To allow for a structured insight into infanticidal behaviour of baboons, these annotations are organized according to the themes addressed in each article. The first four articles delve into the evolution of male-female friendships as well as father-offspring bonds in the context of infanticide.

Palombit, R. A. (1999). Infanticide and the evolution of pair bonds in nonhuman primates. *Evolutionary Anthropology: Issues, News, and Reviews, 7*(4), 117–129. https://doi.org/10.1002/(SICI)1520-6505(1999)7:4<117::AID-EVAN2>3.0.CO;2-O

Summary: This review article explored infanticide (killing of unweaned young by conspecifics) in non-human primates. Previously, protection from male infanticide was proposed as a benefit to male-female bonds in various primates. Polygynous primates were known to have less direct and substantial paternal care patterns than monogamous primates. In many non-human primates, it is unclear whether male care of infants serves a paternal effort or mating effort. Thus, the prospective adaptive causes of male-female bonds were also investigated in this review. Palombit (1999) used a comparative analysis between non-human primates to evaluate the costs and benefits of social relationships between the sexes. Field studies provided a quantitative basis of comparison between "friendships" in chacma baboons and "pair bonds" in hylobatids (sympatric, white-handed gibbons, and siamang). The field study about responsibility for proximity maintenance between males and females revealed a greater female responsibility in baboons and more male responsibility in hylobatids. The field analysis about male and female contribution to grooming exercises indicated higher female contribution to grooming in baboons and higher male contribution to grooming in hylobatids. Chacma baboons tend to share close bonds to reduce the risk of infanticide, though males invest little effort into the relationship. The infanticide-protection hypothesis was used to explain that a cohesive relationship with males was beneficial to female chacma baboons, even though they invest more effort into the relationship. Infanticide was also observed in monogamous birds using male-removal experiments. The findings suggested that sexually selective infanticide may be a selective force even in monogamous species, and that strong heterosexual bonds may evolve as a response to this pressure. The author suggests future research to focus on infanticidal behaviour in gibbons, as the current data provides little/equivocal support to the infanticide-protection hypothesis, and further research based on comparative data can strengthen these predictions.

Contribution: In this review article, Palombit (1999) summarized the understandings of male-female relationships that have evolved in non-human primates, namely in response to infanticide. The selective influence on infanticide was supported in baboons and mountain gorillas, which had females maintain friendships, but was contradicted in hylobatids which had mostly males maintaining pair-bonds. This article was selected for my literature review due to its comparative approach to the topic of infanticidal behaviour, which sets the animal of interest (baboons) apart from other primates that have adapted to infanticide using different forms of social relationships between the sexes.

Weingrill, T. (2000). Infanticide and the value of male-female relationships in mountain chacma baboons. *Behaviour, 137*(3), 337–359. https://doi.org/10.1163/156853900502114

Summary: Social factors, primarily infanticide, are thought to have selected for the evolution of inter-sexual relationships in primates. Savannah baboons are known to maintain long term male-female relationships but live in multi-male troops and breed with multiple males, so they do not meet the conditions for infanticide to occur. Females benefit from close male connections, as they pose as powerful partners during aggressive and infanticidal situations. Males benefit by potentially increased chances of future mating with he female (in line with the pre-mating hypothesis) and increasing the fitness of the offspring sired with the female by protected the infant (in line with the post-mating hypothesis). In this study, Weingrill (2000) studied male-female associations in a Drakensberg Mountain chacma baboon troop at Natal Drakensberg, South Africa from September 1993 to August 1995. Troop sizes were between 29 and 36 individuals, with 12 adult females and 3 to 7 adult males (an average of 5.6 males/month of the study period). Grooming was observed ad-libitum throughout the study. Groups scans over 980 hours were used to collect data on proximity of nearest male and female neighbours and the distance between them. 12-minute focal animal samples of males were collected between group scans. It was found that the main benefit of male-female bonds observed in the mountain chacma baboon troop was of infanticide avoidance. While the highest-ranking male rarely interacted with his infant, only the other two fathers carried their respective inferred offspring. This evidence supports the prediction that infanticide avoidance is the main factor resulting in long-term male-female relationships. Weingrill (2000) suggests that infanticide is an adaptive strategy of dominant males against high paternity certainty and alpha-male tenure. Future studies can focus on an offspring's possible inheritance of an infanticidal trait, which would increase its future reproductive success.

