Adriana Lowe

INFANT KILLERS OF BUDONGO REVISITED: INFANTICIDE AND COUNTERSTRATEGIES IN WILD, EASTERN CHIMPANZEES

Abstract:

Infanticide, the killing of infants, is well documented in chimpanzees. However, despite multiple reports of this behaviour, no comprehensive study has attempted to explicitly test the various different hypotheses for its adaptive function in this species. In this thesis, I use records from the Sonso community of chimpanzees in the Budongo Forest, Uganda, to address the question of the function of infanticide. While infanticide has been recorded in several communities of chimpanzees, rates vary dramatically. In order to shed light on this variation, this thesis investigates risk factors for infanticidal behaviour and counter-strategies by parents. I found that the majority of infanticides adhere to the predictions of the sexual selection hypothesis for male committed infanticide, that instability in the male hierarchy is a key risk factor, and that mothers, but not fathers employ counterstrategies to protect their infants. Avoidance of potentially infanticidal individuals appears to be a key maternal counterstrategy to infanticide. Mothers are responsive to the varying risks posed by different individuals and how they change over time and they selectively avoid high risk individuals, both at the between and within party level.

Living Primates Research Group
School of Anthropology and Conservation
University of Kent, UK

December 2018

159 pages

Thesis submitted for the degree of
Doctor of Philosophy in Biological Anthropology

Acknowledgements

Firstly I would like to thank my supervisor, Dr Nick Newton-Fisher, who has for the last three and a bit years provided the perfect combination of encouragement, support and constructive criticism. As well as excellent supervision, he also provided much of the data used in this thesis, which was a lifesaver when many of our plans went slightly awry. Without Nick none of this would have been possible, nor would it have been so much fun.

I am also immensely grateful to the team at Budongo, particularly Geresomu, Robert and Kizza, who introduced me to the chimpanzees and gave me advice, practical help and friendship. Thanks also need to go to the researchers and staff at Budongo who helped to make it feel like home.

For permission to work in Uganda, I thank the Uganda National Council for Science and Technology and the Uganda Wildlife Authority.

Lastly, thanks to my parents, for everything.

To the chimpanzees of Budongo

Author's Declaration

I affirm that this thesis is my own work, except where indicated otherwise. The thesis was written by myself, with comments from my supervisor, Dr Nicholas Newton-Fisher. Data were collected by Dr Newton-Fisher, Mr Geresomu Muhumuzu and Adriana Lowe. All data analyses were run by Adriana Lowe. Chapter Four was prepared for publication with the input of Dr Catherine Hobaiter, who provided comments on the manuscript. Risk assessment and ethical approval were provided by the University of Kent, and permission to conduct research in Uganda was provided by the Uganda Wildlife Authority, the Uganda National Council for Science and Technology and the President's Office.

Table of Contents

1. Introduction: infanticide and counterstrategies

Infanticide is the killing of un-weaned infants by conspecifics (Hrdy 1979). It is common in mammals, occurring across several orders including rodents (Blumstein 2000), carnivores (White 2005; Singh et al. 2014), bats (Knörnschild et al. 2011), primates (Takahata 1985; Mori et al. 1997; Struhsaker & Leland 1985; Watts 1989b) and even-toed ungulates (Patterson et al. 1998). It has also been observed in birds (Moller & Cuervo 2000; Heinsohn et al. 1997) and reptiles (O'Connor & Shine 2004). Infanticide is a major cause of infant mortality in some species, for example accounting for the full or partial loss of 39% of prairie dog litters (*Cynomys ludovicianus*: Hoogland, 1995), 44% of infant deaths in Venezuelan red howler monkeys (*Alouatta seniculus*: Crockett and Rudran, 1987) and up to 63% in Hanuman langurs (*Semnopithecus entellus:* Borries, 1997).

The study of infanticide, particularly within primatology, has been dogged by critiques, both scientific and moral (e.g. that reports are too sparse for meaningful analysis; Sussamn et al. 1995, and that focusing on adaptive explanations "plays into the culturally overdetermined lust for sexualized violence"; Haraway, quoted in Sommer, 2000). When infanticide in wild non-human primates was first reported (Sugiyama 1965), it was largely ignored. However, when Sarah Hrdy hypothesised that frequent infanticide amongst Hanuman langurs (*S. entellus*) was a sexually selected behaviour born out of male competition over mates (Hrdy, 1974), the subject began to garner attention. Those researchers whose thinking was still influenced by group selection struggled to reconcile these ideas with the concept of adults killing conspecific infants for personal gain (e.g. Vogel 1979, quoted in Sommer, 2000). Infanticide was dismissed in some quarters as "inconsequential epiphenomena of aggressive episodes" (Sussman et al. 1995) or as a pathology, potentially stemming from overcrowding or human interference (Curtin &

Dolhinow 1978). This was bolstered by evidence from rats which suggested that artificially elevated population densities led to an increase in aberrant behaviour, including infanticide (Calhoun 1962).

While infanticide reduces the number of infants (which are the mechanism by which genes are replicated in the next generation), rather than increasing it, this does not preclude an adaptive explanation. If perpetrators use infanticide to enhance their own fitness, albeit at the cost of the victim's, then the behaviour may not be maladaptive. Rather, it may be a product of Natural Selection. The discipline of behavioural ecology seeks to understand the behaviour of animals in terms of Darwinian fitness (Krebs & Davies 1987), i.e. how does a particular behaviour help or hinder an individual in the attempt to successfully pass on its genes and protect that genetic investment? It employs a logic derived from economics, weighing fitness costs and benefits to determine whether, and under what conditions, a behavioural strategy will be favoured by selection. It is this consideration, rather than subjective impression, that allows for an objective determination of the adaptive value of any particular behaviour, and in this case, infanticide.

The impact of infanticide, particularly non-parental infanticide, should not be underestimated. If conspecifics can significantly reduce another individual's fitness by killing their infant, then relationships between potential killers and parents (particularly mothers) will by necessity be shaped by this conflict of interest, as each attempts to improve their fitness at the other's expense. This creates a cycle of counter-strategies and counter-counter-strategies, which have major implications for social behaviour and structure. For instance, some analysis has suggested that the risk of infanticide has led to social monogamy multiple times in various primate lineages (Opie et al. 2013). However, this may not apply to other mammals where other factors, notably female density and range sizes, make defending multiple females impractical for males, and infant defence may be a result of, rather than the reason for, social monogamy (Lukas & Clutton-Brock 2013). Infanticide risk has also impacted sexual strategies, leading to promiscuous mating in some species (Struhsaker & Leland 1985) and subsequent attempt to limit promiscuity by males (Knott et al. 2010; Muller et al. 2007). Both inter-sexual and intra-sexual relationships are markedly shaped by infanticide risk, with it linked to either the formation of affiliative relationships with certain individuals (e.g. yellow baboons (*Papio cynocephalus*): Palombit et al., 1997) or aggressive behaviour towards conspecifics and territoriality, (Wolff 1993; Wolff & Peterson 1998; Maestripieri 1992).

Parental infanticide (manipulating investment)

In species with internal fertilisation, mothers must invest time and energy in gestation and, in the case of mammals, lactation (Pond 1977), with one or both parents providing ongoing provisioning and care in many species (Moller & Cuervo 2000; T. Clutton-Brock 1991). Since infants represent costs for parents then they will need to also represent a good return on the investment for it to be adaptive for parents to incur that cost. For instance, offspring that are unlikely to survive to sexual maturity and be able to produce offspring themselves are evolutionary dead ends and parents would be better served by saving their energy for potential future offspring who will be able to enhance their parents' inclusive fitness by producing offspring themselves (Hrdy 1979). Similarly, in species with multiple reproductive events, an offspring or litter which will over stretch the parents to the extent that it damages future reproductive prospects is a poor investment. For instance, in unusually harsh environments it could be adaptive for parents to abandon offspring and use their energy reserves to maintain their own body condition in order to be able to breed in future, rather than risk their lives providing for offspring which may not survive anyway (Hrdy 1979).

Females of many species manipulate their reproductive output based on the viability of particular embryos and social/ecological conditions. Poor nutrition is linked to reduced female fecundity in animals as diverse as birds (Gustafsson et al. 1994), bovids (Perera 2011), humans (Ellison 2008) and insects (Awmack & Leather 2002), which reduces the likelihood of pregnancy in harsh environments which are unlikely to be able to support the increased energetic demands of the mother and those of the infant(s). Evidence from humans that fecundity is negatively impacted by increases in physical exertion even when energy balance is neutral (Jasienska & Ellison 1998) and that moderate, chronic malnutrition only mildly reduces fecundity (Bongaarts 1980) indicates that this variation is an adaptive response to environmental change, not merely a proximate outcome of poor environments or negative energy balance. Mothers, particularly in species with potentially long reproductive lifespans, would be better served by investing energy in their own survival when times are hard, so they can breed later when conditions have improved, rather than attempting to breed in suboptimal conditions (Jones 2011). This manipulation of parental investment continues after conception. In humans for example, more than 70% of conceptions do not survive past 6 weeks of gestation (Boklage 1990). Genetic abnormalities are a significant cause of spontaneous abortion in humans (Rubio et al. 2003) and non-human animals (e.g. domestic pigs (*Sus scrofa*) and mice (*Mus musculus*): Akesson and Henricson, 1972; Schreiner and Hoornbeek, 1973) which cuts off investment in these embryos. The functional consequence of this is that mothers curtail energetic expenditure on pregnancies which are unlikely to produce healthy young. This is evident again after birth as parents continue to evaluate offspring quality and the impact on their own condition of further investment. For example, 42% of common eider (*Somateria mollissima*) mothers abandon their broods with such abandonment linked to poorer maternal body condition (Bustnes & Erikstad 1991). Similarly, female moustached tamarins (*Saguinus mystax*) kill or abandon their infants when fewer alloparents are available to help with infant care (Culot et al. 2011). These examples indicate that mothers are shifting investment from their young to themselves when ecological or social conditions are unfavourable.

The cost of reproduction hypothesis, central to life history theory (Williams 1966), argues that there is a trade-off between current and future reproduction. Females must allocate resources accordingly, ending investment by reducing time spend feeding, or abandoning/killing, non-viable, small or weak offspring, who offer low returns on parental investment. This represents reallocation of resources to other, stronger offspring in the brood where applicable or potential future offspring, instead of low quality current progeny. Such behaviour has been documented in many species, including boas (*Epicrates cenchria maurus*: Lourdais et al., 2005), common marmosets *(Callithrix jacchus:* Tardif et al., 2002) and a variety of birds (Caro et al. 2016; Klosowski et al. 2002). In a similar vein, parents of some species tolerate siblicide, in which stronger offspring kill weaker siblings, achieving much the same outcome for the parents as infanticide (e.g. black eagles *Aquila verreauxii*: Gargett, 1978). The phenomenon of parental infanticide is also particularly well documented in humans. Historical accounts of children being abandoned/exposed are common e.g. ancient Romans, Athenians and Spartans reportedly abandoned weak new-borns or those the family could not afford to keep (van Hook 1920; Patterson 1985; Brennan 2002). Unmarried European mothers historically left their illegitimate babies, which they would be unable to support and would damage their chances at a future marriage and legitimate children, at foundling hospitals or sent them to wet nurses/baby farms where the death rates often made this tantamount to infanticide (Rose 2015; Wilson 1989; Viazzo et al. 2000).

Non-parental infanticide

As well as parents, who may selectively kill some of their own offspring in order to reallocate reproductive effort, unrelated conspecifics pose a significant risk to young in many species. Non-parental infanticide has been recorded across the multiple taxa, including in primates (*Homo sapiens*: Daly and Wilson, 1984; *Gorilla beringei beringei:* Watts, 1989; *Pan troglodytes schweinfurthii:* Kirchhoff et al., 2018), felines (*Panthera leo:* Packer and Pusey, 1983; *Panthera tigris:* Singh et al., 2014), birds (*Tachycineta bicolor:* Robertson, 1990), rodents (various, see: Ebensperger and Blumstein, 2007), meerkats (*Suricata suricatta*: Clutton-Brock et al., 1998) and fish (*Neolamprologus pulcher*: Jindal et al., 2017).

Resource competition

One key reason for non-parental infanticide is resource competition (Hrdy 1979). Since certain resources, such as food and nest sites, are directly or indirectly related to the ability to successfully rear offspring (Townsend, Slocombe & Thompson 2007; Wiebe & Martin 1998), females in particular (whose reproductive success is limited largely by access to such resources, while males' is limited by access to females: Janicke et al.; Bateman, 1948; Collet et al., 2014), are prone to compete over them (Hrdy 1979). Much as parental infanticide should improve the perpetrator's overall fitness, if it is the consequence of Natural Selection, resource competition motivated infanticide should result in the perpetrator having better access to resources than they would otherwise have had.

Social rank is associated with resource quality in many species, with higher ranking individuals having preferential access to feeding or nesting spots (Banks et al. 1979; Murray, Mane, et al. 2007; Ekman & Askenmo 1984; Post et al. 1980). As well as limiting lower-ranked females' access to resources themselves, high-ranking females of some species suppress the ovulation of other females, thus limiting subordinates opportunities to produce offspring who represent more competition (Hackländer et al. 2003; Creel et al. 1992). While strictly speaking not infanticide, this behaviour functions in the same way. In species in which subordinates do breed, high ranking females have been known to kill those females' young (e.g. dingos (*Canis lupus dingo*) and common marmosets (*C. jacchus*): Corbett, 1988; Digby, 1995). While adult individuals will compete physically over resources (e.g. tufted capuchins (*Cebus apella*)*:* Janson, 1985, and stingless bees (*Trigona spp*)*:* Johnson and Hubbell, 1974), targeting infants (future competitors) rather than adults (current competitors) could be beneficial if it minimised costs for the attacker (e.g. if adult individuals do not defend the infant and the risk of injury to the attacker is therefore low). To maximise the effectiveness of this behaviour, perpetrators should target those individuals who pose the biggest threat to their resources. In female philopatric species, female infants represent greater future competition than do male infants, as they will remain in the group to breed, and thus these should be the targets. In the female philopatric toque macaque (*Macaca sinica*), young females receive more aggression than young males, suggesting that resource competition is a factor (Dittus 1977) and in bonnet macaques (*Macaca radiata*), daughters of low ranking females are most vulnerable to aggression, again indicating that resource competition plays a role (Silk et al. 1981). Evidence from mice (*M. musculus*) that pregnant females are more infanticidal than non-pregnant adults or pre-pubertal females suggests that the increased energetic costs of reproduction trigger infanticidal behaviour by females (McCarthy & Vom Saal 1985).

While food and space are key resources for females, by contrast male fitness should be more influenced by access to mates (Trivers 1972). Males could theoretically benefit from removing future competitors by killing infant males but allowing unrelated infant females to survive as such females could be future mates (Hiraiwa-Hasegawa &

Hasegawa 1994; Nishida & Kawanaka 1985). Despite being proposed as an explanation for the male bias in victims recorded in early investigations of infanticidal behaviour in chimpanzees (Nishida & Kawanaka 1985), overall, evidence for males removing future sexual competitors through infanticide is weak in primates. It requires that males maintain breeding access until female infants mature sexually and male infants are able to compete sexually and is therefore a poor fit for long lived species. For example in langur monkeys (*S. entellus:* Agoramoorthy and Mohnot, 1988), males are not capable of copulatory behaviour until around 4 years old and females langurs do not reach sexual maturity until they are 2.5 years old, while the length of male tenure in harems averages 2.3 years (Author et al., 1995) meaning that this is unlikely to be particularly successful strategy. Evidence for the male bias in victims predicted by this hypothesis in this species is mixed, finding that that either infanticidal males target male and female infants equally (Sommer & Mohnot 1985) or identifying a male bias in victims (Agoramoorthy & Mohnot 1988).

Sexually selected infanticide

While the evidence is patchy for male-committed infanticide motivated by resource competition, infanticide by males remains common across a range of animals (e.g. primates: Borries, 1997; Wilson et al., 2014; Zipple et al., 2017, rodents: Mennella and Moltz, 1988; Graziani, 1995, bats: Knörnschild et al., 2011, birds: Robertson, 1990, carnivores: McLellan, 2005; Bellemain et al., 2006). A key hypothesis that seeks to explain this phenomenon is the sexually selected hypothesis for male committed infanticide (Hrdy 1974). This hypothesis holds that in species in which mothers provide parental care (e.g. lactation in mammals and provisioning in birds), males can create mating opportunities by killing infants as this results in the mothers of those infants becoming reproductively available sooner than they would otherwise have been (Sommer 1987; Hrdy 1974; C. van Schaik 2000a). In order for this behaviour to be adaptive, males must be unlikely to kill their own offspring, the infant's death must reduce the time before the mother is ready to mate again, and when she is, the male must have a reasonable chance at conceiving a new infant with her (Sommer 1987; Hrdy 1974; C. van Schaik 2000a). Therefore, in species in which males can identify their offspring and mothers do not conceive while they have young dependent offspring, males who have a reasonable likelihood of securing mating access to a mother in the near future will gain adaptive advantages from killing infants. Lactational amenorrhoea in mammals makes them vulnerable to infanticide, particularly in species with extended inter-birth intervals, as the longer the interbirth interval, the greater the potential benefit to the infanticidal male (C. P. van Schaik 2000b). The benefits of committing infanticide, rather than waiting for females to resume cycling again, depend on the inter-birth interval and lactation period (how much time is being saved) and social structure. In species with short lactation/provisioning periods, such as the harp seal (*Phoca groenlandica*, ~12 days lactation: Lydersen and Kovacs, 1996), infanticide would provide little to no benefit to males. However, in species with long, slow life histories such as primates (Jones 2011), late weaning ages will make infanticide highly beneficial for males. For example, chimpanzees (*P. troglodytes*) wean their offspring at ~4.5 – 5.5 years (Bădescu et al. 2017a; Pusey 1983) and gorillas (*G. b. beringei*) at ~3.3 years (Eckardt et al. 2016), meaning infanticide could create a mating opportunity years earlier than it would have otherwise occurred. In species in which male access to mates is fluid and depends on rank or impermanent group membership, the difference between committing infanticide or not may have a major effect on the perpetrator's fitness. For example, in female philopatric species such as lions (*P. leo*) and langurs (*S. entellus*), males frequently kill infants after a group takeover (Hrdy 1974; Packer & Pusey 1983). Incoming males can be sure the current infants are not theirs, and waiting until the current infants are weaned would mean losing most, if not all of their mating opportunities, given that that their tenure in the group is time-limited. A male Hanuman langur maintains his position in a group for an average of 2.3 years (Author et al. 1995), while pairs of male lions do so for 18 months, with larger coalitions lasting longer (Bygott et al. 1979); the median tenure across all coalitions is around 24 months (Pusey & Packer 1987). Takeovers by newer males eventually occur and often involve the deaths of any un-weaned infants. Therefore, the sooner a male can impregnate the group's females, the more likely his offspring are to have been weaned, and therefore be safe from attack by incoming males, by the time he is deposed. In langurs, interbirth intervals are reduced by ~60 days in cases of early infant death. Interbirth intervals when infants survive are ~15.4 months in this species (Harley 1985). Killing an infant would therefore result in a 13% reduction in the interbirth interval. If new males waited until all current infants are weaned before mating with the group females, they could even be expelled or killed before they had a chance to mate at all. Since some males manage to maintain tenure in a group for only a few days (Author et al. 1995), this is not unlikely.

Cannibalism (nutritional benefits)

One common feature of infanticidal attacks is the consumption of the victim. This has been observed in both parental infanticide (e.g. moustached tamarins (*S. mystax*): Culot et al., 2011, and American kestrels (*Falco sparverius*): Wiebe et al., 2011) and non-parental infanticide (e.g. New Zealand sea lions (*Phocarctos hookeri*): Wilkinson et al., 2000, and chimpanzees (*P. troglodytes*): Goodall, 1977; Nishie and Nakamura, 2018). There may be cases in which the main motivation for the attack is resource acquisition (cannibalism), but when the attacker is unrelated to the victim it is hard to separate this from other hypotheses, such as resource competition, because the behaviour will function both to provide food and remove a competitor. For instance, while female mice can remove competitors by killing unrelated infants, pregnant and lactating females (who have higher energetic requirements) are more likely to eat their victims, suggesting that the behaviour has a dual function (Wolff & Cicirello 1989). In cases of parental, specifically maternal, infanticide, cannibalism fits well within the framework of manipulation of parental investment: when mothers choose to stop investing in an infant or brood, consumption serves to avoid wasting further energy. The energy involved in gestation, lactation (in the case of mammals) and any other parental investment has already been spent and it would be adaptive to recoup some of these losses by eating infants. Since harsh environments should be a trigger for parental infanticide, and perpetrators are often in poor physical condition (Bustnes & Erikstad 1991), infanticide victims may be a valuable energy source. Cannibalising victims may also provide an additional benefit: carcasses are a vector for disease (Ogada et al. 2012) and attract predators (Cortés-Avizanda et al. 2009) so mothers might be protecting themselves and any remaining offspring by removing carcasses in this way.

Non-adaptive explanations

Despite the potentially adaptive benefits of committing infanticide, not all infant deaths can be attributed to an evolutionary strategy on the behalf of the perpetrator. Those which cannot, can be broadly categorised as either by-products of other adaptive behaviours or accidental deaths not associated with any adaptive behaviour.

