females is

against females in the immediate context of courtship. The scarcity of coercive mating could be due to the risk of retaliation from females who are supported by other females and males. [17], [21]. Females are not coerced into matings or consortship [30]. **Suggested that sexual coercion is absent in bonobos** [17] Males generally performed strong advances toward females during periods of high excitement, but they never used their physical strength to force females into a sexual contact [17], [23]. Female alliances causes to inhibited male sexual coercion. Males therefore benefited	Male never use their physical strength to force females into sexual contact[17]	No intimidation to improve future copulation[17]. No aggression to discourage females from mating other males[17].	and females, compared to chimpanzees [17]. Intensity did not differ significantly between males and parous females and males and nulliparous females [17].	[17]. There are cases of males being severely wounded by one or several females [30].	due to the tendency of bonobos to mask the timing of ovulation. This was eventually responsible for the relaxed social conditions that allowed the evolution of 'communication sex' [28]. Some 'sexual coercion' by females towards males has been reported – not in the strictest sense, in which there are beatings and/or forced copulation, but there is one female in particular that makes very strong advances to males for oral or manual stimulation [17]. Aggression by females against males is a response to male coercion. Females direct aggression against approaches by

less from being dominant over other males and more by being socially attractive to females (grooming and protection) [28].					unwanted males. Towards males they have friendly relationship they will not show aggression [21].

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Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Rhesus macaques *(Macaca mulatta)*					
Only mate guarding when females are in oestrus [20] They frequently chase and occasionally bite oestrous females [55], [58]. Infanticide is rare [59].	Females suffer higher rates of male attack while in proximity to low-ranking males than while in proximity to high-ranking males [55], [58].	Males punish females that attempt to mate with subordinate male s[10]. Threats, chases and biting [59].	There are seasonal varying levels of aggressive behaviour [66]. High levels of aggression and social instability during the fall reproductive period [66]. Male aggression as frequent or more often towards females than towards other males [3]	Incidents of wounding were classified involving punctures and/or cuts and slashes. Slashes and cuts were significantly larger number of wounding incidents than punctures were [59]. Significantly more wounds on the head [59]. Females receive the most wounding during the birth and mating	

				season. This was research in which they studied wounds that were at least 4 cm in lengths [66]. In the birth season the most females died [66]	
Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Japanese macaques *(macaca fuscata)*					
Punishment, chasing. herding do occur [3], [60], [63], [64]. Forced copulation does not occur [60]. Harassment may occur in the form of possessive following [60], [64]. Only mate guarding when females are in oestrus [20]. Male to female aggression during the breeding season appeared to be a side	High ranking males closely following oestrous females from 1 to 7 days, preventing males from approaching [60]	Males punish females that attempt to mate with subordinate males[10] Males use aggression to coerce reluctant females into mating [60], [65]. This results in female proximity maintenance and an increase in mating and time in proximity [60].	Male aggression toward females did not vary significantly across male rank categories. Although there was tendency for top ranking males to behave more aggressively toward their partners than other males did [111] Male aggression as frequent or more often towards females than towards other males [3]. Males more likely to act aggressively toward periovulatory mating partner than toward	There are numerous reports of severe sexual aggression, which can result in damage on the female [10], [63]. Many females which are in oestrus or pre-oestrus are attacked and get wounds [65].	Female proceptive behaviour during the fertile phase of the ovarian cycle, suggesting that female behaviour did not clearly signal the probability of conception [61]

effect of time in proximity, but a minority of male aggressive acts may have served to coerce females into mating with them [60].			females in general [60]. Frequency of chasing increased in the mating season. Chasing focused on oestrous females and non-oestrous females. [63]. There are seasonally different patterns of aggressive behaviour [66].		
Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Stump-tailed macaques *(macaca arctoides*)					
No instances of infanticide reported [59]. Harassment in the form of threats, chases and bitings [59].		Threats, chases and biting [59].	Increased aggression during the breeding season [59]. Incidents of wounding were classified involving punctures and/or cuts and slashes. Slashes and cuts were significantly larger number of wounding incidents than punctures were reported [59]. Lower incidence of	Incidents of wounding were classified involving punctures and/or cuts and slashes [59]. Significantly more wounds on the head [59].	

			violence than rhesus monkeys [67].		
Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Crested black macaque *(Macaca nigra)*					
Low ranking males have higher degree of harassment than higher ranking males [70].			Frequency and intensity of aggression towards females was greatest for mid-ranking males [70]. High-ranking males are the least aggressive toward females [70]. Males in all rank displayed significantly more aggression toward sexually receptive females than toward female sin other oestrous states [70].		High-ranking males may offer several benefits to females. First, high-ranking male may deter low-ranking adult and subadult males from harassing them. This protection may be important because low-ranking males are more aggressive toward females than high-ranking males are. Second, the females may suffer less feeding competition by other males when they are near a high-ranking male. Lastly, high-ranking males are usually preferred sexual partners [70].
Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Formosan rock macaque *(Macaca cyclopsis)*					

Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Barbary macaques (Macaca sylvanus)					
Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Long-tailed macaques *(Macaca fascicularis)*					
Only mate guarding when females are in oestrus [20]		Aggression as frequent or more often towards females than towards other males [3]		Biting between member of an estabilised group was never seen to result in deep wounds, whereas biting between stranger caused extensive and deep wounds on a few occasons [73]. In cases of heavy physical assault in the observation period females suffered 1,35 wounds per animal per periods, compared to males receiving 1,56 and juveniles receiving 0,29 wounds per animal [73].	Females bark and present their hindquarters toward the alpha male when it bit their screaming child [73]. High position in the hierarchy is expected to yield real benefits to a female and her progeny [50]

Forms of Sexual coercion	Degree of sexual coercion	Forms of aggression	Intensity aggression	Physical and physiological consequences	Female counter strategy
Tonkean macaques *(Macaca tonkeana)*					
Only mate guarding when females are in oestrus [20]. Dominant males mate guard females to monopolise sexual access to parous females that were in fertile stage of their reproductive cycle[72]. Higher ranking males may use threats and attacks to prevent them from expressing possible preference for rival, and thus reinforce their own reproductive success [72]. Mate-guarding males successfully prevented fertile females from expressing direct mate choice in Tonkean macaques [72].	Mate-guarding males use mild coercive behaviours to prevent females from mating with other males at conception time [72]. Mate-guarding males	Aggression as frequent or more often towards females than towards other males [3]	Mild threats towards females at low frequencies (0.01 occurrences per hour), which was sufficient to dissuade them from continuing to interact with male rivals.	Females did not suffer any physical costs, nor did males use aggression to force reluctant females into copulation [72]. No injuries or violent attacks reported to females [72].	Sexual presentations indicated that females accepted different types of partners, supporting the weak-selectivity hypothesis regarding direct mate choice [72]. At the evolutionary level, female sexual advertising and thus indirect choice promoted competition between males. The outcome is that indirect mate choice appears to be more important than direct mate choice in females [72].

Lower-ranking males monitored only nulliparous females [72].					
Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Chacma baboon *(Papio ursinus)*					
Chasing, mate guarding, sexual intimidation [19], [86]. No support for short-term harassment and punishment [19]. Males preferentially targeted cycling females [19] Direct coercion more important than indirect coercion *(males attempt to increase their own mating rates rather than to decrease those of others)* [19]. However, the aggressive behaviour does not lead to immediate copulation, nor do they lead to immediate formation	Males are vigorous mate guarders [84]. Females who receive more aggression throughout her cycle by certain male is more likely to be mate-guarded by him during ovulatory window. Resulting in a higher mating success in long term for the male aggressor [19]	Supplant, displacement, threat, chase and attack [19]. Aggression used against females to both compete with other males and coerce females into mating with them[20], [86] Males often engage in aggressive loud calls ("wahoo"), which functions as intra- and intergroup male-male competition. During most wahoo displays males chase females [86], [132]	Males direct violent aggression at females at times when the females are relatively likely to conceive [19]. Swollen females received the most injuries [19], [86]. Lactating females receive just as much aggression as other non-swollen females [20], [86].	Females that received higher rates of aggression from males suffered more injuries [19]. Male aggression represent a major source of injuries for fertile females [19]. No strong evidence found that attacks had substantial fitness costs to females [86]. Females rarely exhibit obvious injuries following an assault [86]. Open cuts, punctures of the skin, swelling, limps[19]. Male have capability of doing great damage	

of consortship. Therefore there is an **indirect coercion effect** [12], [86]**.** Male mating success may be related to placement in the male **dominance hierarchy and infanticide strategies (indirect coercion)** [86] Only mate guarding when females are in oestrus [20]. The females are often mate guarded when approaching ovulation. High ranking males more likely to chase females than low-ranking males [86]				with their canines, and their size relative to females. Males seem to restrain themselves and avoid inflicting injuries that could harm a female's reproductive potential [86]. However the attacks can lead to serious wounding. These injuries can in turn compromise the survival of females, due to reduced foraging/traveling efficiency and increased risk of infection [19], [86].	