Contribution: In this article, Weingrill, T. (2000) showed that the occurrence of infanticide in chacma baboons is in line with the theory that infanticide is adaptive strategy for many species of male primates. However, this theory was previously only backed by research on the hanuman langur. Thus, this research advances on the knowledge that infanticide by new males can be attributed to the strong correlation between rank and mating success and consequently increased paternity certainty. This article was chosen for its focus on infanticide as an adaptive male reproductive strategy, and its significance of male-female bonds to improve reproductive success.

Nguyen, N., Van Horn, R. C., Alberts, S. C., & Altmann, J. (2009). "Friendships" between new mothers and adult males: Adaptive benefits and determinants in wild baboons (*Papio cynocephalus*). *Behavioral Ecology and Sociobiology*, *63*(9), 1331–1344. https://doi.org/10.1007/s00265-009-0786-6

Summary: Non-monogamous mammals rarely maintain friendships between males and females with newborn infants; however, polyandrous primates exhibit these friendships regularly. Mating exclusivity is not observed in male-female friendships, suggesting that males should minimize paternal care towards infants. Thus, the authors explored the adaptive significance and determinants between adult males and mothers with dependant infants. To address this, they examined four yellow baboon groups (multi-male, multifemale) in Amboseli, Kenya for male mating effort and joint parental care. Over 16 months, 29 mother-infant dyads and their associated male friends (from four distinct multi-male group) were studied. 20-mintute focal animal sampling was used to observe pregnant females 2 months before and after birth, wherein affiliative and antagonistic interactions between females and infants/other group members were recorded. Post-birth bouts of infant distress and infant handling were also continuously recorded. Infant handling behaviours were recorded as either touch or rough handling (pull or contact breaking). Measures of grooming were observed since grooming intensity is an indicator of strong and persistent associations. Measures of proximity (within 5 m) were also observed since spatial pattering can indicate partner preference as females have increased reproductive success with "preferred" males. A male "friend" and "non-friends" were established for each mother-infant dyad. The findings significantly indicate that friendships help mother-infant dyads gain protection from harassment and infanticide, showing how friendships are used as a counterstrategy for infanticide. Almost half of male friends were genetic fathers of offspring and consorted with mothers during the most probable period of conception. These findings demonstrate that friendships between mothers and non-fathers did not result from paternity confusion, since all non-father friends were not involved in mating with the mothers during conception. Future research can investigate a father's decision to form a friendship with a mother-infant dyad, as they were not clearly predicted in this study.

Contribution: Nguyen et al. (2009) advanced research in this field as they were the first to find evidence that females gain social benefits from early associations with adult males. This study was significant towards the understanding of male-female associations, as it provided evidence that friendships are beneficial to both mothers and infants and are a form of biparental care of offspring. During periods of instability and consequent risk of infanticide, mothers tend to seek protection from male friends. This article was chosen for its insight on adaptive friendships and how they serve as a counterstrategy to social threats to infant safety.

Huchard, E., Charpentier, M. J., Marshall, H., King, A. J., Knapp, L. A., & Cowlishaw, G. (2013). Paternal effects on access to resources in a promiscuous primate society. *Behavioral Ecology, 24*(1), 229–236. https://doi.org/10.1093/beheco/ars158

Summary: Low paternity certainty in promiscuous mammals results in rare cases of paternal care. In contrast, recent research has found that juvenile baboons with present fathers exhibit faster maturation in promiscuous societies. To address this, father-offspring associations of wild chacma baboons were explored to see how they promote the offspring's access to resources. Researchers studied baboons in the semidesert region of Tsaobis Leopard Park, where they foraged in the closed woodland area (large trees and shrubs with multiple foragers at one patch). Data was compiled from October 2006 to January 2007 with 2 study groups: a large group with 9 adult/subadult males, 16 adult females, and 32 juveniles, and a small group containing 7 adult/subadult males, 9 adult females, and 16 juveniles. Dominance ranks were instituted using ad libitum focal observations of approach-avoidance and agonistic interactions within adults. One-hour focal animal sampling was conducted for each individual and scans were reformed every 5 minutes. All individuals were genotyped at 16 microsatellite loci to establish paternity and genetical analyses were conducted using tissue biopsies. Offspring were found to preferentially associate with their genetic fathers as opposed to other males. Father-offspring associations were more pronounced in the vicinity of other adult males and when mothers were absent. Offspring associated with father more frequently while feeding, which allowed them better access to richer food patches. Stronger father-offspring associations were observed in subordinate males and their offspring. These findings indicate that fathers can buffer the ecological and social environment faced by their offspring, paternal presence can mitigate the risk of attacks from predators and conspecifics. This study is significant as it highlights how fathers invest in their offspring at a low cost while still enhancing offspring fitness. Future research can investigate other paternal strategies that increase offspring fitness without compromising future paternal reproductive success.