Infant death as a by-product

In species in which infants require parental care, separation from the caregiver can involve serious injury and quickly result in death from starvation. Kidnapping, resulting in infant injury or death, is well documented, for instance in emperor penguins (*Aptenodytes forsteri:* Jouventin et al., 1995), yellow baboons (*P. cynocephalus:*

Shopland and Altmann, 1987), Lowe's guenons (*Cercopithecus campbelli Lowei:* Bourliere et al., 1970) and olive baboons (*Papio anubis:* Collins et al., 1984).

Emperor penguins without chicks of their own frequently "adopt" the chicks of others, either finding lone chicks or forcibly taking them from their parents; this can occasionally be violent enough to result in a chick's death (Angelier 2006; Jouventin et al. 1995). The majority of adoptive parents do not feed the chicks, who as a result quickly become emaciated (Jouventin et al. 1995). These deaths appear to be an incidental side effect of misplaced parenting behaviour, linked to the high residual prolactin levels (a reproductive adaptation to their harsh environment) of parents who have lost their own young (Angelier 2006), rather than targeted attacks as described in other species.

Similarly amongst primates, some cases of infant injury/death during kidnapping has been suggested to be a by-product of an adaptive behaviour called "aunting" (Quiatt 1979; Hrdy 1976; Hunt et al. 1978; Kuester & Paul 1986). "Aunting" has been proposed as an opportunity for young females to practise infant care in preparation for when they have their own offspring (Hrdy 1976). In species which require extensive parental care, this experience could be the difference between survival or death of a first born infant and therefore highly valuable. Primate females separated from their mothers, with no behavioural model for parenting, have poorer reproductive outcomes (Harlow et al. 1966) and even amongst free-ranging, mother-raised individuals, multiparous females have much higher infant survival rates than primiparous females (Drickamer 1974). Practise therefore seems to be valuable for primate mothers and nulliparous females (who should benefit most from practise) are overrepresented as "aunts" in several species (see Hrdy, 1976). In these cases the proximate cause of this behaviour appears to be attraction to infants, as is the case with the penguins. However, regardless of proximate causes, since being taken from the mother can be dangerous and infants can be injured or killed during these transfers (Quiatt 1979), this behaviour may serve to reduce competition for the attackers and their own future offspring, making it ultimately adaptive and perhaps better categorised as a form of adaptive infanticide. In addition, some aunts or allomothers are actively aggressive to their charges (Sommer 1989), further supporting the idea that at least some cases of aunting are a form of infanticidal behaviour.

Male primates have been observed carrying infants when interacting with other adult males, a behaviour known as “agonistic buffering” (barbary macaques (*Macaca sylvaus*): Whiten and Rumsey, 1973, Kümmerli, 2004, and geladas (*Theropithecus gelada*): Dunbar, 1984). According to the agonistic buffering hypothesis, infants serve to dampen aggressive responses from adult males and are thus used to regulate behaviour between males (Deag & Crook 1971). While this provides obvious benefits to the males, who reduce their chances of being injured, infants can be killed either in the process of being snatched from their mothers or from ensuing violence when their presence fails to de-escalate the male aggression (Shopland 1982).

Accidental infant deaths

Opponents to adaptive explanations for infanticide have argued that infant deaths categorised as infanticide may instead have been accidently caused during violence between adults, for instance during group takeovers or mating seasons (Curtin & Dolhinow 1978). However, this hypothesis was explicitly proposed in opposition to the sexually selected hypothesis in langur monkeys, and subsequent research has indicated that infant deaths in this species follow a pattern suggesting a male sexual strategy, rather than accidents (Borries, Launhardt, Epplen, Jîrg T Epplen, et al. 1999). That is not to say that infants never die accidentally at the hands of conspecifics, however. Adult walrus (*Odobenus rosmarus*) occasionally crush infants on crowded beaches, and young elephant seals (*Mirounga sp.*) have been killed during male-male dominance contests

(LeBoeuf and Campagna, 1994). In addition, elevated aggression during the mating season in rhesus macaques (*Macaca mulatta*) has been linked to infant deaths in the first year of life (Drickamer, 1974).

Counterstrategies

In cases of infanticide in which the parent is not the perpetrator, the parents suffer a fitness cost from the death of their infant. Counterstrategies are likely to have evolved in response to infanticidal behaviour as parents tried to avoid the loss of their reproductive investment. The selective pressure of infanticide should be strongest in species with extended periods of gestation, lactation and infant provisioning, since infant deaths represent a significant amount of wasted reproductive effort. While an initial criticism of Hrdy's sexual selection hypothesis (1974) was the lack of evidence for counterstrategies (Sussman et al. 1995), subsequent research has identified a variety of male and female behaviours which function to reduce the risk of infanticide (below).

The Bruce effect

The Bruce effect – the phenomena of pregnant females spontaneously aborting embryos in response to the presence of an unfamiliar male (Bruce 1959) – has been recorded in species in which males commit sexually-selected infanticide (e.g. mice (*M. musculus)*: Bruce, 1959; vom Saal, 1985, geladas (*T. gelada)*: Mori et al., 1997; Roberts et al., 2012 and bank voles (*Myodes glareolus*): Eccard et al., 2017). Abortion of embryos reduces energetic and time costs for the mother in situations where infanticide is highly probable. Energetic savings may have significant impacts on body condition and therefore fitness; in marmots (*Marmota marmota*), females who abort pregnancies when introduced to novel males are in better condition the following year and have higher reproductive success than females who do not (Hackländer & Arnold 1999). While this does not serve to ensure the survival of the embryo, it is a response to infanticide risk and ultimately achieves the goal of reducing fitness costs to the mother. There is no evidence of the Bruce effect in chimpanzees. This may be due to the fact that in a male philopatric species, where novel males do not suddenly appear and pose a threat to infants, infanticide risk is less clearly defined. However, it may also be simply due to the difficultly of recognizing early stage pregnancy in this species, where not all females are seen regularly.

Aggression and territoriality

Active use of aggression to defend infants, while the most direct way of preventing infanticide, is also potentially costly since it risks injury. This potential cost needs to be offset against the benefit of protecting one's genetic investment. Therefore the benefit of defence for males will vary depending on paternity certainty. In a uni-male group all infants are sired by the one male. This male therefore has high paternity certainty and when he is challenged by a new male, risking losing access to the females, defending his offspring may be adaptive, even if costly, as he could be protecting the entirety of his reproductive output. Even though infant defence is less beneficial for the protector when paternity certainty is reduced, paternal defence does sometimes occur in multi-male groups such as langurs (*S. entellus*), which appear to use mating history as an indicator of paternity (Borries, Launhardt, Epplen, Jörg T Epplen, et al. 1999). As well as reduced paternity certainty making infant defence less beneficial for males in multi-male groups, male hierarchies can have an effect. Defending an infant against a lower ranked male will be a lower cost activity than defending against a higher ranked male (where there is a higher risk of injury) and so, while male defence is observed in multi-male groups, and does deter attacks, though this should generally only be adaptive when the attacker is lower in rank than the protector (Broom et al. 2004).

Mothers, who, unlike fathers, have no ambiguity around relatedness to infants and generally invest more heavily in their infants (Trivers 1972), should benefit from protecting their infants from attack (protecting their investment), assuming they are not likely to incur injuries which could reduce their future fitness. Accordingly, an increase in aggression is a key behavioural feature of the lactation period in mammals, which serves at least in part to protect infants from conspecifics (Bosch 2013; Maestripieri 1992; Wolff 1985). Aggression as a counter-strategy to infanticide can extend to territoriality, in which mothers defend an area against intrusion by potentially infanticidal individuals. Territoriality is exhibited by many female rodents and has often been considered to be primarily about resource competition (Ostfeld 1990). However, territorial aggression is heightened during the breeding season when food is relatively abundant (Wolff 1993; Ostermeyer 1983), indicating that this behaviour primarily functions as an infanticide defence, rather than as resource competition (Wolff 1993). Altricial species, in which mothers must park their infants, are more vulnerable to infanticidal intruders than mothers with precocial young who can keep them with them while foraging. Accordingly, female territoriality is found more commonly in species with altricial than precocial young (Wolff & Peterson 1998) further indicating that it is an anti-infanticide strategy. This behaviour is not limited to rodents or solitary species; group-living female lemurs (*Lemur catta*) also attack incoming males but only after they have conceived, which functions to repel potentially infanticidal males (Pereira & Weiss 1991).

Mate choice

In the face of sexually selected infanticide, one key female counterstrategy is mate choice.

According to Van Schaik's (2000a) model of adaptive, sexually selected infanticide, the net benefit to a male will be positive when:

$$[(t_n - t_i) / t_n] P_i > p$$

$(t_n - t_i)$ is the time until the female is available to mate if no infanticide is committed, minus the time if infanticide is committed (i.e. the time saved), P_i is the probability of siring the replacement infant and p is the probability of having sired the current one. Broadly, females can distribute their mating effort in two ways, by widening or narrowing their choice of sexual partners. On one end of the spectrum is promiscuity in which, by mating with multiple males within a single conceptive cycle, females give each a non-negligible chance of paternity. This should make infanticide less beneficial for males, since benefit in is derived partially from the probability of fathering a subsequent infant after infanticide (P_i) being greater than the probability of having fathered the current one (p). Therefore, the higher a male's chance of having fathered potential victims, all other things being equal, the lower the benefit of infanticide will be. Despite female promiscuity offering some benefit to males (their infants are more likely to survive if paternity confusion deters males from killing infants: Boyko and Marshall, 2009) successful, sexually selected infanticide often offers much larger fitness benefits and accordingly, males have developed coercion as a counter-strategy to promiscuity. In baboons (*Papio ursinus*) and chimpanzees (*P. troglodytes*) for example, males use coercion to limit female promiscuity (Muller et al. 2011; Muller et al. 2007; Baniel et al. 2017), increasing their likelihood of paternity, thus making infanticide more likely.

Alternatively, females may choose to mate selectively, rather than promiscuously. This concentrates paternity certainty in fewer males, generally those who are high ranking (e.g. *Lemmus trimucronatus*: Huck and Banks, 1982). High ranking male mice (*M. musculus*) are more likely to be infanticidal and infanticide appears to be triggered by unfamiliarity with the mother (William Huck et al. 1982), so mating with these males would mitigate the risk of infanticide as the $P_i > p$ condition of the model would not be met since they have a high chance of having fathered existing infants. In addition, high ranking males may offer better protection against attackers as they are more likely to repel intruders (Jones & Nowell 1973). The most extreme form of this mating strategy is monandry when females mate with only one male (either in a monogamous or polygynous system). Under polygynous mating, males defend mating access to a group of females and expel intruders (e.g. gorillas, *Gorilla gorilla:* Watts, 1996) limiting opportunities for potentially infanticidal males to access the females. By concentrating P_i in one male, females ensure that he will not pose a risk to their infants. However, since all other males have a higher p than P_i, this makes non-group males highly dangerous. Females therefore trade infanticide protection for exclusively mating with a single male (Robbins et al. 2013). Under a socially monogamous system, males forgo new mating opportunities in order to associate continually with a single female (Black 1996). This continuous association means that males are able to provide infanticide protection. In altricial species, which are more vulnerable to infanticide due to a longer lactation period (C. P. van Schaik 2000b), infanticide risk may be high enough for males to benefit more from a high investment strategy in which they provide constant protection, rather than a low investment strategy in which they attempt to impregnate as many females as possible and risk their infants being killed by other males. Phylogenetic analyses of primates indicate that the presence of infanticide reliably predicts a shift to social monogamy among primates (Opie et al. 2013), indicating that social monogamy has emerged as a counter-strategy multiple times. An additional benefit for both sexes is that social monogamy and associated biparental care reduces energetic costs for mothers, facilitating shorter interbirth intervals (Lappan 2008).

Avoidance

In sexually dimorphic species, the smaller sex will likely to be unsuccessful and incur costs (injuries) if they attempt to defend against attacks from the larger sex. Mothers may therefore often have little chance of physically protecting their infants from attack. In this case, avoidance of dangerous individuals may be the most effective, lowest cost strategy. For example, tiger (*P. tigris*) mothers have been observed leaving their territory when it is invaded by a new male (Singh et al. 2014), presumably because the cost of losing the territory is lower than cost of encountering the male. Similarly, female red howler monkeys (*A. seniculus*) and lions (*P. leo*) leave groups which have too many females as these are more attractive to potentially infanticidal incoming males (Crockett & Janson 2000; Pusey & Packer 1987). By avoiding spending time in groups which are liable to be joined by dangerous males, these females are reducing infanticide risk. However, this is not without cost, for example, emigrating female howler monkeys delay reproduction and have poorer quality diets and increased mortality in the solitary period between groups (Crockett 1984). A fission-fusion social structure may allow individuals to reap the benefits of an avoidance strategy, without incurring many of these costs. Fission-fusion, in which social groups contain fluid subgroups of varying size (Y Sugiyama 1968), offers the opportunity for individuals to preferentially associate with or avoid each other, even while maintaining membership of the same social group and thus avoiding the costs of emigration. By avoiding joining subgroups containing dangerous individuals (e.g. adult males) mothers may be able to reduce the risk of infanticidal attacks (Otali & Gilchrist 2006). It has been suggested that female hyenas (*Crocuta crocuta*) employ this strategy (Smith et al. 2008) and that a reduction in female gregariousness during the perinatal period in chimpanzees *(P. t. schweinfurthii*) is an adaptive response to infanticide risk (Nishie & Nakamura 2018). Bottlenose dolphin (*Tursiops truncatus*) mothers also avoid males, tending to form subgroups with other mothers, based on their infants’ ages (Wells et al. 1987). This strategy would still include some costs, e.g. increased travel time if mothers have to regularly leave groups which are joined by dangerous individuals and potentially reduced feeding access if preferential feeding patches contain individuals they are avoiding. Such costs mean it would be adaptive for mothers to be very selective about which individuals to avoid and sensitive to variations in the risk posed, in order to maximise the benefits of avoidance while minimising the costs.

Infanticide in chimpanzees

Chimpanzees, polygynandrous great apes that live in patrilocal communities of 20 – 150 members (Goodall 1986; Boesch & Boesch-Achermann 2000; Watts 1998; Nishida 1990) are well documented as being infanticidal (Wilson et al. 2014; Townsend, Slocombe & Thompson 2007; Nishie & Nakamura 2018; Murray, Wroblewski, et al. 2007; N. Newton-Fisher 1999b). Between 1965 and 2014 there were 85 accounts of infanticide in this species (40 inter-community, 45 intra-community; reviewed in Wilson et al. 2014). Comparisons of frequency with other species are difficult due to differences in the number of study sites and observation methods. However these 85 accounts were across 16 communities and 426 study years indicating a rate of 0.01 per year. In comparison, a four year study of three langur (*P. entellus*) groups reported 11 infanticides (Sommer 1987) indicating a rate of 0.9 per year. Infanticide in chimpanzees is therefore well documented but, comparatively, not very common. Accounts of infanticide in chimpanzees are varied and not all consistent with one specific hypothesis, with cases variously supporting the sexual selection hypothesis (Nishie & Nakamura 2018), the nutritional benefit hypothesis (Watts & Mitani 2000), the resource competition hypothesis (Townsend, Slocombe, Emery Thompson, et al. 2007; Wilson et al. 2004) and none of the above (Murray, Wroblewski, et al. 2007).

Despite patchy evidence, chimpanzees are prime candidates for sexually-selected infanticide, in part because of the long period of lactational amenorrhea (Thompson et al. 2012) during which time the mother cannot conceive again, and the fact that more than 80% of victims are young (< 1 year old), meaning their deaths would lead to the biggest reductions in lactational amenorrhea (Hrdy 1974). Promiscuity is often suggested to be a counterstrategy to sexually selected infanticide (Palombit 2015; Ebensperger 1998), but it is debatable how effective this would be in chimpanzees as males appear to manipulate female mate choice, limiting female promiscuity (Muller et al. 2011). There is also the suggestion that males may offer protection to their own infants, preferentially associating with them, which may deter attackers (Murray et al. 2016), despite paternity confusion. In addition, there is some evidence that mothers exploit the fission-fusion social structure of chimpanzees to avoid risky individuals (Otali & Gilchrist 2006), although research on who exactly poses the biggest risk to infants is lacking.

Aims

Mixed evidence for the function of infanticide in chimpanzees is likely to be due to its relative rarity and the fact that it is underreported (17 of the 45 cases in a recent review by Wilson et al. (2014) were from unpublished data). This makes it difficult to spot trends, such as biases in the age or sex of attackers/victims. In this thesis I use long term data from the most infanticidal community of chimpanzees on record (the Sonso community in the Budongo Forest Reserve, Uganda: Wilson et al., 2014) to tackle this problem. Twenty-four years of data on this community have provided ample evidence of infanticidal behaviour and offer a unique opportunity to investigate the nature and function of this behaviour and related counter-strategies. In Chapter Three, I give a full and detailed description of every recorded infanticide and attempted infanticide at the site in order to understand who is at risk of being attacked and who the perpetrators are. I test which adaptive hypothesis best fits the observed cases and find strong evidence that most of the infanticide in this community fits with the sexual selection hypothesis. Chapter Four investigates a possible counterstrategy by mothers, specifically male avoidance, looking at individual relationships to test whether mothers avoid males based on relative risk. Since rank predicts paternity in chimpanzees (Newton-Fisher et al. 2010; Wroblewski et al. 2009; Boesch et al. 2006), any males who increase rapidly in rank will have a low chance of having fathered current infants compared to potential future infants, and therefore should benefit from infanticide. I find that mothers responded to this and selectively avoided a male who rapidly rose in rank, indicating that they are sensitive to the different levels of risk posed by various members of the community. The results also suggest that high-ranking males might offer protection to high risk infants. In Chapter Five, I look more closely at maternal avoidance. I interpret low association between mothers of young infants and a high risk male in Chapter Four as female driven so, in order to test this interpretation, in Chapter Five I use methods that will identify the directionality of social relationships so I can come to firm conclusions about which sex is responsible for low inter-sexual association. In this chapter I find further support for the hypothesis that female chimpanzees avoid males as an anti-infanticide strategy. Based on the indication in Chapter Four that some males might protect infants, Chapter Six addresses the counter-strategy of paternal care. Evidence from other chimpanzee communities has offered mixed support for the hypothesis that chimpanzee fathers invest in their offspring, perhaps protecting them against infanticide (Lehmann et al. 2006; Murray et al. 2016), but I find no evidence that fathers preferentially associate with their own infants.

Overall, in this thesis I provide new evidence that infanticide in my study community of chimpanzees largely fits the predictions of the sexual selection hypothesis and show that mothers are highly sensitive to male risk, employing various forms of avoidance to mitigate risk, while fathers appear to offer no direct protection.

2. Study Site, Population and General Methods

The Budongo Forest

The Budongo Forest Reserve is an area of 793km^2 near Lake Albert in Western Uganda which comprises both forest and grassland (Newton-Fisher 1997). The forested portion of the reserve is 428km^2 and, according to estimates made in the early 2000s, contained roughly 600 chimpanzees, a number which had remained static since a decade earlier (Plumptre et al. 2003; Plumptre & Reynolds 1996). The forest is a medium altitude, semi-deciduous, tropical forest (Eggeling 1947). Rainfall is frequent and heavy throughout the year, aside from a three month dry season from December – March and a brief, "little dry season" which occurs somewhat unreliably during June and July and is in fact is characterised by somewhat lighter rain, between periods of regular heavy rain (Newton-Fisher 1997). The dry season has average temperatures of over 30°C, which drop to the mid-20s at their lowest, during the middle of the year (Newton-Fisher 1997).

The Budongo Conservation Field Station (BCFS) is based at a now unused logging station. The Budongo Forest was logged as part of an attempt at sustainable harvesting between the 1930s and 1990s (Plumptre & Reynolds 1994). This was not the first time the area had been logged, as timber was taken, although at much lower levels, from around 1910 (Plumptre 1996). Most portions of the forest have been harvested at least once and mahogany was the primary focus (Plumptre & Reynolds 1994). This has resulted in an increase of "mixed forest" at the expense of "Cynometra forest" (Plumptre and Reynolds 1994; for definitions see: Eggeling 1947). This kind of selective logging can benefit chimpanzees, as the secondary forest increases opportunities for fruiting trees, such as figs, which provide food. There is however evidence suggesting that chimpanzee densities may be lower in secondary forest than in mature forest (Plumptre & Reynolds

1994). As well as logging, chimpanzee diets at Budongo have also been influenced by the introduction of exotic species, notably *Broussonettia papyifera*, which is the largest single dietary item for Sonso individuals and was imported by the British in the 1950s as a possible cash crop for paper manufacturing (Reynolds et al. 1998).

Research at Budongo

In the early 1960s Vernon and Frankie Reynolds studied the chimpanzees of the Budongo Forest, (Reynolds & Reynolds 1965). Due to war and unrest, chimpanzee research in this area ceased during the 1970s and 1980s but began again in the early 1990s and focused on a community named Sonso, after the river that passes through their territory (Reynolds 2005; Newton-Fisher 1997). The Budongo Forest Project, now BCFS, was established formally in 1991 (Newton-Fisher 1997).