Forms of Sexual coercion	Degree of sexual coercion	Forms of aggression	Intensity aggression	Physical and physiological consequences	Female counter strategy
Kinda baboon *(Papio kindae)*					
Only mate guarding when females are in oestrus [20]. No male infanticide suspected [75]					
Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Yellow baboon *(Papio cynocephalus)*					
Only mate guarding when females are in oestrus [20]. Infanticide is rare [74], [133]. Alpha males more likely to guard females on conceptive, rather than no conceptive cycles [88]. Alpha males achieved higher conception rates than expected apparently because they exercised mate choice more effectively			Males guard females during conceptive period [20], [88].		

than lower-ranking males [88].					
Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Olive baboon *(Papio anubis)*					
Only mate guarding when females are in oestrus [20] Infanticide is rare [74], [133] Direct female coercion has more impact on mating success [86]		Female frequently assaulted during feeding competition or when a male defended a third-party female, many attacks occurred during male-male competitive context (26%) or were seemingly unprovoked (32%) [86]	Areas bitten were neck, back and tail during aggressive interactions [59]	Direct female coercion has high impact on mating success, which could explain the severity of male-female attacks in olive baboon population [86].	
Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Hamadryas baboons *(Papio hamadryas)*					
Mate guarding their females at all times [20] Male hamadryas baboons are the both the main protectors and the main aggressors of their females . Females likely benefit from this	Males are vigorous mate guarders [84]. In general males directed aggression toward females at especially high rates during takeovers [20].	Threatening, chasing, hairpulling, biting, grabbing [20]. Neck-biting most common form of aggression [20]. Males seem to use aggression in more directed fashion. They	No aggression of any kind was observed under baseline conditions [20]. Aggression rates are far higher during takeovers. They exhibit also more kinds of aggression used during takeovers *(biting on back, possession grip*	Neck-biting rarely breaks the skin or produce blood. It does not seem to physically harm females in most cases. However, in animals victim of frequent neck-biting in short time will become hairless and covered	Females appear to live in constant fear of aggression by males [20].

association with a protective male because it increases the survival prospect of their offspring[20], [31], [85]. The relationship between male leader and female can be described as permanent consortship [20], [85]. Hamadryas baboons males mainly do coercive mate guarding *(via herding, punishment an sequestration).* With this behaviour males will increase their chance copulation and conception in the future, meanwhile also decreasing the female's chance of conception and copulation with other males [20] Rare form of sexual		use aggression primarily during takeovers, as a means of conditioning females [20].	*and pushing only observed in takeover context)* [20]. Aggression functions to control female sexuality, females receive more aggression when they are more fecund [3], [20]. Lactating females receive least aggression overall. Both mountain gorillas and hamadryas baboons, compared to other baboons and chimpanzees are characterized by a high degree of paternity [20], [31]. Outside takeover context: leader male is aggressive toward his females when they move too far away or leave the social boundaries of the one-male unit. But this is	with wounds in various stages of healing [20]. Females appear to live in constant fear of aggression by males [20].	

coercion is infanticide. This has an more quantifiable cost to female recipients [20], [134]. Even though it is rare[74] →*Unusual with respect to the **multi-layered social system**, which distinguishes them from other baboons* [20]			variable, males are not uniform [20]. Females receive the most aggression from their leader males shortly after being taken over, and then receive less aggression over time. Especially if additional females have joined their one-male-unit [20]. Females that stay closer to their leader male and spend more time grooming him will receive less aggression from him [20].		
Forms of Sexual coercion	**Degree of sexual coercion**	**Forms of aggression**	**Intensity aggression**	**Physical and physiological consequences**	**Female counter strategy**
Guinea baboon *(Papio papio)*					
Only mate guarding when females are in oestrus [20]. Ritualized greetings involved touches, embraces, hip touches, genital manipulations,		Aggressive behaviour between males and females occurred at a rate of 0,1 events/h. They mostly occurred between the primary male and the female and consisted of male	More than half of the time, no male was found within 5 m of the female. Pointing to more relaxed relationship between males and females than in hamadryas		Counter aggression was observed in 20% of the cases in which males directed aggression toward them [87].

and mounting were mainly restricted to the primary male [87]. No infanticide was observed [87]. Male form relatively stable relationships with one or several females, but these relationships appear to be much looser than hamadryas baboons.		aggression against female [87]	baboons. Each female was mainly found in close proximity (<2 m) of one specific male [87]. Male guinea baboons generally less aggressive than male chacma baboons, towards males and females [87]. Male-female interactions patterns not strongly affected by female reproductive state. Neither grooming nor aggression patterns changed with female reproductive state [87]. Only the likelihood of observing greetings was significantly lower when the female was lactcting.		Female transferred to other males both between and within parties. Changes occurred irrespective of reproductive state [87]. There was no clear pattern prediciting female transfer, and no obvious fighting of males over females; the few available observations tentatively suggest that within generally stable periods, shorter instable phases of multiple transfers occur.