Contribution: This article advanced on the significance of father-offspring bonds in wild desert baboons. Huchard et al. (2013) found that the facilitation of resource acquisition by fathers is a mechanism though which males increased offspring fitness without facing high costs and compromising their future reproductive success. research is supported by the research-acquisition hypothesis and supports previous finding that fathers and offspring in promiscuous primate societies can recognize genetic relationship. This article was selected to provide a perspective on the protective services that males can offer to offspring which can reduce the risk of conspecific aggression including infanticide.

The next two articles examine the hormonal effects of the risk of infanticide on male and female baboons, and the stressful conditions that promote infanticide.

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

Summary: Female chacma baboons are faced with a multitude of stressors daily that manifest themselves as hormonal changes. Previously, these increases were associated with the threat of infanticide, male immigration, and female reproductive stages. Engh et al. (2006) conducted a general linear mixed model analysis to determine the effect on glucocorticoid (GC; stress hormone) levels in response to seven predictor variables: age (young, middle, or old), dominance ranks (approach-retreat interactions), female reproductive states (cycling, pregnant, or lactating), male immigration, infanticidal attacks (canine punctures), female dominance hierarchy (stable or unstable), and predation. 70 individuals (an average of 22 adult females and 9 adult males) were studied over 16 months in the Moremi Game Reserve. 630 fecal samples went through hormonal analysis and were assayed for GC metabolites. 10-minute focal samples were used to record social interactions including grooming and aggression. Male immigration, infanticide, reproductive state, female rank instability, and predation significantly contributed to elevated GC levels, whereas dominance rank and age did not. Fecal GC levels were about 20% higher in pregnant females compared to cycling or lactating females. Male immigration resulting in the instability of the top two ranks also increased female GC levels, as this involved the threat of infanticidal immigrants. Higher levels were also seen during infanticidal months since infanticidal attacks pose an immediate threat to infants. Lactating females' GC levels significantly increased in response to immigration and infanticide, contrasting with cycling and pregnant females. In both the first and second periods of instability, only females who were susceptible to changing ranks showed increased GCs. The significance of this study is that it investigates how baboons mitigate their stress levels in response to normal stressors. Future studies can examine mechanisms by which stress levels are adaptively minimized in females to target specific stressful conditions and avoid chronic stress.

Contribution: The authors expanded on the concept of elevated GC levels in females by testing additional stressors including female rank instability and actual infanticide. Pregnant females' lack of elevated GCs opposed previous findings, suggesting that females may not foresee the risk of infanticide until they have susceptible offspring. A smaller increase of GC levels was found during infanticidal periods in lactating females, supporting the hypothesis that females form friendships to minimize infanticidal risk from immigrant males. This article was chosen to explore how the risk of infanticide can have potentially similar/different effects on GC levels than actual occurrences of infanticide.

Cheney, D. L., Crockford, C., Engh, A. L., Wittig, R. M., & Seyfarth, R. M. (2015). The costs of parental and mating effort for male baboons. *Behavioral Ecology and Sociobiology*, *69*(2), 303–312. https://doi.org/10.1007/s00265-014-1843-3