This research described in this thesis complied with regulations set by the Research and Ethics Committee of the School of Anthropology and Conservation, University of Kent, the protocols of the Budongo Forest Project (now BCFS) and the legal requirements of Uganda.

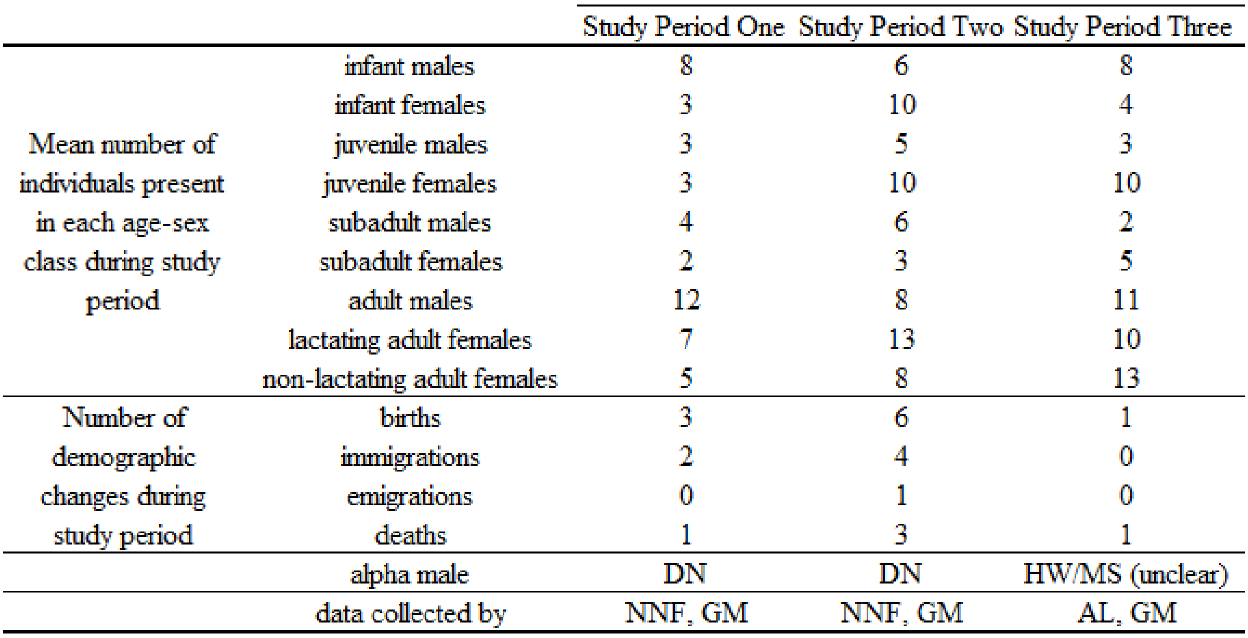
The Chimpanzees

The chimpanzees of the Budongo Forest are of the Eastern subspecies (*Pan troglodytes schweinfurthii*). There are currently two habituated communities of chimpanzees at BCFS: Sonso and Waibira. Sonso community has been under continual observation by researchers since the early 1990s (Reynolds 2005; Newton-Fisher 1997). Since around 1993 the majority of community members have been fully habituated to human observers and have been individually recognised, making behavioural research possible (Reynolds 2005; Newton-Fisher 1997). Habituation of Waibira community began in 2011 and due to the presence of Sonso born females who were well habituated at the time of their emigration, has progressed very rapidly (Samuni et al. 2014).

The Sonso chimpanzees' home range covers ~7km^2 of the forest. It is a mosaic of multiple different forest types, including *Cynometra* forest, mixed forest, colonising forest and swamp, as well as open areas including the research camp as well as farm fields and gardens along the forest edge (Newton-Fisher 2003). The fact that the Sonso community's home range extends to the limits of the forest means that crop raiding is common (Tweheyo & Lye 2005).

This thesis uses data from three different study periods (see below). Due to the long life span of chimpanzees, several individuals are represented in all three data collection periods. Because of births, deaths, immigrations and emigrations, the composition of Sonso community has changed between these study periods (Table 2.1).

Table 2.1. *Demographic information for the three study periods; average number of individuals in each age-sex category in Sonso community across the three study periods as well as any changes during the study period, the identity of the alpha male and the researchers who collected the data (NNF = Dr Newton-Fisher, GM = Mr Muhumuza & AL = myself).*



		Study Period One	Study Period Two	Study Period Three
Mean number of individuals present in each age-sex class during study period	infant males	8	6	8
	infant females	3	10	4
	juvenile males	3	5	3
	juvenile females	3	10	10
	subadult males	4	6	2
	subadult females	2	3	5
	adult males	12	8	11
	lactating adult females	7	13	10
	non-lactating adult females	5	8	13
Number of demographic changes during study period	births	3	6	1
	immigrations	2	4	0
	emigrations	0	1	0
	deaths	1	3	1
	alpha male	DN	DN	HW/MS (unclear)
	data collected by	NNF, GM	NNF, GM	AL, GM

Data used in this thesis

The data used in Chapter Three to compile a full history of infanticides at Sonso were extracted by me from PDF scans of log books belonging to BCFS. These books contained written records of any novel or interesting behaviours exhibited by the chimpanzees and were filled in by researchers, field assistants, the veterinary team and any other observers who happened to be present. I received scans of all pages of all books since records began in 1993 and went through everything, making notes on incidences of infanticide and non-lethal attacks on infants or mothers in order to create the dataset used in Chapter Three (Appendix 2).

Chapters Four, Five and Six use behavioural data collected at Sonso over three time periods: a period of 14 months in the early days of research at the site (period one: October 1994 – December 1995), a period of 16 months a decade later (period two: October 2003 – January 2005) and a shorter, three month period more recently (period three: April – June 2017). During the first two periods, data was collected by Dr Nicholas Newton-Fisher and field assistant Mr Geresomu Muhumuza. In study period one, party composition was recorded using scan samples every 15 minutes and in study period two it was recorded every five minutes. In both periods, aggression was recorded using all occurrence sampling. During these periods, data were collected during nest to nest focal follows (as much as possible). When a focal individual was lost, a new focal was selected from the next party observed. While these periods were a long time apart, data were collected by the same two people and was therefore appropriate to be used together, as in Chapter Five. I also worked with Geresomu during my data collection period, ensuring some consistency between the earlier and later periods. The data from study periods one and two were provided to me by Dr Nicholas Newton-Fisher in the form of both raw excel files and original paper data collection sheets. I entered the data in the same format as the excel files with which I was provided in order to expand the raw dataset which I then worked with.

For this thesis I spent 11 months in the Budongo forest. Two of these (August – September 2016) were for an initial pilot to investigate the possibility of collecting behavioural data on a second, newly habituated, community of chimpanzees at the site, called Waibira. I returned at the beginning of April 2017 and stayed until the end of the year. I spent April, May and June collecting behavioural data on the Sonso community and the rest of the year collecting faecal samples from the Waibira community for additional projects which did not eventually form part of this thesis. Chapter Five used the three months of behavioural data I and Mr Geresomu Muhumuza collected together in 2017. In this period we worked an eight day work cycle comprised of three days on, one day off, three days on and two days off, in accordance with BCFS regulations. A full work day, as set by BCFS was 7am until 4pm, during which we followed the first of our pre-selected focal individuals until we lost contact, then switching to the next pre-selected focal we encountered. Geresomu and I worked together, following the same focal animal. He collected party composition and nearest neighbour data at 15 minute intervals, while I collected directional spatial data. The directional spatial data involved considering a 2m radius around my focal animal and recording all incidences of other adult individuals entering it and the directionality (i.e. who approached whom), as well as any responses from the approached individuals which were then categorised into “affiliative” (groom, touch, present: taken from Goodall, 1989), “non-affiliative” (aggression or threat behaviours: detailed in Newton-Fisher, 2017), “other” (all other behaviours), or “none”. These broad categories were used because responses were very rare since most close spatial association appeared to be incidental (i.e. individuals were feeding on the same food source, rather than individuals approaching each other and initiating social interactions).

Together Geresomu and I collected 708 party composition scan samples representing 177 hours and 1162 spatial interactions. These were collected during 137 focal samples. Of these focal samples, 46.6 hours were of females exhibiting no sexual swellings or indications of pregnancy, 23.1 hours were of pregnant females and 8.5 hours were of females with sexual swellings. The remainder were of the lactating mothers.

Limitations of the data

Because much of this thesis used pre-existing data and long term site records, I was limited in the questions I could ask and the analyses I could run by the nature of the data. Two key limitations are the lack of reliable long term rank data and absence of paternity data for many of the infanticide victims and some living individuals. A lack of rank data prevented me from looking in more detail at the relationship between male hierarchy and infanticide rates, which would have been a valuable addition to this thesis. A lack of information on paternity for many of the living individuals limited the sample size in Chapter Six, however, as discussed there, for paternal care to offer meaningful benefits it would have to be a large effect, visible even in a relatively small sample. In addition, it was also rarely possible to retrieve the bodies of infanticide victims for paternity analysis. Attackers either carried the body all day and were then observed the next day without it, or observers lost sight of them. In most cases it would have been impossible to collect the carcass without interfering. This meant that it was not possible to directly test two of the key predictions of the sexual selection hypothesis, that of males not targeting their own infants and killers fathering subsequent infants. However, there is enough other support for this hypothesis, presented in Chapter Three that this does not significantly weaken my conclusions.

Due to BCFS only allowing me limited time in the field (due to rules about the number of researchers who can work with the chimps at any one time), my own data collection was somewhat constrained. I had to collect dense data to have a large enough dataset for meaningful analyses after only three months. The directional data, due to being all occurrence recording of a very frequent behaviour allowed me to create a dataset of 1162 observations in a short period of time. This novel approach allowed me to investigate spatial association in a new way, was sufficient to answer my research questions in Chapter Five and was valuable in validating my interpretation of results in Chapter Four. However, this short period of data collection with only a small number of focal individuals meant I could not address additional questions, such as the effect of reproductive state on close spatial association of individuals and I was limited to only addressing a very specific research question.

Since the data in this thesis was collected by multiple different people, reliability is a concern. The log books used in Chapter Three are the least reliable of the various data used, since they are qualitative reports from a variety of different observers. In an attempt to reduce potential issues stemming from this, I created specific, conservative definitions of all behaviours extracted from these reports (i.e. what counts as “defence” of an infant) and excluded observations which were ambiguous for any reason (for full details of this process, see Chapter Three, Materials and Methods). Mr Geresomu Muhumuza collected data in all three study periods, creating some consistency, and data which were combined for analysis (that of study periods one and two, in Chapter Six), were both collected by the same observers, Dr Newton-Fisher and Mr Muhumuza.

Statistical analysis

All data were organized and analysed in R, version 3.4.3 (R Core Team 2013), and all graphs were produced in R, using the package “ggplot2” (Wickham 2016). In this thesis I make extensive use of linear mixed effects models using the R package "lme4" (Bates et al. 2015). These are a powerful statistical tool which, due to the ability to control for repeated observations of the same individuals, are ideal for analysing behavioural data from wild animals. These models make specific assumptions about the data: that variables are not co-linear (i.e. variance inflation factor (VIF) is < 2), that the data follows a straight line, that the residuals are normally distributed and that there is homogeneity of variance (homoscedasticity) (Zuur & Ieno 2016). In all cases where these models are used, these assumptions were verified by calculating VIFs and plotting residuals and assessing for temporal and spatial dependency.

3. Infanticide at Sonso: a review

Published as: Lowe A, Hobaiter C, Asiimwe, C, Zuberbuehler, K & Newton-Fisher N (2019) Infanticide in wild, eastern chimpanzees: a 24 year review. Primates

*The use of "we" in this chapter reflects the contribution of my co-authors who all provided comments on the manuscript. I devised this chapter, extracted the data from the long term records, analysed the data and wrote the chapter, with the help of my co-author's comments.

Abstract

Infanticide by chimpanzees has been documented at multiple research sites but no clear pattern indicating an adaptive function has yet been identified. While the sexual selection hypothesis for infanticide is generally assumed to explain some cases, no attempt has been made to test this hypothesis in chimpanzees and there are also a variety of recorded cases in which the predictions of this hypothesis do not apply (i.e. infants are comparatively old or attackers are female). Here I use 24 years of records from the Sonso community of chimpanzees in Uganda to test several hypotheses for infanticide: the sexual selection hypothesis, the resource competition hypothesis, the resource exploitation hypothesis, and the male mating competition hypothesis. I also consider the possibility that infanticide in chimpanzees is not adaptive at all. I found that a) infanticide is very common in this community, occurring much more frequently than at any other site and b) the vast majority of infanticides fit with the prediction of the sexual selection hypothesis. There were also infanticides which did not fit the sexual selection hypothesis however, predominantly those committed by females. These were too rare to identify a likely adaptive function.

Introduction

Intra-community infanticide is well documented in chimpanzees *(Pan troglodytes)*. In a 2014 review of 12 eastern (*P. t. schweinfurthii*) and six western (*P.t verus*) populations of chimpanzees, as well as 4 bonobo (*Pan paniscus*) populations, 45 observed, inferred, or suspected intra-community infanticides by chimpanzees were reported (Wilson et al. 2014). Of these, only one was from a West African population and none were from a bonobo population. Since then, one further East African case has been reported in the literature (Nishie & Nakamura 2018), although it is likely that there have been other unreported incidences in the intervening years: this behaviour appears to be under-reported, with 17 of the 45 cases complied by Wilson et al. (2014) drawn from previously unpublished data. It is also possible that other cases go not only unreported but unobserved, particularly if they occur immediately after birth, with the infant(s) never seen by researchers. Infanticide is likely to be an important selective pressure, given the slow reproductive rate of chimpanzees and the substantial energetic costs for mothers of pregnancy and lactation (Emery Thompson 2013; Murray et al. 2009), and detailed information on the nature of infanticidal attacks is therefore particularly valuable.

The sexual-selection hypothesis for infanticide states that males should kill infants when they are unrelated, and when doing so will increase the attacker's chances of reproducing with the mother (Hrdy 1979; Sommer 1987; C. van Schaik 2000a). Support for this hypothesis has been found in a variety of primate species (Borries, Launhardt, Epplen, Jîrg T Epplen, et al. 1999; Daly & Wilson 1984; Palombit et al. 2000; Watts 1989a), but not explicitly in chimpanzees. The adaptive benefits of sexually-selected infanticide will be reduced in multi-male groups, due both to higher paternity uncertainty making it more likely a male will kill his own infant, and competition for the mating opportunity created. Despite this, male infanticide is documented in several primate species which live in multi-male groups (for example: red colobus *(Piliocolobus badius)*: Struhsaker and Leland, 1985; Hanuman langurs *(Semnopithecus entellus)*:

Borries, 1997; chacma baboons *(Papio ursinus):* Palombit et al., 2000), and chimpanzee infanticide is often assumed to be sexually selected. However, and despite frequently being used as an explanatory factor when interpreting chimpanzee behaviour (Murray et al. 2014a; Murray et al. 2016; Otali & Gilchrist 2006), the hypothesis has not been tested explicitly in this species.

Predictions can be generated from this hypothesis to test whether instances of infanticide are likely to be part of an adaptive reproductive strategy by male chimpanzees. Lactation prevents females from ovulating (McNeilly et al. 1994), meaning that infants are an obstacle for males seeking reproductive opportunities. A younger infant is a larger obstacle, as it represents a longer period until the mother will be sexually receptive again. This is quantified in van Schaik (2000)'s model for sexually selected infanticide in which *B* (benefit for the perpetrator of committing infanticide) is the reduction in time until the mother is free to mate again which a male could bring about by killing her present infant. *B* will be largest when infants are youngest and therefore this hypothesis predicts that the majority of infants be very young (infants << one yr). In addition to infants being very young (sexual selection hypothesis prediction one (S1)), killers should not kill their own infants (prediction S2) and should often father replacement infants (prediction S3). Attackers should be males (prediction S4), and victims should be neither predominantly male nor female since both represent an equal obstacle to mating with the mother (prediction S5). All predictions are summarised in Table 3.1. Mothers should generally be unharmed (prediction S6): they are not the primary targets, and severely injuring a female may compromise future mating opportunities. Existing data provide mixed support for the sexually-selected infanticide hypothesis. Of the 35 intra-community infanticides reported by Wilson et al., (2014), excluding those from our study site (the Budongo Forest Reserve, Uganda), in eight instances the attackers were male, in six instances they were female, while both sexes were attackers in two instances; the sex of the attackers was unknown in 19 cases. The mean age of victims where age was known (31 cases) was 0.46 years (SD 0.79) and infanticide would, therefore, shorten the mother's period of lactational amenorrhoea by several years (average weaning age 4.5 – 5.5: Pusey, 1983; Bădescu et al., 2017). While the sexual selection hypothesis predicts that males will benefit from killing young infants, the age of victims killed by females (who do not benefit from shortening a female's period of lactational amenorrhoea) was even lower (mean age 0.09 years, SD 0.07) than that of those killed by males (0.80, SD 0.38). Male infants were killed more frequently than female infants (19 versus seven incidences respectively), although these data were not adjusted for potential short-term variation in the birth sex ratio. Mothers were often unharmed, even when the infants were taken in circumstances where the attackers seemed capable of killing them as well (Wilson et al., 2014). Based on existing data, predictions S1 and S6 (infants are young and mothers are often left unharmed) are supported, but not predictions S4 and S5 (no sex bias in attackers, and a bias towards male victims, although this may not be statistically significant and in many cases no data is available on attacker or victim sex). Data on paternity is often lacking in cases of infanticide, partly due to the difficulty of retrieving corpses for analysis. Infants were deemed unlikely to be, or definitely not, sired by attackers in some cases (Nishie & Nakamura 2018; Murray, Wroblewski, et al. 2007) but attackers were considered possible fathers in others (Wilson et al. 2004; Nishida & Kawanaka 1985). Data on whether killers commonly sire subsequent offspring with the mothers of their victims are also lacking, so there is not enough evidence to evaluate predictions S2 and S3.

Table 3.1. *Summary of predictions generated by different hypotheses for the function of infanticide in chimpanzees*

Hypothesis	Prediction	Prediction Details
Sexually Selected Infanticide	SS1	victims are very young
	SS2	killers do not target their own infants
	SS3	killers often father replacement infants
	SS4	attackers are always male
	SS5	no sex bias in victims
	SS6	mothers are generally unharmed
Resource Competition	R1	attackers are predominantly female
	R2	no sex bias in victims, or a trend towards male victims
Meat Acquisition	M1	victims are always eaten and eaten in their entirety
	M2	the killer always eat the carcass
	M3	attackers are predominantly female
Male Mate Competition	MC1	attackers are always male
	MC2	victims are always be male

An alternative, although not incompatible, hypothesis for infanticide is competition over food resources (Hrdy 1979). According to this resource-competition hypothesis, individuals may kill infants who are, or will become, competitors for resources (Hrdy 1979), and, in order for such killing to be adaptive, it must result in greater access to resources, such as food for the killer and/or their kin (Hrdy 1979). Resource-competition motivated infanticide is often between females (e.g. Belding's ground squirrels (*Urocitellus beldingi*) in which infanticidal females can gain access to better nest sites by killing the young of other females who then abandon their "unsafe" burrows: Sherman, 1976). As female fitness is linked to resource quality in chimpanzees (Emery Thompson, Kahlenberg, et al. 2007), females may benefit by removing future competitors for these resources. Female committed, resource competition motivated, infanticide in chimpanzees would therefore be typified by a pattern of female attackers (resource competition hypothesis prediction one (R1)) and no bias in the sex of victims or a trend towards male victims (prediction R2), since both sexes represent food competition while resident in the group but males will stay resident their whole lives, representing longer period of competition. Of the reported cases of infanticide at all sites excluding our study community, there was no sex bias in attackers: six attacks were by females only, eight by males only and two had attackers of both sexes (Wilson et al. 2014). Twice as many attacks had male victims (eight vs four: Wilson et al. 2014). Females were no more likely to attack male infants than female infants (female only attackers killed two male and two female infants, as well as two of unknown sex: Wilson 2014). Resource competition is unlikely to account for the infanticides committed by males but may be a factor in the female-committed infanticides.

It is also possible that rather than, or in addition to, being a competitor *for* food resources, the infant could *be* the resource. Meat is an important source of protein for chimpanzees and may provide necessary micronutrients (Fahy et al. 2014; Tennie et al. 2009). Hunting is not always successful and success rates vary between communities, from 42% in the Sonso community (Hobaiter et al. 2017), 52% at Gombe (Stanford et al. 1994), 60% at Mahale and Taï (Hosaka et al. 2001; Boesch & Boesch 1989) and 72% at Ngogo (Watts & Mitani 2002). Hunting frequency is correlated with fruit abundance (Mitani & Watts 2001; Gilby & Wrangham 2007), indicating that it involves an energetic cost, and since unsuccessful hunts yield no compensatory benefits, opportunistically snatching conspecific infants may be a comparatively lower cost way to obtain meat. This hypothesis predicts that the carcasses of victims will always be eaten and eaten in their entirety, as the primary motivation will be to acquire meat (meat acquisition hypothesis prediction one (M1)). In addition, the killer should always be the one (or at least one of the individuals) to eat the carcass, if cannibalism is the underlying cause (prediction M2). This hypothesis does not predict a bias in sex or age of the victims, unlike in hypotheses such as sexual selection, where infant age is a key factor. Younger infants may be easier to snatch as they are less able to defend themselves, but chimpanzees regularly hunt *Pilocolobus tephreosceles* and *Colobus guereza* which reach up to 13 and 23kg respectively (Kingdon 1997; Newton-Fisher et al. 2002; Stanford et al. 1994) and since a five year old chimpanzee weighs an average of ~20kg (Grether & Yerkes 1940), adults should be able to prey on them throughout the infancy period. In addition, larger infants could be preferred as they are less likely to be in direct contact with the mother and would make a more substantial meal. Overall, the main factor in selecting a victim would be the opportunity to snatch it from the mother, meaning victims would be a mix of different ages.

In most communities, female chimpanzees are less likely to be actively involved in hunting and consequently eat less meat (Mitani and Watts, 2001; Watts and Mitani, 2002; Reynolds, 2005; but see also: Pruetz and Bertolani, 2007; Newton-Fisher, 2015). Mitani and Watts (2002) reported only five kills by females of prey animals (red and blue duiker, red colobus) during a 32-month observation period in which 131 predation episodes were witnessed, indicating that females especially could benefit by targeting the young of conspecifics as an alternative source of meat. If meat acquisition is the primary motivation for infanticide in chimpanzees, attackers should be predominantly females (prediction M3) as they have reduced access to other meat sources, and, unlike males, who do not know which infants they have fathered, will not risk accidentally killing their own offspring when targeting infants as a food resource. This hypothesis does not preclude the possibility of attacks by males, but attacks should be primarily perpetrated by those individuals who have fewer alternative sources of meat. Cannibalism is well documented in infanticide cases (Goodall 1977; Nishie & Nakamura 2018; Watts & Mitani 2000; N. Newton-Fisher 1999b; Kirchhoff et al. 2018; Takahata 1985; Walker et al. 2018), and is the norm in at least two populations (12 of 14 within group incidences in the Kanyawara study community, Kibale, Uganda: Arcadi and Wrangham, 1999, and all cases in which the infanticide was successful at Gombe, Tanzania: Murray et al., 2007). However, infanticide victims tend to be exploited less fully than prey animals with less meat-rich areas (such as hands and feet) more likely to be eaten (Kirchhoff et al. 2018).Infanticide without cannibalism has also been reported, including at Budongo (Townsend, Slocombe, Emery Thompson, et al. 2007; Arcadi & Wrangham 1999). While a lack of a sex bias in victims supports this hypothesis, the bias towards younger victims and the frequency of male attacks (Wilson et al. 2014) suggests that in many cases, resource acquisition is not the primary motivation for most infanticides.

A fourth hypothesis for explaining infanticide in chimpanzees is male mating competition. While females should compete over food, male fitness is primarily constrained by access to females (Bateman 1948), making fertile females their most valuable resource. Males could potentially target male infants who will one day be competitors for this resource, and this has been proposed as an explanation for infanticide in both chimpanzees (Takahata 1985) and langurs (Agoramoorthy & Mohnot 1988). This hypothesis generates the predictions that infanticides should be committed by males (male mating competition hypothesis prediction one (MC1), and that they should target male infants (prediction MC2). Of the eight male committed intra-community infanticides reported for chimpanzees at sites other than Budongo, five involved male victims and one had a female victim, while the sex of two victims was unknown (Wilson et al. 2014). These data offer some support for the male sexual competition hypothesis, although the attack of the female infant by males, and the attacks by females, require alternative explanations.

Materials and Methods

Data collection

The Budongo Conservation Field Station (BCFS, previously Budongo Forest Project) has collected behavioural data on the Sonso community of chimpanzees since 1993 (Plumptre 1996; Reynolds 2005; Newton-Fisher 1997), alongside demographic information tracking births, deaths, immigrations and emigrations. The Sonso community's territory comprises ~7km^2 of moist, medium altitude, semi-deciduous rainforest within the 428km^2 Budongo Forest Reserve (Newton-Fisher 1997; Eggeling 1947; Newton-Fisher 2003). During the study period (1993 – 2017), the Sonso community consisted of 34 – 71 individuals (median: 60). The number of adult males (≥ 16 yrs) ranged from 5 – 15 (median: 10) and the number of adult females (≥ 14 yrs) ranged from 16 – 28 (median: 23).

Ages of individuals who were adults when data collection began were estimated (by comparison to known-age individuals in other habituated communities, particularly the Kasakela community, Gombe National Park, Tanzania: Reynolds 2005)., as were those of females who emigrated into the community. Infant ages were calculated from the birth date when known, or the midpoint of a date range when the exact date was unknown.

Data analysed here were collected by field assistants and researchers studying this community between 1993 and 2017. Both field assistants and researchers recorded unusual or rare events in a series of log books maintained by the field station. While such qualitative reports form an imperfect record, infanticides are an event of sufficient rarity and interest that they are typically recorded in considerable detail. We used these records to compile as comprehensive a history as possible of intra-community infanticides among the Sonso chimpanzees. We collated all accounts of infanticide and extracted, for each case: date, identity, age and parity of the mother, age and sex of the infant at the time of the attack, injuries sustained, whether the attack was successful or not (i.e. did the infant survive), whether the infant was cannibalised, age and sex of the attacker(s), injuries to the mother, and whether or not other community members defended the victim.

Long-term demographic records from BCFS show 103 infant births, and 50 deaths or disappearances of individuals aged under five years, since data collection began (1993

– 2018). Of these 50 cases, we excluded four where uncertainty around birth and/or disappearance dates made it possible that they were no longer infants at the time of disappearance, and five that were definitely or likely to be infants from neighbouring communities. We also excluded three further, more ambiguous, instances (for example: where Sonso-community individuals were found with an infant chimpanzee carcass within the peripheral areas of their territory). The final dataset for analysis consisted of 38 deaths/disappearances of infants between 1993 and 2017. It was not always clear whether an attack was inter- or intra-community when it was not observed directly, so we used location to infer in some of these cases, i.e. attacks that occurred inside the community territory were assumed to be intra-community attacks, even if it was not obvious to which female the infant belonged. Given the fission-fusion nature of chimpanzee social organisation, particularly in East African chimpanzees, peripheral female chimpanzees in the Sonso community may not be seen for months or (rarely) years. As a result it is likely that both births and infanticides are missing from the data, and an infanticide may be intra-community, even where the mother cannot be identified.

Data analysis

Calculating frequency of infanticide

We categorised each death/disappearance according to the likelihood that it was due to an infanticidal attack (Table 3.2, for full details of all attacks see Appendix 2). Only those incidences when the moment of death, fatal wounding, or permanent separation from the mother were observed were listed as definite infanticides. When attacks were observed and infants disappeared or died days later, these were listed as "almost certain." We considered incidences in which infants had severe injuries to be indicative of infanticide, particularly when those injuries were unlikely to be sustained by a fall and were reminiscent of those sustained in observed attacks (e.g. bite marks, disembowelling).

These were listed as “almost certain” or “suspected” depending on the injuries sustained and behaviour of other individuals in the vicinity. Leopards (*Panthera pardus*) are absent from the study area (Schel & Zuberbühler 2009) and crowned-hawk eagles (*Stephanoaetus coronatus*), despite killing monkey prey of up to ~11kg, appear not to prey on chimpanzee infants (Sanders et al. 2003). Predation pressure is therefore low in the Sonso community and injuries that are not consistent with a fall (e.g. limbs or scalp torn off) are likely to be inflicted by conspecifics. Where mothers were seen carrying dead infants but no attack was observed, this was categorised as “suspected” if an infanticidal attempt had been observed in the previous days. We consider the majority of “unknown” deaths to be relatively unlikely to be infanticides: Sonso community chimpanzees are observed by researchers almost every day, and most observed infanticide events have included multiple, loud vocalisations and substantial commotion. Field assistants are in the habit of investigating when the chimpanzees’ vocalisations indicate an unusual event and are likely (although not certain) to be alerted to infanticidal attacks.

Attempted infanticides

We also considered failed attempts to commit infanticide and attacks on the mother with the potential to cause infant death, but in which the infant survived (i.e. severe, prolonged physical attacks on mothers who were currently holding infants). There were nine such cases. In four of these nine cases, an attempt to snatch the infant was explicitly recorded. One of these four infants was killed at a later date. Of the five infants whose mothers were attacked but no clear attempt on their own life was made, three were later killed. We therefore consider all these attacks to be attempted infanticides, regardless of whether an attempt to take the infant was observed.

Defence of infants

On several occasions, records indicated that third parties provided some form of defence for the mother and infant. We excluded cases in which observers only attributed motivations to individual chimpanzees but did not provide behavioural details (for example: simply stating that X wanted or tried to defend). We retained cases in which named individual chimpanzees were recorded as either attacking the infanticidal individual(s), or chasing them away. In one instance an individual who initially acted as a ‘protector’, subsequently attacked the mother himself; we did not count this as defence.

Results

Example one: Male-committed infanticide.

Date: 08/04/2016

Adult female Irene is in a party with three other adult females. She has a six day old male infant. At 10:30 adult male Frank joins the party and approaches Irene. She pant grunts to him. A few minutes later Frank moves closer and Irene pant grunts again. At 10:45 Frank chases Irene into the undergrowth and emerges holding her infant, followed immediately by Irene, who is screaming at him. The infant’s belly is ripped open. At 10:50 Frank begins to eat the infant. After a few minutes, he swings the carcass against the undergrowth and throws it away. No other individuals intervened or became involved.

Observers: Geresomu Muhumuza, Charlotte Grund

N.B. male committed infanticide (a different incident) is depicted in Figure 3.1

Example two: Female committed infanticide

Date: 06/09/2013

Observers hear screaming at 15:25. On investigation they find a party containing two adult females, an adolescent female and two males. There is lots of blood and pieces of flesh on the ground. Night, the adolescent female is dragging a newborn male infant along the ground. The infant is still alive at this point. The infant dies soon after, by around 15:30. Night and her mother sit with the carcass and defend it by barking at other individuals when they approach. An hour later, at 16:30 Night and her mother leave. For ten minutes from 16:30, another adult female, Mukwano, feeds on the carcass.

Observers: Monday Gideon, Geresomu Muhumuza, Chandia Bosco, Carol Asimwe

Example three: Male committed infanticide; attempted defence by female relative

Date: 27/09/2017

At 14:30, alerted by vocalisations, observers come across a party of five adult females, an adolescent female and one adult male. The adult male, Musa, is attacking Ramula, a young natal female who is holding a new-born infant of undetermined sex. Ramula is attempting to shield the infant and Musa is repeatedly beating her on the back and attempting to grab the infant. The baby has a large head wound; much of the scalp has been ripped off. Ramula's mother, Ruhara, gets between Musa and Ramula and attacks Musa. Musa's mother Nambi becomes involved, screaming and attacking Ramula. The adolescent female approaches Ramula and is bitten by Nambi. The attack dies down and Ruhara sits between Musa and Ramula. The infant son of one of the other females picks up pieces of the victim's scalp from the ground and plays with it. Other individuals approach the group and as Musa looks towards them, Ramula runs away. She is followed by several adult males who have just arrived. They all surround her and look at the baby *which is still alive and whimpering. Ramula then drops the baby, which is retrieved by her mother, Ruhara. They travel together and observers lose sight of them.*

Observers: Adriana Lowe, Geraldine Ischer, Monday Gideon

Figure 3.1. *Two adult males (Hawa, left, and Frank, right) with a freshly killed infant. Credit: Mathilde Grampp*

Frequency of attacks

There were a total of 11 ‘definitive’, four ‘almost certain’, and nine ‘suspected’ infanticides, as well as nine ‘attempted’ infanticides (Table 3.2), making a total of 33 attacks on 30 victims. We hereafter consider all these together and refer to them throughout as “attacks.”

Table 3.2. *Categories of infant deaths and attacks on mothers/infants*

Category	Definition	Frequency
definite	Kill, fatal wounding or separation from mother observed	11
almost certain	Attack observed, infant subsequently died or disappeared	4
suspected	evidence points towards infanticide (injuries, behaviour of mother/other individuals)	9
unknown	no evidence either way	11
non-infanticidal	evidence for alternative explanation	3
attempted infanticide	The mother is violently attacked. An attempt to snatch the infant may or may not have been recorded.	9

Attacks were not evenly distributed across time (Figure 3.2). There were between zero and seven intra-community infanticidal attacks per year (median = two). The highest number occurred in 2013 and 2017, with these years seeing seven and five attacks respectively. In addition there were six non-intra-community infanticides (cases which were either certainly inter-community or there was no evidence to suggest whether it was inter or intra-community) and one non-intra-community attack in which the outcome was uncertain (the infant may have survived).

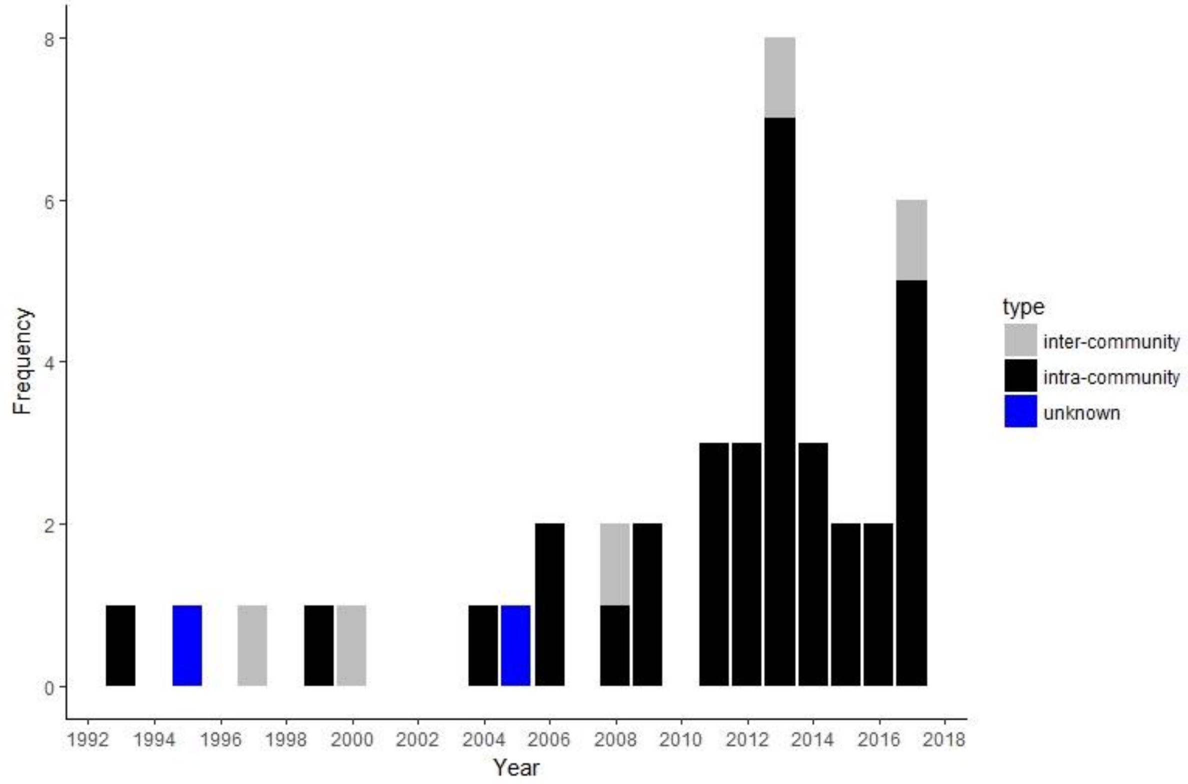


Figure 3.2. *Attacks (failed and successful) by year and type*

Age and sex of victims of attacks

In general, victims of attacks were very young (Figure 3.3). Excluding two infants whose age was unknown, victims had a mean age of 29 (+/- 85) days. There were three outliers where the targeted infants were aged 120, 180 and 439 days. Excluding these, the mean age of victims was six (+/- eight) days. All but three incidences occurred when infants were under five weeks old and 2/3 of the attacks for which the age of the victim was known were on infants under one week in age. Of the 33 attacks, 11 of the victims were female, eight were male and 11 were unsexed (30 victims total despite 33 attacks as three infants survived only to be killed in a subsequent attack). The difference in the number of male and female victims was not significant (exact binomial test: p = 0.58). Infanticidal males did not preferentially target male infants (adult male only attacks where infant sex was confirmed: 10 female infants, five male infants: exact binomial test p = 0.67) and female only attacks with victims of confirmed sex were too rare to identify any trend (one female victim, two male victims).

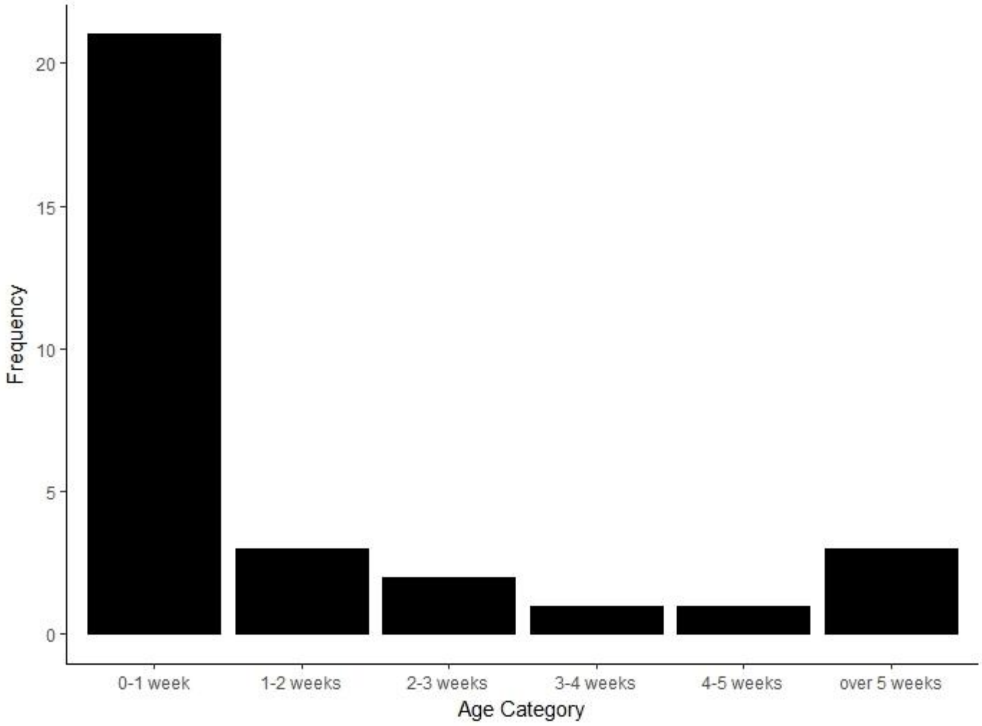


Figure 3.3. Frequency of attacks (failed and successful) by age category of the victim

Cannibalism

In some instances, victims of infanticide were cannibalised. In 19 cases, observers were able to ascertain whether the victim was cannibalised because either the whole attack was observed, or the carcass of the infant was seen by observers subsequently. Cannibalism was observed in six (32%) of cases: in three, the attacker(s) cannibalised the victim, in one case an individual who may or may not have been the attacker cannibalised the victim and in two cases individuals who were not involved in the attack cannibalised the victim. Cannibalism was probable in one further case (due to the absence of some body parts), giving an estimated cannibalism incidence of 37%. In most cases, records did not describe the amount of the carcass which was eaten but in one case only the eyelids were consumed and in another an individual is described as feeding for nearly ten minutes, indicating that the amount eaten varied. In another case, the cannibalistic individuals moved off "leaving only the head behind", but it is not clear if all other parts were cannibalised or the remaining parts were taken by the individuals who left or simply scattered and left behind. Body parts specifically mentioned being eaten are eyelids, fingers and a limb and in once case an attacker is described as biting into the belly. Mothers and maternal kin of the victims were not observed cannibalising their kin.

The mother

Mothers whose infants were subject to attacks were aged between 14 and 39 years (median = 21 years, mode = 15 years). The mean age did not vary between mothers of infants who survived attacks and those that were killed (23 and 24 years respectively).

Of the 37 Sonso community females recorded giving birth since 1993, six were natal females. Of the 33 attacks, 10 were on natal females and their offspring, 22 were on non-natal females, and in one case the mother was unidentified. Despite only 8% of births being from natal mothers, and their infants making up 30% of victims, natal females were not statistically more likely to lose infants to infanticide than immigrant females. The difference in the proportion of natal females in the community overall and the subset of females whose infants were attacked was not significant (2-sample proportion test $p = 0.09$).

Some infanticidal attacks involved considerable aggression towards the mother, with the mother suffering visible injuries in 10 of the 33 attacks. Injuries included bleeding and limping but nothing visibly more serious. In the remaining 23 cases, mothers sustained no visible injury. No mother died at the time of or within several months (or indeed years) of these attacks. No females disappeared in the immediate aftermath of an attack but one female disappeared seven months after her infant was killed and is presumed to have emigrated.