Summary: The sexual selection theory suggests that male mammals in polygynous relationships will invest less effort into paternal investment and more into mating competition. This article investigated the stress response in male chacma baboons (indicated by elevated levels of glucocorticoids (GCs)) in response to paternal effort and mating effort. Cheney et al. (2015) aimed to identify how variables including stable/unstable periods (stable period exists after the top two ranks are established), immigration/non-immigration periods (of males within the top two ranks), dominance rank (approach-retreat interactions), friendship status (grooming, infant handling/defense with lactating females), and consort status (males mating with and guarding females) are involved in the trade-off between mating effort and paternal effort. A 32-month study was conducted using focal animal sampling of approximately 25-29 female and 4-14 male chacma baboons. Male feces were collected and assayed for fGC metabolites. Linear mixed models were used to assess the correlation between fGC and the five predictor variables listed above. The results revealed significant interactions between stability/instability and friendship status, and between dominance ranks and both friendship and consort status. During periods of instability, males expressed higher fGC levels. Unstable periods were marked by high rates of infanticide (or attempts at infanticide), which posed a direct threat to infants. An inverse relationship was observed between fGC levels and dominance rank during unstable periods. Low-ranking males formed fewer friendships, had higher fGC levels while involved in sexual consortships, and had lower fGC levels in friendships, as opposed to high-ranking males. This study was significant as it shows that even in highly polygynous species, males must balance paternal effort with mating effort. Future studies are required to determine the mechanisms behind elevated fGCs, and its relation to the loss of mating opportunities and risks of injuries.

Contribution: Cheney et al. (2015) provide new insight into the trade-off between paternal and mating efforts in chacma baboons. This research advances the role of glucocorticoid as an indicator of stress, along with its importance in examining the best allocation of male reproductive effort. This article was chosen to gain a better understanding of the circumstances in which infanticide would be most beneficial, since males who invest heavily into mating often lose their own infants to infanticide. Future research could investigate why baboons exemplify the potential costs of mating and paternal effort, as opposed to other polygynous species.

The last three articles look at female counterstrategies to infanticide and the role of infants in preventing infanticide.

Clarke, P. M. R., Henzi, S. P., & Barrett, L. (2009). Sexual conflict in chacma baboons, *Papio hamadryas ursinus*: Absent males select for proactive females. *Animal Behaviour, 77*(5), 1217–1225. https://doi.org/10.1016/j.anbehav.2009.02.003

Summary: Infanticide by males is a leading cause of infant mortality in chacma baboons. Thus, females develop counterstrategies such as paternity confusion and manipulation of paternal behaviour. Clarke et al. (2009) suggest that when there is no infanticidal threat from resident male chacma baboons, females opt for polyandry as a source of protecting their infants from infanticidal immigrant males. However, additional protection of an infant may be required due to the absence of a principal protector during the infant's vulnerable period To address this, researchers examined two troops of chacma baboons in the De Hoop Nature Reserve of South Africa: the first troop: average 10.32 adult females and 6.31 adult males; second troop: average 11.61 adult females and 5.71 adult males). The Kaplan-Meir estimator was used to residency patterns of putative fathers during the infant's first year when the risk of infanticide is highest. This mate-guarding data assigned paternity to 64 infants. Behavioural data was collected over 18 months through 20-mintue continuous focal animal sampling of 14 adult, non-natal males covering 21 adult females. Frequency of female mating initiations and refusals were recorded. The researchers found that 47% of principal protectors were at least partially absent during an infant's period of vulnerability. Through polyandrous mating behaviour, females aim to confuse paternity among males to influence their mating patterns and gain extra protection. Females were observed to mate with any guarding males regardless of their rank or probability of ovulation which allowed them to increase the mating success and confuse paternity of these males. This research significantly emphasizes how limited female choice forces females to take on an indiscriminate strategy to optimize their mating success. Future research can investigate other female counterstrategies infanticide such as adsorption of the fetus when exposed to replacement males that will likely kill the offspring at birth.

Contribution: Clarke et al. (2009) have advanced upon the female counterstrategies to sexual conflicts and attempts to influence male choice. The results demonstrate how females augmented the mating success of guarding males and how polyandry was favoured because it increases protector availability. The findings support selection driven by sexual conflict, and favours females who can increase the number of protective males around them to lessen the risk of infanticide. This article was chosen to delve into the female mating strategy that leads to active and passive mating approaches that not only promote polyandry, but also counter the selection pressure of infanticide.