Excluding females who lost infants during the final year of the study period, who would not have had time to conceive and gestate another infant, 89% went on to successfully give birth again in the community. The average time from infant death to next conception (calculated by subtracting 225 days, the average gestation period for this subspecies (Wallis 1997b), from the birthdate of the subsequent infant), was 251 days; much lower than the average interbirth interval in this community when infants survive (1907 days: Emery Thompson et al., 2007b).

Infants of primiparous mothers made up 39% of victims (12 out of 31 cases in which the mother's history was known: Table 3.3).

Table 3.3. *Parity of the victim's mother*

Birth order of victim	Frequency
unknown	2
1	12
2	4
3	3
4	4
5	6
6	1
7	1

The attackers

Unfortunately, there is very limited data on paternity. Paternity of the victim and paternity of the mother's next infant is not known for any of the cases in which the identity of the attacker was recorded.

Not all community members were equally likely to commit infanticide. Any individual who attacked the mother/infant, or who carried or fought over the infant while it was still alive, was categorised as 'involved'. Inspection of the infant (peering at, sniffing), before or after death, was not counted as involvement, nor was interacting with the carcass (touching, carrying).

Infanticide was a more common behaviour for males than for females: 12 adult males (of 34: 35%) were involved in at least one attack, whereas only 5 adult females (of 50: 10%) were involved (Table 3.4). The sex of attackers was known in 20 cases (11 definitive infanticides and nine observed attempts/non-lethal attacks). In cases where the attacker(s)' identity was not certain, we categorised it either as "probable" – where it was not conclusive e.g. the early stages of the attack were observed but the actual killing was not observed or an individual was seen holding the victim after the attack, or "suspected" – where certain individuals had previously attacked or harassed the mother, or "unknown." In all but two such cases the death was less than three days after the initial harassment or attack. In one case the infant died two months later and in another it was three weeks later. In the first case there was no indication of sickness or other potential causes of death, leading us to believe that infanticide was the likely cause, and in the second case the infant was injured in the initial attack, making it a possibility the death was related to the initial attack, not a subsequent one. Males were observed, probably, or suspected to be involved in 23 occurrences, females in four, and both sexes in three. For three cases the sex of the attacker was unknown. Excluding the two joint attacks, males were significantly overrepresented as attackers (exact binomial test, $p = 0.003$).

Table 3.4. *Individuals involved in infanticidal attacks*

ID	Sex	Number of attacks involved in
FK	Male	5
HW	Male	6
NK	Male	5
MS	Male	4
SM	Male	3
MG	Male	1
JM	Male	1
KZ	Male	1
PS	Male	1
ZL	Male	3
SQ	Male	1
KT	Male	1
HT	Female	2
NB	Female	4
NR	Female	1
NT	Female	1
ZM	Female	1

Defence by other community members

Some level of defence or protection of the mother/infant by other community members was record in five cases (male protector = two cases; female protector = three cases). In 13 cases the attack was not clearly seen and in 15 cases there was no observed defence by individuals other than the mother. Of the two cases where an adult male provided defence, one involved the adult male FK defending his mother FL and her infant from attack by multiple other adult males, while in the other, the adult male KT chased SM, another adult male, who had been attacking the adult female OK and her infant. All female protectors were close maternal kin of the infant being attacked (grandmother or sibling). Two of these instances of protection were by the same female, RH. Two of her daughters (RS and RM) remained in Sonso community to reproduce, and experienced four attacks on their offspring: RM's infant was killed, two of RS's infants were victims of failed attempts, with one of these later killed. RH was present for two of the four attacks and in both cases, despite being an estimated 48 and 52 years old respectively, she physically defended the infants from attack, blocking the attacker's path and chasing attackers away. The third female to receive kin support was KY, a mother whose 15 and six year old daughters attacked and injured one of the adult male attackers. The females who received support from female kin were all natal females, and kin intervened in three of the five attacks on natal females that were clearly observed.

Discussion

Infanticide was the most common cause of infant death in the Sonso community, accounting for 63% of infant mortality. Of the 103 total known infant births, 23% were victims of infanticide. Even at a more conservative estimate, excluding suspected cases, the 15 remaining infanticides still account for 39% of infant deaths and mean that 15% of all infants were killed by intra-community conspecifics.

The evidence from Sonso community suggests that the majority of infanticidal attacks can be explained by the sexual selection hypothesis (Hrdy 1979; Sommer 1987; C. van Schaik 2000a). This hypothesis predicts that infants will be young, and in this community 2/3 of infants were under one week old at the time of the attack. The sexual selection hypothesis also predicts that infanticide will reduce the time until the mother is sexually receptive. The average time until next conception after an infanticide was 241 days. The average inter-birth interval when infants survive at Budongo is 1907 days (Emery Thompson, Jones, et al. 2007a), making the time until next conception 1682 days (average gestation period = 225 days: Wallis, 1997b). Females who lose an infant to infanticide therefore conceive on average around seven times quicker than if their infant had survived. Since the vast majority of females (89%) who lost infants to infanticide went on to breed again within the community and did so much sooner than they would have been able to had their infants survived, the infanticides did create reproductive opportunities that would not otherwise have existed, as predicted by the sexual selection hypothesis. Further predictions of the sexual selection hypothesis are that attackers will be male and infants will be neither predominantly male nor female. Attacks by males were indeed more common (23 male only attacks, four female only), and there was no significant sex bias in victims. In addition, this hypothesis predicts that mothers not be seriously harmed, as they are not the prime target of attacks and represent future reproductive opportunities for the attacking male. In 23 of 33 attacks, mothers were not visibly injured and none died, offering further support for sexual selection as an explanation.

Attacks were more commonly directed towards females' first-born offspring than any other birth order, and towards the offspring of young mothers (median age 23, mode 15). This further lends support to the sexual selection hypothesis for infanticide. Male chimpanzees prefer mating with older, parous females (Muller et al. 2006) and high ranking males have higher mating success (Tutin 1979; Nishida 1983). If high ranking males focus their mating effort on older, parous females, then the infants of primiparous females should be more likely to be sired by lower ranking males. The risk of infanticide to these infants will then be high because high ranking males have a low chance of having fathered them compared to their chance of fathering a replacement infant, assuming they invest more in mating effort during subsequent fertile periods, which they should do if female attractiveness increases with age and parity (Muller et al. 2006). Unfortunately looking at the effect of male rank on the likelihood of killing primiparous females' infants is beyond the scope of this study but is a question that deserves further attention. Targeting nulliparous females' infants could indicate that coercion is used to enhance a killer's chance of fathering future infants. As a form of male aggression which is costly to females and results in mating opportunities, sexually selected infanticide in general should be considered as a form of male sexual coercion (Smuts & Smuts 1993; Muller et al. 2009b). However, targeting nulliparous females may be a more specific strategy which encourages females at the beginning of their reproductive career to subsequently preferentially mate with the infanticidal males (enhancing a male’s chance of fathering future infants relative to their chance of having fathered the existing infant). Something similar has been observed in gorillas where females have been recorded transferring groups after infanticidal attacks to join the attacker (Yamagiwa et al. 2009).

While this offers circumstantial evidence that killers are more likely to father replacement infants, due to a lack of available data on paternities, both of the infanticide victims and subsequent infants born to their mothers, I cannot test the final two predictions of the sexual selection hypothesis: that killers will not target their own infants and will father replacement infants. It seems highly unlikely that males are killing their own infants since these are not rare incidents but common occurrences accounting for the majority of infant mortality. It would therefore be highly maladaptive for males to practise infanticide if they were regularly killing their own infants and the behaviour would be selected against. The carcasses of victims were only rarely recovered and DNA samples were not taken as standard protocol. While DNA samples are on record for the potential sires and attackers, without samples from the victims we cannot entirely rule out the possibility that males are killing their own offspring. While the available evidence does indicate that male committed infanticide in chimpanzees is sexually selected, future research is needed. Attempts should be made to recover corpses of victims for paternity analysis as this data will be valuable in providing a further test of the sexual selection hypothesis.

The predictions of the resource competition hypothesis were not met. The male bias in attacks and lack of a sex bias in victims indicates that infanticide in this community is not primarily driven by resource competition by females. Only four attacks were perpetrated solely by females, making this too small a sample to identify any trends in this behaviour which might give clues as to its function. It seems unlikely that the rarity of female committed attacks is simply due to a lack of opportunities, since adult natal females with potential coalitionary support from their mothers were never observed committing infanticide, despite the fact that coalitionary support should make it easier for females to overpower other females (Goodall 1983) who, unlike infanticidal males, have no size advantage. One female only attack included a mother daughter pair, reminiscent of multiple infanticidal attacks at Gombe by a mother and her adolescent daughter (Goodall 1977), however the daughter in the case reported here was 10 years old at the time and therefore her coalitionary value would have been limited. The fact that even females who are likely to be successful in their attempts (due to the presence of adult female kin) rarely kill infants suggests that there are fewer benefits for female perpetrators than there are for males. The motivation for the female committed infanticides in this community remains unclear.

The meat acquisition hypothesis predicted that attacks would be primarily perpetrated by females which was not the case. It also predicted victims would be of varying age while in fact infants were predominantly very young and that victims would be of both sexes, which was the case. Crucially, this hypothesis predicted that victims always be eaten which did not happen. The relative rarity of cannibalism (occurred in seven out of 24 lethal attacks), suggests that meat acquisition (Hrdy 1979) is an unlikely explanation for infanticide in this community. It is unclear why infanticide victims are more likely to be eaten in other chimpanzee communities (e.g. 100% of victims in the Kasekela community at Gombe: Murray et al., 2007 vs 37% at Sonso). The chimpanzees of Gombe eat meat more frequently than Sonso (24 successful hunts annually: Stanford et al., 1994, vs 11 successful hunts annually: Hobaiter et al., 2017, respectively), so it may be the case that individuals at Gombe have greater need of the calories and nutrients found in meat than are the chimpanzees of Sonso. However, at both sites cannibals did not consistently effectively exploit infanticide victims as a food resource. In one instance, a Sonso female ate only the eyelids of a victim and at Gombe, infanticide victims are eaten less completely than prey items (Kirchhoff et al. 2018), suggesting that while there are undoubtedly nutritional benefits to consuming infanticide victims, this does not fully explain cannibalism of infants in chimpanzees.

The male mate competition hypothesis was also not borne out by the evidence; males were the attackers in the majority of cases, but there was no sex bias in victims. While attacking male infants has been proposed as a method of removing future reproductive competitors in both chimpanzees and langurs (Agoramoorthy & Mohnot 1988; Takahata 1985), this does not fit with the pattern here where male attackers did not target male infants preferentially. The long life history trajectory of chimpanzees also makes this an unlikely hypothesis for infanticidal behaviour in this species as an infant male will not reach adulthood until 16 years old (Goodall 1986). Males who survive until adulthood in Sonso community live to an average of 29 years, meaning that an infant males is unlikely to be a major reproductive competitor for any males who are adults at the time of his birth.

It is not clear why there was no sex bias in infanticide victims at Sonso, while findings from other sites suggest that males are more frequent victims (Wilson et al. 2014). There is evidence from another East African community that mothers of sons may be more gregarious and spend more time with adult males (Murray et al. 2014a). While potentially having socialisation benefits (Murray et al. 2014a), such behaviour may also expose infant males to greater infanticide risk. It is possible that in a comparatively low infanticide risk scenario, the socialisation benefits for infant males may outweigh the risk of death, whereas at Sonso, due to higher risk, mothers of sons may be more wary of associating with adult males, meaning attackers do not have more opportunities to kill infant males than females. It may also be possible that a trend in previous reports towards male victims is simply the result of small samples sizes and the high number of unsexed victims (Wilson et al. 2014).

The attacks in Sonso were not evenly spaced throughout the study period, varying between 0 and seven per year with more attacks in more recent years. While research intensity has increased over the years and the community has become generally more habituated to human observation (although this has fluctuated), *inter*-community infanticides were observed in the early years of the study period when *intra*-community attacks were rare, suggesting that the lower number of attacks prior to 2011 was not due to a lack of observation. The increasing frequency of attacks was therefore unlikely to be an artefact of habituation, suggesting that particular social or ecological factors were responsible.

It is not yet clear why this community appears to be so much more infanticidal than others. The study site with the next highest number of intracommunity infanticides, Gombe Stream National Park, reported 16 intracommunity infanticides during a 49 year study period (1965–2014) across two study communities (Wilson et al. 2014), while I report here 24 over a 24 year study period with one study community (one per year compared to 0.33 per year for Gombe, see Table 3.5). Assuming that infanticide at other sites also generally conforms to the sexually selected hypothesis, variation in rates of infanticide between communities would be due to variation in either the reduction in the interbirth interval (IBI) achieved by committing infanticide (B in van Schaik (2000)'s model for sexually selected infanticide) or the chance of siring a replacement infant, minus the chance of having sired the existing one ($P_i - p$). A review of IBIs across six wild chimpanzee communities found that these lasted from 63 – 71 months when infants survived and 23 – 37 months when infants were killed (Emery Thompson, Jones, et al. 2007a). While such variation in IBI could be a factor in varying infanticide risk, killing infants resulted in the smallest IBI reduction at Sonso (Emery Thompson, Jones, et al.

2007a) indicating that variation in *B* is not the crucial factor. This leaves $P_i - p$. Paternity uncertainty should disrupt evaluation of both P_i and *p*, making infanticide less likely. Sexual coercion limits female choice in chimpanzees (Muller et al. 2011), limiting promiscuity and giving more paternity certainty to coercive males. Sonso males are more coercive than those in some other communities such as Mahale (Kaburu and Newton-Fisher, 2015), where only 12 infanticides were reported between 1981 and 2014 (Wilson et al., 2014). With this in mind, variables influencing male sexual strategies, such as hierarchy steepness (Stefano S K Kaburu & Newton-Fisher 2015) may be the key factor. Since $P_i - p$ is about the *change* in likelihood of fathering the current vs the potential future infant, rank stability will be important. Since rank predicts paternity in chimpanzees (Newton-Fisher et al. 2010; Wroblewski et al. 2009; Inoue et al. 2008; Constable et al. 2001), changes in rank will create variation between P_i and *p*. The highest changes between P_i and *p* will occur when a male increases rapidly from low to high rank in communities with steep hierarchies in which high ranking males effectively limit lower ranking males mating access. Some level of hierarchy instability is therefore necessary to create the conditions for sexually selected infanticide to be adaptive and rates should be highest where the male hierarchy is both unstable and steep.

Table 3.5. Table showing the number of infanticides and the rate per year at six chimpanzee research sites. Rates are calculated from the date of the first recorded infanticide to 2014, the date of publication of Wilson et al.'s review of lethal aggression in chimpanzees, from where this data is extracted. *In the case of Budongo, because we have accurate records of when data collection first began, we calculate from this date instead. We have not calculated a rate for Goulougo since only one attack has ever been observed or Taï since their one attack had no date associated with it.

Site	Infanticides	First recorded infanticide	Rate
Gombe	16	1965	0.33
Mahale	12	1977	0.32
Kibale	5	1997	0.29
Budongo	24	1993*	1
Taï	1	unknown	-
Goualougo	1	2006	-

Due to its frequency, infanticide is likely to be a major selective pressure on this population. Considering that female chimpanzees give birth on average every five to seven years (Emery Thompson, Jones, et al. 2007b) and typically have one infant at a time (rate of twinning reported from Gombe is one in 91 births: Wallis, 1997; there are no records of twinning at Sonso) the loss of an infant is likely to have a serious, quantifiable impact on fitness. Sonso mothers conceive again, on average 241 days post infanticide. Since a pregnancy averages 225 days (Wallis 1997a), a mother who loses an infant has lost the combined time of gestation and the period post infant death before she resumes cycling again (average 466 days) plus the length of the infant's life. The average reproductive lifespan for Sonso females is roughly 28 years (average age of first conception in eastern chimpanzees is 12.4 years and the oldest Sonso female to have given birth to a live infant did so at 40.6 years: Emery Thompson et al., 2007). If an infant is killed at one week old, the infanticide results in a loss of 473 days of the mother's reproductive career, with costs steadily increasing the longer the infant survives prior to the infanticide. The most fecund Sonso female had eight recorded births and four surviving infants. She lost infants at one week, one week, one day, and 65 days post-partum, a total loss of 1944 days to pregnancies, inter-birth intervals and lactation. These four infant deaths cost this female 19% of her 28-year reproductive career. While not all of these fatalities are confirmed as being a result of infanticide, it is clear how the loss of an infant can be a major reproductive cost to the mother.

One interesting feature of the infanticides in the Sonso community was the lack of active defence by other community members. Although fathers should have a strong motivation to defend their own infants, males only very rarely protected infants from attack. I had only two records of males intervening in attacks: one case of a male protecting his mother and sibling and one case of an unrelated male defending a mother and infant. Intervening in attacks, particularly in those by other males, may be costly as there is a chance of injury to the protector. Defence may be a poor strategy for fathers, however. As well as the potential for injury, a physical altercation with another male could lead to a change in rank. Since male rank is linked to reproductive success (Newton-Fisher et al. 2010; Boesch et al. 2006; Constable et al. 2001) and males increase in rank through winning aggressive interactions (Newton-Fisher 2004), competing with another male always carries the risk of dropping in the hierarchy and losing future mating opportunities. Males should therefore be risk averse, only initiating contests that they are likely to win. Defending infants may simply be too costly, depending on the relative rank of the attacker to the father. As well as being costly, paternity uncertainty reduces the benefit of intervening in conflicts on behalf of an infant as there is always the possibility that the effort is misdirected towards a non-kin infant. Were males sure of the paternity of infants, defence would be a more beneficial strategy, although this would not necessarily outweigh the potential risk of a reduction in rank. The rarity of female defence and the fact that natal females received support while non-natal females did not is not surprising, as most female Chimpanzees emigrate on sexual maturity (Constable et al. 2001; Nishida et al. 1990; Boesch & Boesch-Achermann 2000) and do not live with close kin who would gain inclusive fitness benefits from protecting them during attacks. Natal females however were defended by kin more often than not (three out of five cases in which the attack was clearly observed). One mother (RH) was heavily involved, risking injury to herself. In one of these cases, the infanticide was not successful. In one instance of kin support, a juvenile and young adult female (six and 15 years old) defended their mother and infant sibling from attack, even wounding one of the attacking adult males. Despite the rarity of active defence, several attempted infanticides were prevented. Of the nine failed attempts, six of the targeted infants survived infancy, while three were killed at a later date. It is worth noting that in four of the nine failed infanticidal attempts, individuals other than the mother defended the infant and three of these four infants survived long term, while one was killed at a later date, so it is possible that infanticidal individuals are effectively deterred by protectors. This suggests that protection is an effective strategy, but that individuals other than the mother do not generally gain enough from protecting infants for them to incur the costs.

This review provides the first detailed description of all infanticidal behaviour from a single community, showing that infanticides in Sonso are a major cause of infant death and are common enough to be considered a significant selective pressure. The majority of cases are adult males killing very young infants which supports the sexual selection hypothesis although this conclusion would be bolstered by genetic data on relatedness between attackers and victims. The evidence did not fit the patterns predicted by either the male mate competition hypothesis or the resource competition hypothesis. Sonso individuals are less cannibalistic than those at other sites and females are only relatively rarely the perpetrators in attacks. An interesting feature of these infanticides is that defence of infants by individuals other than the mother can be effective in ensuring infant survival but that mothers rarely receive this support.

Since a large proportion of infanticides are unreported (Wilson et al. 2014) and attempted infanticides even more so, it seems likely that sexually selected infanticide is more prevalent in chimpanzees in general than previously thought. However there does seem to be variation between communities (Wilson et al. 2014), which is likely to be due to variation in male mating strategies and rank instability.

Note: Since the completion of this study two further intra-community infanticides and one further attempted infanticide have been reported from the Sonso community (E. Holden & A. Soldatis personal communication).

4. Countering infanticide: chimpanzee mothers are sensitive to the relative risks posed by males on differing rank trajectories

Published as: Lowe A, Hobaiter C, Newton-Fisher N (2018) Countering infanticide: chimpanzee mothers are sensitive to the relative risks posed by males on differing rank trajectories. American Journal of Physical Anthropology 1–7. doi: 10.1002/ajpa.23723

*The use of "we" in this chapter reflects the contribution of my co-authors who provided comments on the manuscript. I devised this chapter, extracted the relevant data from raw data files and hard copies, analysed the data and wrote the chapter, with the help of my co-author's comments.

Abstract

Infanticide by males is common in mammals. According to the sexual selection hypothesis, the risk is inversely related to infant age because the older the infant, the less infanticide can shorten lactational amenorrhea; risk is also predicted to increase when an infanticidal male's chance of siring the replacement infant is high. Infanticide occurs in chimpanzees (*P. troglodytes*), a species in which male dominance rank predicts paternity skew. Infanticidal male chimpanzees (if low-ranking) are unlikely to kill their own offspring, while those who are currently rising in rank, particularly when this rise is dramatic, have an increased likelihood of fathering potential future infants relative to any existing ones. Given that mothers should behave in ways that reduce infanticide risk, we predicted that female chimpanzees, and specifically those with younger, more vulnerable infants, would attempt to adjust the exposure of their infants to potentially-infanticidal males. Specifically, mothers of young infants should reduce their association with adult males in general, and to a greater extent, with both low-ranking males and those rising in rank from a position where paternity of current infants was unlikely, to a rank where the probability of siring the next infant is significantly higher. We also investigated the alternative possibility that rather than avoiding all adult males, mothers would increase association with males of stable high rank on the basis that such males could offer protection against infanticide. We examined data on female association patterns collected from the Budongo Forest, Uganda, during a period encompassing both relative stability in the male hierarchy and a period of instability with a mid-ranking male rising rapidly in rank. Using linear mixed models, we found that mothers reduced their association with the rank-rising male, contingent on infant age, during the period of instability. We also found evidence that females preferentially associated with a potential protector male during the high-risk period. our results support the sexually-selected hypothesis for infanticide, and demonstrate that female chimpanzees are sensitive to the relative risks posed by adult males.

Introduction

Infanticide by males is common in mammals (Lukas & Huchard 2014). According to the sexually-selected infanticide hypothesis (Hrdy 1979; Sommer 1987), the risk of infanticide increases when (a) males can kill unrelated infants; (b) infanticide reduces the interbirth interval of the targeted infant's mother; and (c) infanticide increases the male's likelihood of achieving paternity (i.e. the chance of siring the replacement infant relative to the infant killed). Infanticide should generate significant selective pressure, and so females are expected to employ counterstrategies, such as promiscuity and post-conceptive swellings to confuse paternity, as well as maternal vigilance and aggression (Hrdy 1979; Parmigiani et al. 2010; Treves et al. 2003; C. van Schaik 2000b; Wolff & Macdonald 2004).

Infanticide occurs in multiple communities of East African chimpanzees, with most cases perpetrated by males (*P. t. schweinfurthii*: Arcadi and Wrangham, 1999; Newton-Fisher, 1999a; Murray et al., 2007; Newton-Fisher and Emery Thompson, 2012, Chapter Three). Female promiscuity is conventionally interpreted as a strategy aimed at confusing paternity and protecting against male-committed infanticide (Hrdy 1981). However, adult males may be able to track variation in the size of female sexual swellings, suggesting that ovulation is not entirely concealed (Deschner et al. 2003), and in some communities male coercive aggression may place restrictions on females' ability to determine the males with whom they mate (Muller et al., 2007; Feldblum et al., 2014), although the use of coercion varies between sites (Kaburu and Newton-Fisher, 2015a). More critically, however, male dominance rank typically predicts paternity across multiple communities, including this study group (Boesch et al. 2006; Newton-Fisher et al. 2010; Wroblewski et al. 2009; Langergraber et al. 2013b). This raises a particular problem for females: while promiscuity might reduce rank-related paternity skew (and might be responsible for the relatively moderate degree of skew: 60% of paternities achieved by males of ranks one – three in Sonso community: Newton-Fisher et al., 2010), it cannot protect fully against infanticide by confusing paternity. Infanticide becomes an adaptive strategy where the chances of a male having sired an existing infant are low, and when changes in social dominance rank increase the probability of him siring a replacement infant (the value of *P* in van Schaik's [2000a] model of adaptive infanticide). As a consequence of the probabilistic relationship between rank and paternity, males who employ infanticide as a strategy contingent on their relative dominance rank (and recent changes thereof) will do so, on average, in an adaptive fashion. At a proximate level, tracking outcomes of recent agonistic interactions with other males and thus relative rank is likely to be less challenging than tracking mating history, or estimating likelihood of paternity, under a fission-fusion social system with promiscuously mating females. While such a reliance on rank as a proxy may in some cases be negated by specific mating strategies such as consortships (in which mating is restricted and paternity certainty is potentially high), the existence of a statistical relationship between rank and paternity, itself the outcome of the interplay of male and female mating strategies, will in most cases provide males with a reliable cue (at least considered from the perspective of the evolution of the strategy) which females cannot directly counter. The proposed female strategy of concentrating mating efforts, when most likely to conceive, on preferred males (Stumpf & Boesch 2005) will only worsen this problem if these preferred males are high ranking, as it will reinforce or exacerbate the rank-related skew in paternity. If females cannot fully reduce paternity skew through promiscuous and frequent copulation, either because they cannot overcome male coercive aggression (Muller et al. 2007; Muller et al. 2011), or because they seek high quality mates (Stumpf & Boesch 2005; Stumpf & Boesch 2006; Tutin 1979), additional or alternative strategies will be needed to counter the risk of infanticide.

A consequence of this link between male rank and paternity skew is the correlated link between male rank and infanticide risk. While low-ranked males generally have a low likelihood of siring any given infant, and would have less to lose by pursuing an infanticidal strategy, the greatest risk to females comes from males who rise in rank, all other factors being equal (cf. *Macaca fuscata*: Soltis et al., 2000). In particular, those males who rise from a rank at which paternity was unlikely when an infant was conceived to a sufficiently high rank that the probability of siring the next infant is non-negligible have both little to lose and a lot to gain (C. van Schaik 2000a). Female chimpanzees, who are 20 – 25% lighter than males (Bean 1999; Goodall 1986) and socially subordinate (Goldberg & Wrangham 1997; Goodall 1986), are in a poor position to defend their infants directly from attacks by males, although in some cases they may receive coalitionary support (Kahlenberg et al. 2008; Newton-Fisher 2006).

These arguments assume that male chimpanzees are not able to identify paternity directly, and while recent studies of chimpanzee from communities in both Taï and Gombe (Lehmann et al. 2006; Murray et al. 2016) have shown that male chimpanzees bias socially-positive interactions towards their offspring, these studies did not explore males' knowledge of paternity. The statistical dependency between rank and paternity, which we argue allows males to be adaptively infanticidal, may allow males to provide paternal investment without offspring recognition by biasing behavior according to their expected probability of paternity according to rank, although other factors, such as previous association with the mother, may also be involved (Langergraber et al. 2013b). Furthermore, the nature of this paternal biasing differs between Taï and Gombe: although males at both sites bias social behaviour (play, reduced aggression) towards their own infants and those infants' mothers, only males at Gombe preferentially associate with their own infants (Lehmann et al. 2006; Murray et al. 2016). Evidence from Sonso community suggests a different pattern again, with paternity having no effect on either association or aggression rates, with adult male-infant play too infrequent to be analysed (Chapter Six). The preferential association of male chimpanzees with maternal, but not paternal, siblings (Langergraber et al. 2007) further questions direct recognition of kin: paternal siblings may be valuable coalition partners rather than reproductive rivals. We suggest, therefore, that it is premature to assume that male chimpanzees have direct knowledge of paternity.

Chimpanzees have a social system characterized by high fission-fusion dynamics, whereby individuals associate with one another in sub-groups ('parties': Sugiyama, 1968) of variable composition and duration (Boesch & Boesch-Achermann 2000; Goodall 1986). Fission-fusion grouping is thought to be a response to managing feeding competition across dispersed patches, particularly of ripe fruit (Symington, 1968), but it also provides individuals with opportunities to adjust their social environment (Murray et al. 2014a; N. Newton-Fisher 1999a; Pepper et al. 1999), subject to the conditions that others may do likewise, and that individuals must satisfy their foraging demands. We suggest that females may make use of this flexibility to counter infanticide risk, as the association of dependent infants with other community members is the direct consequence of decisions made by their mothers to join or leave parties.

We consider three non-exclusive possibilities for female counterstrategies to infanticide risk: (1) that females seek protection from high-ranking males who generally have a greater likelihood of having sired their infants, (the *male protector hypothesis*: (Borries, Launhardt, Epplen, Jörg T Epplen, et al. 1999; Kahlenberg et al. 2008; Palombit et al. 2000); (2) that females adjust the exposure of their infants to potentially-infanticidal males: specifically, that they reduce association with low-ranking and males who are currently rising in rank, contingent on infant age, as vulnerability and desirability as targets are inversely related to infant age (the *risky-male-avoidance hypothesis*); and (3) that females seek protection for their infants by associating with other mothers (potentially benefiting from both dilution and selfish herd effects: Hamilton, 1971). We also consider the *infant safety hypothesis* (Otali & Gilchrist 2006), which proposes that low female gregariousness is due to females avoiding association with males in general, due to their potential for aggression. To test these hypotheses, we take advantage of prior work identifying the link between paternity and rank in Sonso community (Newton-Fisher, Thompson et al., 2010) and the rapid rise in rank of one of the adult males (NK) in June 2004, from mid/low ranking (rank five of eight adult males) to rank two within one month (Newton-Fisher 2017). As paternity in this community is concentrated in the top three ranks and rare below rank 5 (for 13 analysed infants, ranks 1 – 3 sired 8 and ranks 6 – 12 sired 3; Newton-Fisher et al., 2010), this increase in rank represents a significant shift in the likelihood of siring infants, as well as in the level of infanticide risk. Intracommunity infanticide is very common in this community (Chapter Three).

Methods

Data collection

We used data on the Sonso community of chimpanzees from the Budongo Forest, Uganda, collected between October 2003 and January 2005. This community inhabits around $7km^2$ (Newton-Fisher, 2002) of the $428km^2$ semi-deciduous tropical forest within the reserve (Eggeling 1947; Plumptre 1996; Reynolds 2005), and has been studied continuously since 1994 (Newton-Fisher 1997; Reynolds 2005)]. During data collection, the community consisted of 63 individuals, including eight adult males (by definition, ≥ 16 years old), six adolescent males (ranging from 9–14 years old) and 21 adult females (≥ 14 years old). Age categories follow Goodall (1986). Seven of these females had infants under one year of age during the study period; these mothers are our focal mothers. Infants of this age are always in the presence of their mothers (Boesch & Boesch-Achermann 2000). Five of the infants were female and two were male. All focal mothers were multiparous, with between one and four known prior infants. Two infants were of unknown paternity; of the remaining five, adult male BK was the father of three, while MA and BB were fathers of one each (Crockford et al. 2013; L. Vigilant & K. Langergraber unpublished data). Data were recorded using a focal-behaviour sampling regime: parties were followed for as long as possible from first encounter until nesting, with pre-selected focal animals followed when parties fissioned. If contact with chimpanzees was lost due to terrain and/or chimpanzee movement patterns, data were collected from the next party encountered that contained one of the predetermined focal animals. We defined a party following Newton-Fisher's (1999) operational definition: "a collection of independently associating individuals showing coordination in behaviour; a cluster of individuals with a radius of around 35m". Party composition was recorded using 5-minute-interval instantaneous scan sampling. Given that a chimpanzee could travel >240m between scan samples (assuming an average travel speed of 2.95 km/h:

Newton-Fisher 2003, calculated from data in Wrangham, 1977), and easily leave a party in < one min, an individual’s presence in consecutive scans of the same party is not because they are unable to leave within the 5-minute period, and so represents an active decision to remain in the same party (for example when a party leaves a feeding patch and travels together without changes in membership). All occurrence sampling was used to record aggressive interactions within the focal party (Stefano S.K. Kaburu & Newton-Fisher 2015; Newton-Fisher 2017).

Data analysis

Party composition

Party changes were defined after the fact, rather than during data collection, using the party composition data; i.e. when a scan had any new members or had lost any members compared to the previous one, it was classified as the beginning of a new party. For the purposes of analysis, we accorded each of the 1040 parties a unique identifier. This was used to control for multiple observations of the same party. The duration for which party composition remained unchanged was highly variable, with parties lasting between one and 47 scans (mean = 2.82 ± 4.07 scans, median = 2). Our full sample size for analysis was 2930 scan samples of these 1040 parties.

Male rank

To generate a cardinal measure of social rank we constructed Elo-ratings from wins and losses of directed aggressive interactions (Newton-Fisher 2017). We identified several categories of aggression: static threats, approach threats, charging displays, chases and attacks, scaling the impact that these had on Elo-ratings (for further details see Newton-Fisher (2017). We used these Elo-ratings (Fig. 4.1) to identify two consecutive 8-month periods in the dataset: the first, when adult male ranks were relatively stable (October 2003 – May 2004), the second when a mid-ranking (rank five of eight) adult male (NK) rose rapidly and held high (2nd) rank (June 2004 – January 2005). NK then remained high ranking, holding the alpha position from 2006 until 2013. We considered ranks one – three to be "high", four & five to be "mid" and six – eight to be "low." Predicted infanticide risk was low during the stable period and higher during the unstable period.

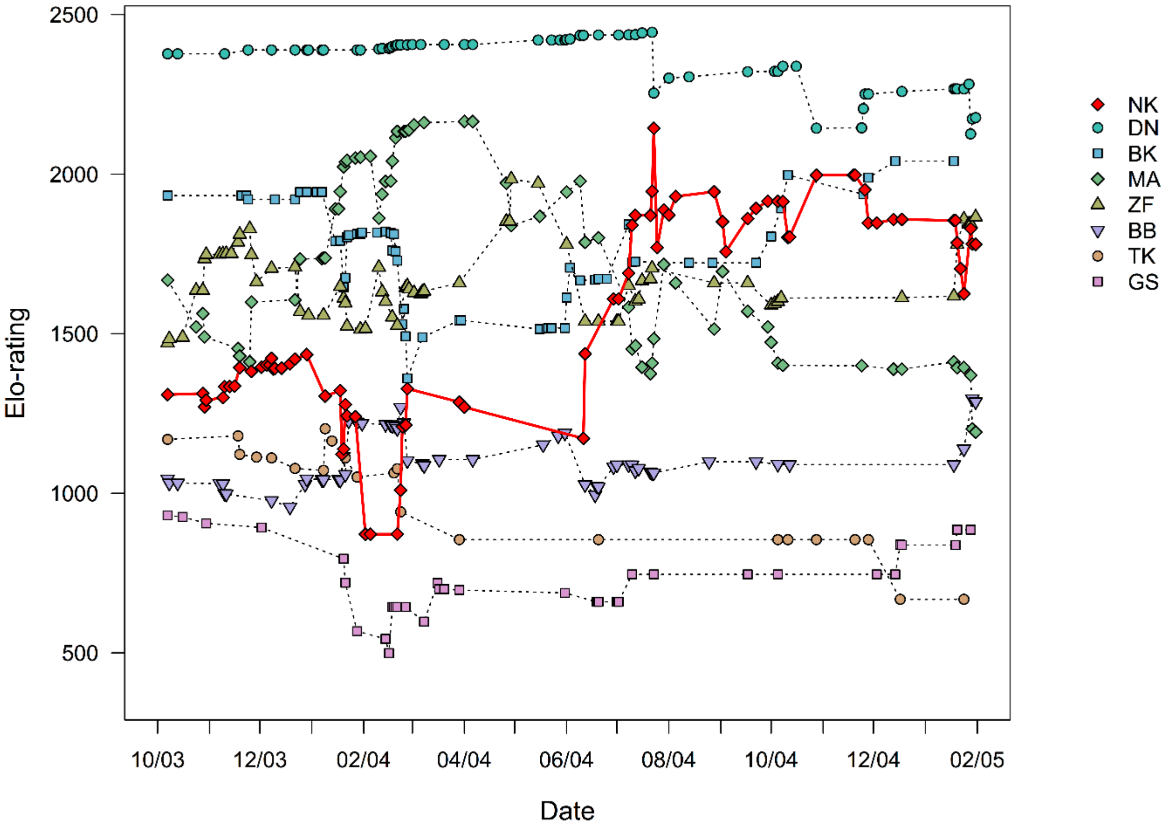


Figure 4.1. *Elo-rating derived dominance hierarchy of all adult males (indicated by 2-letter ID codes) throughout the study period. The individual NK is depicted by thick red line with diamond points.*

Rates of aggressive behaviour

In order to be able to differentiate between rising in rank and general aggression (i.e. are males dangerous because they are rising in rank or merely because they rising in rank is associated with increased aggression), we also calculated aggression rates for each male: (1) aggressive interactions per hour towards all members of the community, and (2) aggressive interactions per hour towards the focal mothers.

Modelling vulnerability and avoidance

Since infant age is a proxy for infanticide risk (Hrdy 1979), and mothers should be sensitive to this, we looked at the relationship between the age of the focal's infant and party composition. This process allowed us to investigate whether female decisions to participate in parties, based on the composition of those parties, varied as a function of infant age. For example, if particular party compositions predicted a decrease in focal female's infant's age, that would indicate that mothers of the youngest infants were spending time in these parties, indicating that the age-sex classes or individuals in these parties are comparatively safe. Conversely, if the presence of particular age-sex classes or individuals predicted an increase in infant age, it would indicate that the infants in those types of parties were older, suggesting that mothers of vulnerable infants were avoiding them. Infant age was therefore selected as the response variable as the age of the infants in a party is a proxy for level of infanticide risk which that party's composition poses to infants. Given that 86% of recorded chimpanzee infanticide victims with confirmed male attackers across communities, including the vast majority of Sonso infanticide victims, were under one year of age (Wilson et al., 2014, Chapter Three), we restricted the analysis to the behaviour of mothers with infants younger than one year. We used linear mixed-model (LMM) analyses to test our predictions, using the function 'lmer' from the R package 'lme4' (Bates et al. 2015). We used mixed models with REML and random intercepts to see how the presence of particular individuals related to the age of the focal mother's infant. We produced two models. In Model 1, age of the focal mother's infant was the dependent variable, with the number of adult males and number of mothers of infants <1 year of age in the party as the predictors. This model was designed to show whether mothers of younger (i.e. more vulnerable) infants spent time in parties with more/fewer adult males and other mothers. In Model 2, we again set the age of the focal mother's infant as the dependent variable, this time with the presence (Y/N) of each adult male and time period (low/elevated risk) as predictors, along with an interaction between these. This model, specifically the interaction between male presence and low/elevated risk, was designed to show whether, after taking into account the fact that infants will necessarily be older in the second of these two periods, younger (more vulnerable) infants were more or less likely to be in the presence of particular males in the unstable versus the stable period. We included, as random effects, the ID of the focal mother to account for repeated observations and possible idiosyncratic variation in behaviour, and party ID to account for multiple samples from the same parties. We tested the significance of the predictors on the dependent variable by using the ‘drop1’ function to compute a likelihood ratio test.

Age of the focal mother’s infant was calculated at each scan sample from either a known birth date or otherwise the midpoint of an estimated date range. Birthdate estimated ranges were 0-14 days, mean: 5.6 days, SD: 6.2.

Results

Our focal mothers spent the majority of their time (52.3% of scans) in parties with no adult males, while one male was present in 19.6% of scans, two males in 9.5% and three to seven males in 18.6% of scans. Mothers were alone, except for their dependent infants for 28.9% of scans. The proportion of time which the focal mothers spent in parties with other mothers of infants <1 year of age was similar to that spent with males. They were with no other mothers of young infants in 58.0% of scans, one other mother in 21.8% of scans, two other mothers in 13.9% of scans and three to six other mothers in 6.3% of scans. We recognise that these percentages may underestimate the total time mothers spend alone, as following lone individuals, in particular females, is typically harder than following larger parties (personal observations). Therefore, time spent with other individuals, or in small all-female parties, may be overrepresented in the data. The mean number of adults in a party was three (SD: four), with a mean of one males (SD: two), and two females (SD: two). On average, one of these two females (mean: one, SD: one) were mothers of infants <one year of age.

During the study period, we recorded a mean rate per male of 0.4 (SD: 0.2) aggressive interactions per hour (h^{-1}), but these ranged from 0.1 to 0.7 (median = 0.4). The three lowest ranking males (GS, TK, and BB) were the least aggressive overall, initiating aggressive interactions at rates of 0.1, 0.1, and 0.3 times per hour of observation respectively. NK was the most aggressive, directing aggression towards other individuals at a rate of 0.7 h^{-1}. The second most aggressive male was BK, who spent the majority of the study period at either rank two or three, with a rate of 0.6 h^{-1}. The other mid- to high-ranking males (ranks 1-5) had rates between 0.3 h^{-1} and 0.4 h^{-1}.

When considering just aggression towards the focal mothers, two low-ranking males (TK and GS) were, again, the least aggressive, with rates of 0.004 h^{-1}, and 0.005 h^{-1}, respectively. MA, ZF and BB (high, mid and low-ranking males) had mid-range aggression rates of 0.009 h^{-1}, 0.2 h^{-1} and 0.03 h^{-1} respectively. The male most aggressive towards mothers (0.053 h^{-1}) was the high-ranking BK, followed by NK, the rank-rising male (0.050 h^{-1}). Aggression rates by the alpha male DN (0.03 h^{-1}) were lower, comparable to the low-ranking BB.

Male intervention was not observed in any of the 567 recorded attacks or threats towards adult females by other adult males. Two females were observed approaching adult males when threatened and chased by another male, on three separate occasions. On one occasion, this female was a mother; the other two occasions involved the same non-mother. The male aggressor was the rank-rising NK in all three instances, while the approached males were all mid- to high-ranking, and in all cases were higher ranking than NK. The mother approached the alpha male, who was not the father of her infant.

Approached males did not offer active support in any of the three incidences, and adult males typically ignored aggression directed towards females by other males.