Zinner, D., & Deschner, T. (2000). Sexual swellings in female hamadryas baboons after male take-overs: "Deceptive" swellings as a possible female counter-strategy against infanticide. ***American Journal of Primatology, 52*****(4), 157–168. https://doi.org/10.1002/1098-2345(200012)52:4<157::AID-AJP1>3.0.CO;2-L**

Summary: Many female non-human primates have evolved reproductive and behavioural alterations to counter the risk of male infanticide, which is known to increase upon the immigration of a new male or a male's increase in rank. Species with dependent infants and female-biased care cannot afford to become fertile and conceive. Higher species of primates can use "deceptive" sexual swellings to falsely indicate ovulation, allowing males to mate without the possibility of female conception, thus reducing infanticidal risk. The authors examined the impact of male take-overs on female post-partum amenorrhea (time between childbirth and the first swellings), and interbirth intervals by following take-overs by new males in a captive group of hamadryas baboons. Reproductive data was collected from a group of 1 to 4 adult males and 4 to 17 adult females at the German Primate Center between 1981 and 1996. Female reproductive states were recorded, including: degree of sexual swelling (5-point scale), menstruation, birth, late abortion, and infant survival. The duration of post-partum amenorrhea, interbirth intervals, and the number of cycles until the next conception were studied during non-takeover periods where the infant survived at least 360 days, non-takeover periods where the infant died within the first week, when the infant survived 7 to 150 days, and after takeovers. Ad-libitum behavioural observations were made during male-takeovers. Following take-overs, 5 out of 6 lactating females developed sexual swellings, consequently shortening their post-partum amenorrhea. Though females mated with new males during the first two cycles, conception did not occur and the length of interbirth intervals did not change. These findings showcase the deceptive use of swellings which significantly reduce female reproductive costs, while providing males with mating opportunities which reduces the proximate incentive of infanticide. Future research could use a bigger sample size and non-experimental setup for further interpretations of the results.

Contribution: The research by Zinner & Deschner (2000) advances on situational sexual swellings in primate species by providing data on subsequent interbirth intervals, which was not provided in previous studies. These findings align with previous research of situation-dependent sexual swellings as a response to group-takeover resulting in reduced PPAs, which is consistent with the infanticide-counterstrategy hypothesis. This article was chosen due to its insight on female counterstrategies to infanticide as it highlighted how females reduce the costs of simultaneous pregnancy and lactation while increasing their offspring's' chances of survival.

Gomendio, M., & Colmenares, F. (1989). Infant killing and infant adoption following the introduction of new males to an all-female colony of baboons. *Ethology, 80*(1–4), 223–244. https://doi.org/10.1111/j.1439-0310.1989.tb00742.x

Summary: Conditions that promote male replacement with new-comers prompts males to kill unweaned infants to bring mothers rapidly back into oestrus and maximize their own reproductive success. In this study, researchers explored infanticide and adoption due to the arrival of male newcomers into established female colonies. Three hamadryas baboons were introduced into a colony of all-female hamadryas and hybrid baboons. 5-minute focal animal sampling was performed to quantitatively analyze 'grooming' and 'mother restrains infant' behaviours. Focal data was collected for 6 juveniles (2 males, 3 females) and 6 infants (3 males, 3 females). Unfamiliar males attacked unweaned infants in all three cases, but only one male committed infanticide. Non-cycling and lactating females continued cycling after the introduction of new males, with some lactating females cycling immediately upon their infant's killing. Infants frequently interrupted interaction between mothers and males. Thus, they stirred up conflict with males who were originally friendly, leading the males to attack the infants. In contrast to infants born before the introduction, infants born after the introduction were friendly with the males. Mothers with dependant infants that develop a male-female bond with a new male are seen to decrease their maternal investment, which drives the infant to create conflict and respond fearfully to the male. Comparatively, if the male-female bonding process was concluded before the infant's birth, no infant-male conflict took take place. Subordinate and young males were less capable of responding to conflict in ways other than infanticide. Independent juveniles and oldest infants maintained distance from mothers and new males, while young dependant infants tried to associate with other caretakers for maternal care. Future research could focus on proximate explanations of infanticide, since mainly casual factors of infanticide have been explored due to the lack of information on the immediate social context of infanticide.

Contribution: Gomendio & Colmenares (1989) found that infants played an important role in producing and maintaining conflict with males and sought for adoption from non-mothers to prevent the risk of infanticide. While other studies primarily focused on mothers and their counterstrategies to infanticide, this research showed the significance of the role of infants in preventing infanticidal risk. This article was selected for its insight on the ultimate influences of infanticide and counterstrategies used by infants that allow them to avoid infanticide and increase their chances of survival.