We found no evidence of a relationship between either the number of adult males (Model one: β ± SE = 8.18e-03 +/- 6.51e-03, p = 0.21 – see Table 4.1), or the number of other mothers of infants <1 year (Model 1: β ± SE = 2.29e-03 +/- 1.27e-03, p = 0.07), in the party and the age of the focal mother's infant. However, we did find (Model 2) statistically significant relationships between the age of the focal's infant and the interaction between the shift from low to elevated infanticide risk and the presence of two of the eight adult males (BK & NK). This reflects which mothers (those with older vs younger infants) were in the presence of these males. Of the three high-ranking males, there was an effect only for BK, who spent time in parties with mothers of comparatively younger infants during the period of elevated risk than before this period (Model two: β ± SE = -0.12 ± 0.03, p < 0.0001 – see Table 4.2. for results for each male). The presence of the male who posed the most likely source of infanticide risk (NK) had the greatest influence: mothers in his presence had infants which were 67.5 days older when risk was elevated compared to the low risk period (Model two: β ± SE = 0.19 ± 0.03; p < 0.0001).

Table 4.1. *Mixed model analyses showing the effect on the age of the focal female's infant on the number of adult males and adult mothers in the party.*

	Model 1				
	β	*SE*	*df*	*t*	*p*
(intercept)	0.710	0.120	9.500	5.924	<0.001
males	0.000	0.003	1987	-0.155	0.877
mothers	0.007	0.006	1208	1.077	0.282

Table 4.2. *Mixed model analyses showing the effect on the age of the focal female's infant as an interaction between the change in infanticide risk and the presence of each adult male. Males are listed in rank order at the start of the study period. Significant results are shown in bold.*

	Model 2				
	β	*SE*	*df*	*t*	*p*
(intercept)	-0.670	0.119	10.200	5.659	<0.01
DN presence * high risk period	-0.020	0.022	2707	-1.105	0.27
MA presence * high risk period	0.010	0.030	1324	0.299	0.77
BK presence * high risk period	-0.120	0.028	1058	-4.394	**<.001**
ZF presence * high risk period	-0.040	0.022	2131	-1.658	0.10
NK presence * high risk period	0.190	0.027	1061	6.869	**<.001**
TK presence * high risk period	0.040	0.043	1029	0.910	0.36
BB presence * high risk period	0.010	0.030	1054	0.412	0.68
GS presence * high risk period	0.000	0.029	1127	0.081	0.94

Discussion

The *infant safety hypothesis* suggests that adult males, by virtue of being potentially aggressive, are a physical and psychological (in terms of stress to the infant and mother) risk to infants, a risk that is heightened when infants are younger (Otali & Gilchrist 2006). However, our results suggest that, when considered as a group, male chimpanzees in the Sonso community were not necessarily treated as dangerous by mothers, or at least that that any danger posed did not vary with infant age in infants under one year old.

Instead, mothers of young infants reacted most strongly to the rapid rise in social dominance rank of the male NK, supporting our *risky-male-avoidance hypothesis*. While we cannot exclude the possibility that our results were the product of this male tending to spend more time with mothers of ‘older’ infants, during and after his rise in rank, we find no convincing explanation why this would be so. It would be difficult to account for such behaviour in terms of future mating effort, since all the infants in our dataset are under one year of age and therefore the mothers of even the oldest are several years away from being sexually receptive: the average interbirth interval (IBI) for chimpanzees, when infants survive, is around five years (Goodall 1986; Kappeler, P & Pereira, M 2003), while the shortest recorded IBI for our study community is 47 months. Furthermore, previous work at Gombe has found that male-female association in chimpanzees does not reflect future mating effort (Murray et al. 2016). While evidence that males may seek out contact with mothers of specific infants was associated with paternity of those infants (Murray et al. 2016), in this study, NK was not the father of any of the five infants under one year of age for whom paternity was known. By contrast, interpreting these results as attempts by mothers to avoid this male is consistent with the *sexually selected infanticide hypothesis* (Hrdy 1979; Sommer 1987). Under this hypothesis, the risk posed by a male depends on the change in his likelihood of achieving paternity with the female's next infant as compared to being the father of her current infant. Risks are greater for younger infants as their death has a greater impact in reducing lactational amenorrhoea (Hrdy 1979; Sommer 1987; C. van Schaik 2000a). An infanticidal male chimpanzee rising in rank will increase his likelihood of achieving future paternities if this rise is post conception and before weaning of the infant(s) at risk. This was precisely the situation for the adult male NK, who was ranked fifth during the first period of our study, only to rise rapidly and sustain high rank in the second period: data from the Sonso community suggest that males of rank five or below have only a low probability of achieving paternity, with most paternity concentrated in males of the top four, and particularly the top three ranks (Newton-Fisher et al. 2010). According to the *sexually selected infanticide hypothesis*, NK's rise should have made him the greatest source of infanticide risk, and the male towards whom mothers should therefore respond most strongly. This is precisely what we found.

My interpretation is supported by our results with respect to males who consistently held high rank: it was the *change* from low to high rank, and thus change in likelihood of achieving paternity, that appeared to be the important factor. Males whose ranks are unchanging between conceptions should not pose an infanticide risk, because without a substantive rise in rank between successive conceptions of a given female, their chance of siring a second infant will be unchanged from that of siring the first, and so they cannot expect to increase their reproductive success through infanticide.

Despite an expectation of higher rates of aggression among high-ranking males (Muller & Wrangham 2004), and thus the likelihood that infants may be at risk from redirected or unintended violence, we found no evidence that mothers reduced association with higher-ranking males when NK was challenging for high rank. Given that rates of aggression by Sonso community males conform to this general expectation, we would have expected such a reduction if females were concerned primarily about their infants falling victim to inadvertent aggression. Even if high-ranking males were only aggressive when around rank-rising males, this male strategy would result in increased levels of aggression during the second period (when NK was rising in rank) and so we would still expect a reduction in mother-male association as females seek to avoid male aggression, which we did not find. Instead, we found opposite effects for the two most aggressive males: while NK was avoided by mothers of young infants, BK, the second most aggressive male, associated more with younger infants during the unstable period. Danger of misdirected aggression cannot explain these patterns of behaviour. We also note that while female chimpanzees will shepherd dependent infants to safety when faced with aggressive males, typically they do not flee from parties under these conditions (personal observations), and it is their older, more independent infants and juveniles who appear to be at most at risk from inadvertent or redirected aggression: the youngest infants – those most vulnerable to infanticide – are more likely to be bodily contact with their mother. Thus, our findings suggest it is the likelihood of infant-directed attacks, rather than misdirected aggression, to which mothers are sensitive. Given that we find both decreased and increased association with particular males, and no general differences in mothers' associations with adult females compared to their association with adult males, we have no reason to suggest that variation in female association patterns is due to infant socialisation (Horvat & Kraemer 1981). Such patterns may be apparent across the period of infancy (0-5years), but for infants < one year, it seems that mothers are attempting to reduce infanticide risk.

We found some support for the *protector male hypothesis* (Borries, Launhardt, Epplen, Jörg T Epplen, et al. 1999; Palombit et al. 2000). Of the high-ranking males, the expected effect (an increase in association when infanticide risk was elevated) was seen only for BK, who was father to three of the five infants < one year old for whom paternity is known. We found no evidence of a ‘protector’ role for the alpha male, although this might have been because the two infants whom he was confirmed to have sired were already over four years old at the start of the study period and therefore at low risk of being victims of an infanticidal attack. Although these results are suggestive of a link between paternity and protector male effect, it is not clear why this was not evident for the other fathers in our dataset, unless the effect is small, visible only because of the cumulative effect of multiple infants, or perhaps because BK had higher paternity certainty than might typically be the case due to coercive curtailing of the mother's promiscuity or through fathering an infant during a consortship. Unfortunately, mating history for the relevant period is not available to test these ideas.

Alternatively, and perhaps more plausibly since it does not require identification of paternity, mothers may have been using BK as a shield, regardless of paternity, on the basis that he could deter potentially infanticidal males. Mothers are unlikely to gain active defence – neither BK nor any other male, was observed intervening in an attack by an adult male on an adult female during this study and only one unrelated male was ever observed to defend an infant against infanticide at Sonso (Chapter Four) – but may benefit if the presence of aggressive high-ranking males deters aggression from other males. If males interpret aggressive displays from others as rank challenges, this is potentially something that mothers could exploit. Since BK was also aggressive towards females, such a strategy would be potentially costly, but tolerating high rates of displays, threats and even contact aggression could be beneficial if linked to protection from infanticidal attacks.

In summary, our results suggest that eastern female chimpanzees in our study community with young infants are sensitive to male rank shifts and respond adaptively to reduce the exposure of their infants to infanticide risk. Mothers reduced their association with (and thus the exposure of their infants to males who have incentives to commit infanticide, as well as associating with safer, potentially protective males, supporting our *risky-male-avoidance hypothesis* and, possibly, the *male-protector hypothesis*. We predict that these findings will be generalisable to other chimpanzee communities with rank-based paternity skew, as this generates potential fitness differentials and associated risks of infanticidal behaviour. our findings support the *sexually-selected infanticide hypothesis* for within-community infanticide by male eastern chimpanzees.

5. Multi-level avoidance of males by mothers: between and within parties

Abstract

Males in many species pose a risk to unrelated infants, as they can, under certain circumstances, improve their reproductive success by committing infanticide. Mothers respond to this risk in a variety of ways, one of which is avoiding those individuals who are most dangerous. For group living species however, when the threat comes from within the group, avoidance may not be possible. Under a fission-fusion social system, mothers can choose to avoid subgroups that contain high risk conspecifics but will sometimes be forced to join subgroups with non-preferred individuals, e.g. at feeding patches. Here I look at the behaviour of female chimpanzees, whose association patterns have previously indicated that they avoid adult males as a counter-strategy to infanticide. I investigate intersexual association in more detail, identifying who is driving association and avoidance to validate previous inferences made from party composition data. Mothers spent time in parties with more females than did females without infants, and were more likely to have females as their nearest neighbours, but they were less likely to approach males than were females without infants, providing evidence that it was mothers who were driving the lower mother-male association rates, rather than males. While mothers did associate more with other females than did females without infants, they were no more likely to respond affiliatively when approached by other females, indicating that high association of mothers with other females is driven by practicality (e.g. ecological factors such as travel costs meaning mothers are left behind in feeding patches by larger groups) rather than social preference, such as the motivation to seek out individuals with which they share affiliative ties.

Introduction

Group-living species benefit from shared territorial and predator defence (Clifton 1990; Watts & Mitani 2001; Molvar & Bowyer 1994; Hass & Valenzuela 2002) as well as increased efficiency finding food and mates (Sueur et al. 2011), while incurring a range of costs, including stress (Pride 2005), increased rate of disease transmission (Alexander 1974) and competition over the food and mates (Wrangham 2010; Mumme et al. 1983) which can result in intragroup aggression/harassment (Asensio et al. 2008; Campbell 2006). One social structure which allows individuals to reap the benefits of group living while mitigating some of the costs is 'fission-fusion', a social system in which individuals vary their group size through the ongoing joining and splitting of units within the whole (Aureli et al., 2008; Kummer, 1971; Sugiyama, 1968). This may take the form of a multi-level society which divides along predetermined lines (e.g. hamadryas baboons (*Papio hamadryas*): Kummer, 1968), or a more fluid system in which membership of subgroups is not fixed (e.g. chimpanzees, (*P. troglodytes*)*:* Sugiyama, 1968). Fission-fusion is somewhat uncommon in mammals (Aureli et al. 2008) but has been documented in a range of taxa, including primates (Asensio et al. 2008; Goodall 1986; Symington 1990b), bats (Rhodes 2007), dolphins (Heithaus & Dill 2002), giraffes (Carter et al. 2013) and spotted hyenas (Smith et al. 2008). When large groups can split into multiple subgroups, membership of which is fluid, individuals can benefit from group living by using shared group territory but also selectively seek out or avoid specific members as and when this is beneficial. This allows, for example, individuals to reduce feeding competition by foraging in smaller groups (Heithaus & Dill 2002), and allows mothers to avoid potentially infanticidal group members (Chapter Four; Smith et al., 2008), or seek out specific individuals who might provide valuable social learning opportunities (Murray et al. 2014b). It also provides an escape to prevent escalating aggression (Smith et al. 2008).

Subgroup (or party: Sugiyama, 1968) composition is therefore a valuable tool for behavioural ecologists, as it provides insight into social relationships by shedding light on which group members are preferentially associating with or avoiding each other. One can use data on joint presence of individuals to infer social behaviour including the relative stability of social relationships across time (Parra et al. 2011), coalitionary and co-operative behaviour (Nishida & Hosaka 1996; Kerth & König 1999), infanticide avoidance (Smith et al., 2008; Chapter Four), mating strategies (Smolker et al. 1992) and parenting strategies (c; Murray, Stanton, Lonsdorf, Wroblewski, & Pusey, 2016; Chapter Six). In this thesis I have used party composition data to infer an anti-infanticide strategy by mothers, in which mothers avoid potentially dangerous males (Chapter Four). However, this interpretation would benefit from evidence which tested whether it is in fact mothers who are initiating this pattern of avoidance.

Party composition data, which I have used previously (Chapters four and five) does not generally provide information about directionality. Subgroup composition and other related measures, such as nearest neighbour, are frequently measured through scan sampling, a form of instantaneous sampling (Altmann 1974) which captures a snapshot of the subgroup at predetermined, regular moments in time. Since changes in group composition between snapshots do not tell us whether an individual joined a group, or was joined by others, any effort to determine directionality from scan sampling data must be based on inference. This causes problems when there is more than one viable interpretation of results, e.g. high association of chimpanzee fathers with their offspring may reflect fathers seeking out their offspring to provide care, or mothers seeking out fathers as protectors (compare: Murray et al. 2016, Chapter Six). Data collected by scan sampling alone cannot help to distinguish between these interpretations and thus Chapter Four relies on inference, rather than direct testing of avoidance behaviour.

As well as these difficulties in interpreting non-directional data, subgroup composition may be influenced by additional confounding factors unrelated to preference or social strategy. For example foraging strategies may necessitate either an increase or decrease in group size (Heithaus & Dill 2002; Connor et al. 2000) and travel costs may be higher for mothers (Altmann & Samuels 1992) meaning that they may spend time with other mothers out of practicality rather than preference. Similarly, in species in which individuals primarily occupy core areas within the group's territory, presence in a subgroup may represent an overlap in these areas, as well as, or rather than, social preferences (Zarin P. Machanda et al. 2013). While in some cases the function of party size variation may be straightforward, for instance when groups increase or decrease during a specific activity, such as feeding (Heithaus & Dill 2002; Connor et al. 2000), in others it may be unclear whether social preference or practicality are underpinning variation. Nursery groups of chimpanzee mothers can be reasonably interpreted as forming either due to travelling costs (Wrangham, 2000) or infant safety (Otali & Gilchrist 2006). With only scan samples of party composition, it is impossible to say whether mothers are choosing to associate preferentially with each other, or are simply unable to keep up with other individuals.

One additional measure which can strengthen and inform inferences from party composition data is directional movement within parties. While Chapter Four identified a pattern of maternal avoidance of a specific male, total avoidance at the level of separate parties is not always practical and may be unnecessarily costly. However, since parties in the Sonso community can contain up to 30 individuals (Newton-Fisher et al. 2000) and span up to around 35 metres (Newton-Fisher 1997), there is still room for preferential association and vigilance regarding potentially dangerous individuals within a party, meaning individuals can be in the same party but still avoiding each other. Joint presence does not necessitate direct interaction, whereas initiating close proximity with other individuals within in the same party provides evidence for preferential association. Here, I consider both static measures of party membership (party composition and nearest neighbour) and movements within parties in the Sonso community. I use these measures to test whether male avoidance by females is evident at the within, as well as between, party level, and test directly who is avoiding whom.

So far I have identified male avoidance at the level of party membership as a response to infanticide in Sonso community under specific conditions (elevated male risk due to a rank increase). I did not find that the number of males in a party with a mother varied as a function of infant age (i.e. there was no generalised avoidance of males by mothers: Chapter Four). This was somewhat surprising as, while risk will vary between males, several males at any given time are likely to pose some level of risk to infants. In this chapter therefore, I look again at mother-male association at the level of party membership, predicting that mothers should spend time with fewer males than females without infants. Further to this, I predict that in accordance with a male avoidance strategy, mothers of infants will associate with fewer males than will females without infants (prediction one), and with more females (prediction two), specifically mothers (prediction three). I also predict that when in parties with these males, mothers will be less likely to initiate close contact with them than will females without infants, (prediction four) since they pose a risk to infants which should be reduced by maintaining a distance. Since the predicted association with mothers would be pragmatic, rather than preferential, i.e. mothers are associating essentially as a side effect of avoiding other community members, rather than gaining any specific benefits from other mothers themselves, that this increased association will not be linked to an increase in affiliative responses to close proximity (prediction five).

Methods

Data collection

Study subjects were the Sonso community of chimpanzees from the Budongo Forest Reserve, Uganda. This community has been under continuous observation since 1993 (Reynolds 2005; Newton-Fisher 1997). I collected detailed data over a 3-month period (April – June, 2017) to test the efficacy of using multiple measures of association in a fission-fusion species and investigate the social preferences of mothers in this species. During the study period, the study community consisted of 11 adult males and between 23 and 25 adult females. I conducted nine hour focal follows of pre-selected individuals: nine focal adult females, five of whom were mothers of infants and four of whom were adult females without an infant under five years old). Party composition was recorded at 15-minutes intervals using instantaneous scan sampling, as was the identity of the focal's nearest neighbour. To determine directionality of within-party proximity, I considered a 2m perimeter around each focal and used all-occurrence sampling to record whenever this perimeter was crossed by another adult, along the directionality of this movement (i.e. whether the focal approached or was approached by another individual). Ambiguous instances, where both individuals moved towards or away from each other, were not recorded. I also recorded the response of the passive individual on being approached as "affiliative" (groom, touch, present: taken from Goodall, 1989), "non-affiliative" (aggression or threat behaviours: detailed in Newton-Fisher, 2017), "other" (all other behaviours), or "none".

Data Analysis

I calculated party composition from the dataset of scan samples as the total number of adult males and total number of adult females in each party as well as the total number of mothers of infants. I used linear mixed model (LMM) analyses (using the R package “lme4”: (Bates et al. 2015) to assess whether I could predict the party composition from maternal state of the focal (mother of an infant coded as Y/N). I created five models. In each of the first three models, in order to test whether the maternal state of the focal predicts her associations, maternal state (has infant/does not have infant) was the predictor variable and focal ID was included as a random effect. In model one, the number of males was the dependent variable; in model two, it was the number of other females; in model three, it was the number of other mothers of infants.

Models four and five used the directional data. For each focal individual I calculated: (1) the rate (occurrences per hour of observation) at which the focal approached adult males; (2) the rate at which the focal approached adult females; (3) the rate at which the focal was approached by adult males and (4) the rate at which the focal was approached by adult females. In model four, I set the rate of approaches as the response variable, while for model five it was rate of being approached. In both of these models, the sex of the non-focal individuals for which the rate was calculated, and whether the focal was the mother of an infant (Y/N), were predictors, with an interaction term between the two. As with the other models, focal ID was included as a random effect. I used the “drop1” function to perform likelihood ratio tests to assess the significance of the predictors in my models.

In order to test whether mothers or other females are biased towards having a particular sex as their nearest neighbour, I used exact binomial tests to see whether, for either group, the ratio of male to female nearest neighbours varied significantly from 50/50.

To test my hypothesis that mothers of infants will associate with other mothers at a higher rate than females without infants do, out of necessity rather than preference, I performed a fisher’s exact test. This was to ascertain whether the proportion of approaches from mothers which elicited an affiliative response from the focals varied based on maternal status.

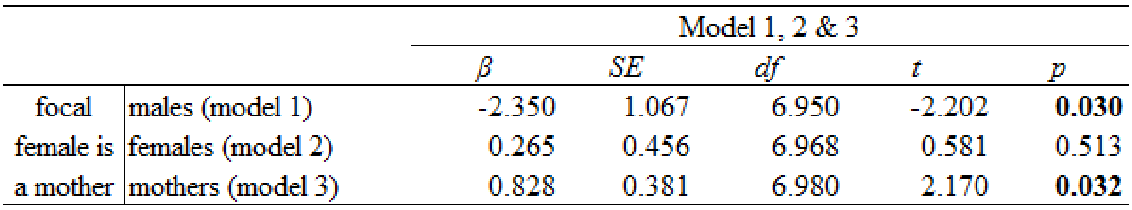
I used 2 sample t-tests to assess whether mothers of infants and other females differed in their rates of approaching other individuals or being approached.

Results

Of 1162 unambiguous approaches involving focal individuals, 526 were adult female to adult female approaches, 437 were adult female to adult male and 199 were adult males approaching adult females. Mothers of infants were less gregarious than females without infants, approaching other individuals at a mean rate of 1.16 times per hour of observation (sd = 0.82), compared to 2.75 times (sd = 1.30). This difference was significant (2 sample t-test: t = -3.26, p = 0.005). Similarly, mothers were approached significantly less frequently than females without young infants (mean rate of 0.77 times per hour, sd = 0.54 and 1.73 times, sd = 0.67, respectively; 2 sample t-test: t = -3.50, p = 0.003). Mothers also spent time in significantly smaller parties on average than females without young infants (mean = 4.96, sd = 4.62 and mean = 6.98, sd = 4.50 respectively; 2 sample t-test: t = -5.85, p = <0.0001). Affiliative responses to approaches were rare, with focal individuals responding affiliatively in only 3% of approaches.

Parties in which the focal female was the mother of an infant over two fewer males (Model 1, p = 0.03, Table 5.1) and more mothers, though this effect was smaller (Model 3: p = 0.03, Table 5.1) than parties where the focal female did not have an infant. Thus both predictions one and three were met. The maternal state of the focal had no relationship with the total number of females in a party (Model 2: p = 0.51, Table 5.1). Thus prediction two was not met. Despite spending time in parties with them, focals who were mothers themselves were not more likely than those without young infants to respond affiliatively when approached by other mothers (fishers exact test test: p = 1). Thus prediction five was met.

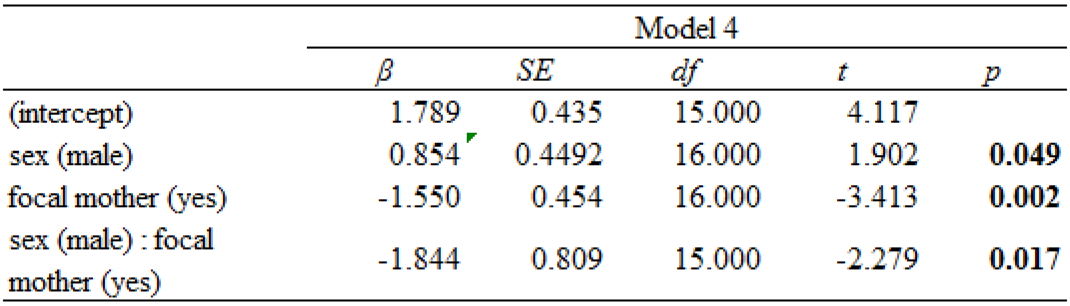
Table 5.1. *Mixed model results from Models 1, 2 & 3 showing the effect on party composition of the focal female's reproductive state (mother/non-mother)*



		Model 1, 2 & 3				
		β	*SE*	*df*	*t*	*p*
focal female is a mother	males (model 1)	-2.350	1.067	6.950	-2.202	**0.030**
	females (model 2)	0.265	0.456	6.968	0.581	0.513
	mothers (model 3)	0.828	0.381	6.980	2.170	**0.032**

In the model which assessed the rate at which the focal females approached others, I found that the interaction between the sex of the individual being approached and whether or not the focal was the mother of an infant was significant. Mothers approached males less frequently than females without infants did with a reduction in rate of -1.84 times per hour, (p = 0.02, Table 5.2). This is in keeping with prediction four. In addition, my focal females were more likely to approach males than other females (p = 0.05, Table 5.2), although this was a smaller effect (an increase in rate of 0.85 times per hour) and mothers approached all other individuals 1.55 times per hour less frequently than females without infants did (p = 0.002, Table 5.2).

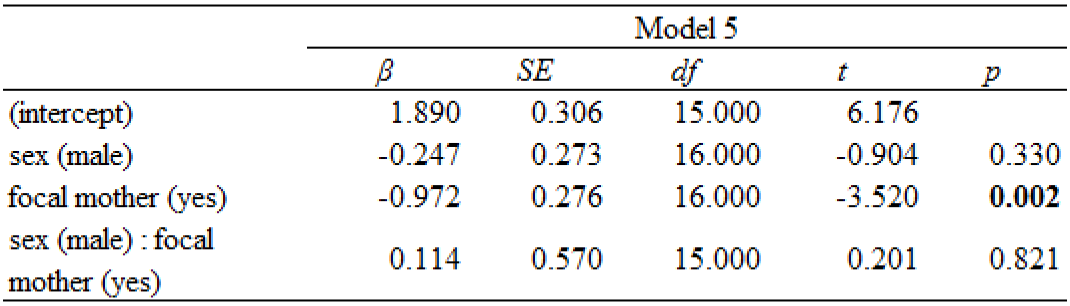
Table 5.2. *Mixed model results from Model 4, showing how reproductive state of the focal (mother/non-mother), sex of the other individual and the interaction between the two affects the focal females' rates of initiating close spatial association. Significant results are shown in bold.*



	Model 4				
	β	*SE*	*df*	*t*	*p*
(intercept)	1.789	0.435	15.000	4.117	
sex (male)	0.854	0.4492	16.000	1.902	**0.049**
focal mother (yes)	-1.550	0.454	16.000	-3.413	**0.002**
sex (male) : focal mother (yes)	-1.844	0.809	15.000	-2.279	**0.017**

In the model which assessed the rate at which the focal females were approached by others, I found that the interaction between sex of the approacher and whether or not the focal female was the mother of an infant was not-significant (Model 5: SE = 0.11 ± 0.57, p = 0.82), indicating that mothers were approached by males as frequently as non-mothers were. The effect of approacher sex was non-significant on the rate at which focals were approached (Model 5: SE = -0.25 ± 0.28, p = 0.33). Whether or not the focal was the mother of an infant had a significant effect on her rate of being approached, with mothers approached significantly less frequently than other females (Model 5: SE = -0.97 ± 0.28, p = 0.002).

Table 5.3. *Mixed model results from Model 5, showing how reproductive state of the focal (mother/non-mother), sex of the other individual and the interaction between the two affects the rate at which focal females are approached by others. Significant results are shown in bold.*



	Model 5				
	β	*SE*	*df*	*t*	*p*
(intercept)	1.890	0.306	15.000	6.176	
sex (male)	-0.247	0.273	16.000	-0.904	0.330
focal mother (yes)	-0.972	0.276	16.000	-3.520	**0.002**
sex (male) : focal mother (yes)	0.114	0.570	15.000	0.201	0.821

Females without infants did not have one sex as a nearest neighbour more frequently than the other (exact binomial test: p = 0.07), although there was a trend towards having male neighbours (171 out of 309 incidences). Mothers on the other hand had other females as nearest neighbours significantly more often than they did males (exact binomial test: p = <0.001).

Discussion

I have found that mothers of infants generally spend time in parties with fewer males than mothers without infants and that mothers are more likely to have females as their nearest neighbours. Non-mothers however do not have the same pattern of association, and have males and females as their nearest neighbours equally as often. There are several potential explanations for mothers associating with more females, and fewer males, when compared to females without young infants. Firstly, it is possible that mothers are preferred companions, which could be linked to infant safety: perhaps other mothers are less likely to be physically violent due to the risk of harming their own infants, for instance. Alternatively mothers could offer social benefits, specifically socialisation for infants. Chimpanzee mothers socialise primarily with other mothers whose offspring are of the same age class (Horvat & Kraemer 1981) and socialisation, particularly infant play, is considered important for development, notably in areas such as communication and navigating social hierarchies (Poirier & Smith 1974). Conversely, rather than preferentially associating with females, this pattern could be a result of mothers actively avoiding males, due to infanticide risk (Chapter Four). I have previously interpreted low mother-male association as a female driven infanticide avoidance strategy (Chapter Four). By this logic, mothers would be clustering by nature of avoiding the same individuals, rather than actively seeking each other out. However, it is also possible that rather than reflecting any social preferences, this pattern could be simply due to elevated travel costs for mothers of infants (Altmann & Samuels 1992; Wrangham & Smuts 1980), making other mothers the most practical travelling companions.

Rather than mother-mother association being the result of a female strategy, it may be a side effect of a male strategy. Rather than mothers seeking out other females or avoiding males, it could be the case that males are seeking out females without infants and spending less time with mothers as a byproduct. Monitoring the reproductive state of non-lactating females might provide males with valuable mating opportunities, making this a beneficial strategy. Male chimpanzees are sensitive to subtle changes in the size of female perineal swellings, which are cues to ovulation (Deschner et al. 2004), so would benefit from tracking these changes in order to identify the most fecund females. In baboons (*Papio anubis*) male-female association may be a form of future mating effort by males (Smuts 1985). Male mating effort might therefore account for the low mother-male association although evidence from another East African population of chimpanzees suggests that this is not the case in this species (Murray et al. 2016). However, behaviour is highly variable between communities (Whiten et al. 1999; Humle & Matsuzawa 2001) and Chapter Six has highlighted potential variation in reproductive/parenting strategies between communities.

Within the context of the frequency of infanticide at Sonso and evidence for maternal avoidance of dangerous males (Chapter Four), it seems most reasonable to interpret the pattern of male-female association seen here as further evidence for an infanticide avoidance strategy by mothers. Low mother-male association would therefore be the result of a maternal strategy, rather than be male initiated, and mothers' higher association with other mothers would be due to a combination of increased travel costs and the side effect of mothers avoiding the same males and therefore spending time in "safe" parties, rather than being due to a desire to association specifically with other females. While static measures of party composition cannot test this directly, directional measures (movements within parties) can test whether mothers or males are responsible for low association and test whether female-female association is due to preference or circumstance. Mothers of infants in this study were both approached and approached others at lower rates than females without infants. Since this effect was bi-directional, this is unlikely to be purely due to a behavioural strategy by mothers and may well be linked to other factors, perhaps lower gregariousness overall due to the energetic demands of lactation necessitating increased time spent foraging (Potts et al. 2011; Dias et al. 2011). However, while there was no sex difference in *being* approached for mothers, i.e. mothers were approached by males and females at a comparable rate, mothers approached males less frequently than they did other females. This is strong evidence that low levels of mother-male association are female initiated, since when mothers were passive (being approached) there were no sex difference, but when they were active (approaching), they chose to avoid proximity with adult males. These results support the hypothesis that mothers pursue a male-avoidance strategy by mothers which would reduce infanticide risk. Furthermore, while mothers associated more other mothers than did females without infants, mothers and females without infants were equally likely to respond affiliatively when approached by other mothers, indicating that mother-mother association was not due to a social preference, but rather incidental. This supports my interpretation that mothers did not seek out other mothers but rather associated with them as by-product of other decisions, e.g. they are avoiding the same males.

It is not entirely clear why in this study period (2017) there appeared to be generalized avoidance of males by mothers and increased association with other mothers, when in Chapter Four (study period 2003 – 2005) this effect was not found. One possibility is that in Chapter Four there was a single male who posed a heightened risk, due to a rank increase, whereas in this case there was no clear alpha male and blurred boundaries between the highest ranks (personal observation based on pant-grunts and aggression, although the data are too sparse to support this statistically), which could mean that overall instability of the male hierarchy made enough males potentially dangerous that a more general avoidance strategy was adaptive.

Male avoidance by mothers is therefore most reasonably interpreted as an anti-infanticide strategy. In response to males' major motivation to attack unrelated infants (Hrdy 1979; C. P. van Schaik 2000a), mothers should have evolved effective counterstrategies, one of which appears to be male avoidance (Chapter Four). However, as previously mentioned, even in fission-fusion species such as chimpanzees, large subgroups do still form (Matsumoto-Oda et al. 1998) and while chimpanzee mothers are often solitary (Wrangham, 2000), there are benefits to spending time in parties with other individuals, including males, even when associated costs are considered. For instance, large groups form at high quality feeding patches, such as ripe fruit trees (Ghiglieri 1984). The benefits of high quality food might outweigh the risks of joining such parties or of remaining in food patches when large parties form around oneself. While feeding in small groups might be preferable due to lower competition (Wrangham & White, 1988), and appears to be part of the reason for low female gregariousness (Wrangham & Smuts, 1980), individuals at high quality feeding patches are likely to be joined by others, regardless of their own social preferences. In this situation, remaining within the party and maintaining a safe distance from undesirable new arrivals may be preferable to leaving and seeking out other food sources. It is also worth considering that being alone is not always safer, even when taking into the account the risk posed by other community members. Lone individuals, particularly when close to the territory edge, are at risk of lethal aggression from strangers who may patrol across borders (Watts, David et al. 2006). Larger subgroups are linked to predator defence (Smith et al. 2008). And while the Sonso community has low predation pressure, predation is a major cause of death at other sites (Boesch & Boesch-Achermann 2000). Essentially, the costs of joining subgroups with potentially dangerous community members may at times outweigh the risks of spending time alone.

In conclusion, Sonso community mothers exhibit not only avoidance of males at the level of party membership but also avoid within-party proximity with males. This suggests that male avoidance by mothers is complex strategy in which highly dangerous males may be avoided almost entirely (e.g. avoiding parties with rank-rising males who pose the biggest threat: Chapter Four) but when mothers must come into association with males, they avoid being in close proximity. Such a strategy should allow mothers to protect their infants (to some extent) from infanticide, without incurring unnecessary costs, such as increased travel time and loss of feeding opportunities that would be associated with complete avoidance of all males.

6. Single mums: no evidence for paternal care in wild, eastern chimpanzees

Abstract

Paternal care is defined as any behaviour selectively directed by males towards their own, rather than unrelated infants, that delivers fitness benefits. Such care is more common in monogamous species, where higher paternity certainty makes a male's investment less likely to be misdirected towards non-kin infants. However, several promiscuously-mating primates reportedly exhibit some form of paternal care. Studies from two communities of chimpanzees (*P. troglodytes*) have claimed to find evidence of such, despite the species' highly promiscuous mating system. In this study, I use data on association patterns and aggression from a third community of chimpanzees, of the eastern subspecies (*P. t. schweinfurthii*) from the Budongo Forest, Uganda, to further investigate this issue. I found that while males directed less aggression towards mothers than non-mothers, they did not distinguish between mothers of their own and others' infants. In addition, I found no evidence of preferential association between mother-infant-father compared to mother-infant-non-father triads. My results contradict claims previously made for chimpanzees, and I suggest that mother-male association in chimpanzees is likely to be underpinned by maternal, rather than paternal infant care strategies.

Introduction

Paternal care is defined as behaviour selectively directed by fathers towards offspring, rather than non-kin, that offers fitness benefits to recipients (Buchan et al. 2003). Paternal care should be rare in species without reasonably high paternity certainty (or the ability to recognise kin), particularly in the case of higher cost behaviours, to avoid wasting investment on non-kin: in order for such behaviour to be adaptive, the energy and time expenditure must offer greater fitness returns to the father than searching for new mating opportunities. Unsurprisingly then, paternal investment is more commonly seen in monogamously mating species with high paternity certainty, across taxa, including birds, rodents, and carnivores (Patris & Baudoin 2000; Sharpe & Rosell 2003; Wright 2006; Kleiman & Malcolm 1981; Gubernick & Teferi 2000; Cant 2003; Moller & Birkhead 1993). Paternal care is common in birds (documented in 81% of species: Cockburn 2006), where both males and females are capable of incubating eggs and feeding young. It is also well documented in fish (Blumer 1979), and present but rare in reptiles and amphibians (Crump 1996; T. H. Clutton-Brock 1991). Amongst mammals, females are adapted to gestate and nurse offspring (Asdell 1946) and therefore have little option but to invest heavily in their young. Males, however, are unencumbered by such adaptations and therefore able to desert females immediately after copulation. Despite this, males of almost 10% of mammal species routinely practise some level of direct paternal care (Kleiman & Malcolm 1981; Woodroffe & Vincent 1994).

Paternal care should be rare or absent in species where females mate promiscuity (mating with multiple males within the same conceptive cycle), a behaviour thought to confuse paternity, largely as a defence against male committed, sexually-selected infanticide (Hrdy 1979). Contrary to this expectation, recent work has suggested that males of several promiscuously-mating non-human primate species appear to bias behaviour towards their own offspring. In mandrills (*Mandrillus sphinx*) and rhesus macaques (*M. mulatta*), fathers' relationships with their offspring are more affiliative than those with non-kin, both in terms of association and through behaviour such as grooming and touching, respectively (Charpentier et al. 2007; Langos et al. 2013). Such increased tolerance may allow infants access to better quality food resources when in the presence of their fathers (Huchard et al. 2013), thus representing a form of low-cost paternal care. More explicit parental care exists in the form of assistance in agonistic encounters, observed in yellow baboons (*P. cynocephalus*: Buchan et al. 2003) and defence against infanticidal attacks in langurs (*S. entellus*: Borries et al. 1999). Previous studies of chimpanzees (*P. troglodytes*) have found that association patterns, and rates of both aggression and play, reflect paternal investment or at least a kin-bias in male behaviour. Patterns were not consistent across communities, however. In one community (Kasakela, Gombe) of the eastern subspecies (*P. t. schweinfurthii)* fathers associated more frequently with their own infants than with those who are unrelated, until these infants were six months old (Murray et al. 2016), while males in a community of the western sub-species (*P. t. verus*) did not (although they were more likely to play and groom with their own infants: Lehmann et al. 2006). The increased association with own infants in Eastern chimpanzees has been proposed as infanticide defence by fathers (Murray et al. 2016). Infants are more vulnerable to infanticide when they are younger (van Schaik, 2000a; d; Chapter Three), supporting this interpretation, however it's not clear exactly how males are defending against infanticide when direct defence of infanticide victims by individuals other than the mother is very rare (Chapter Three). Western chimpanzee males were also less aggressive towards the mothers of their own offspring than they are towards other mothers (Lehmann et al. 2006). The mechanisms for this bias are unclear: while kin recognition is a possibility, it is not a pre-requisite. Both previous association with mothers (Langergraber et al. 2013b), and male rank (Wroblewski et al. 2009), are linked to paternity in chimpanzees, and provide alternative cues to paternity. Given that these findings of paternal kin bias are counter to theoretical expectations, they warrant careful inspection and confirmation.

Association patterns are highly informative, because chimpanzees exhibit a fission-fusion social structure in which individuals associate with one another in sub-groups, or 'parties' (Yukimaru Sugiyama 1968), the composition of which changes throughout the day (Nishida 1968). This means that individuals can selectively associate with, or avoid, other community members. While some male behaviours such as territorial defence may represent a form of indirect paternal care (since the quality of territory is linked to female reproductive success: Williams et al. 2002; Thompson et al. 2007), these do not involve interactions with mothers or infants. In order to provide direct paternal care, fathers must be present in the same party as their offspring. Female chimpanzees are the less gregarious sex, spending upwards of 40% of their time alone (Murray, Mane, et al. 2007; Wrangham & Smuts 1980), which means that males associating with these often-lone mothers will inevitably spend less time with others, and thereby incur potentially significant costs in terms of lost reproductive opportunities and limitations on the male-male associations considered to be a key factor in maintaining alliances and coalitions (Nishida & Hosaka 1996), which are directly linked to mating access (Duffy et al. 2007). However, if direct paternal care improves infant survival, such costs could be mitigated.

In this paper, I investigate the hypothesis that male chimpanzees direct specific, preferential treatment towards their own offspring (and those infants' mothers) compared to unrelated infants. I specifically attempt to replicate the findings of previous research: (1) that mother-infant-father triads associate more frequently than mother-infant-non-father triads, testing the hypothesis that paternity and the age/sex of the infant influences this association; (2) that mothers of young infants (< three yrs of age) receive less aggression from adult males than do other adult females; and (3) that mothers of young infants receive less aggression from the fathers of these infant than they do from other males. I discuss this with relation to infanticide defence by fathers and also consider alternative explanations for previous findings.

Methods

Data collection

Data were collected from the Sonso community of chimpanzees from the Budongo Forest Reserve, Uganda. Habituation of this community began in 1991, and it has been under continuous observation ever since (Reynolds 2005; Newton-Fisher 1997). Data were collected from October 1994 – December 1995 (study period one), when the community consisted of 12 adult females (≥ 14 years old) and 12 adult males (≥ 16 years old); and October 2003 – January 2005 (study period two), when there were 23 adult females and nine adult males. Parties were followed from first encounter to nesting, with pre-identified focal individuals followed when parties fissioned. If visual contact with the chimpanzees was lost, the next encountered party which contained one of the focal animals was then followed. Study period one consisted of 790 hours of focal follows and study period two consisted of 1432 hours. Aggressive interactions were collected using all-occurrence sampling (Altmann 1974) within focal parties, where ‘party’ was defined operationally as a cluster of independently associating individuals with a maximum radius of around 35m, showing coordination in behaviour (N. Newton-Fisher 1999a; Newton-Fisher & Kaburu 2017). Interactions considered to be aggressive were: attacks, chases (with or without contact), directed charging displays, and threats (Goodall 1986; Newton-Fisher 2017). Paternity was taken from previous publications (Newton-Fisher et al. 2010; Wittig et al. 2014; Crockford et al. 2013) and unpublished data (personal communication, L. Vigilant and K. Langergraber).

Data analysis

In order to evaluate whether males preferentially associated with their own offspring versus other infants, I created a measure of association which looked at the proportion of a male’s time which he spent with specific mother-infant dyads. I used pairwise affinity indices (PAIs: Pepper et al. 1999; Mitani et al. 2002) to do this. Log transformation of the final indices meant that a PAI of 0 was equivalent to random association and positive values indicated preferential association while negative values indicated avoidance, creating an easily interpreted measure of association. PAIs were calculated as:

$$\frac{P_{AB}}{P_{A+}P_{B}}$$

where P_{AB} is the total number of times individuals A and B are observed within the same party, while P_A and P_B are the total number of times A and B are observed in all other parties. In each indices A is the male and B is the mother-infant pair.

Following Mitani et al. (2002), all indices were divided by an expected value, produced by the null hypothesis that grouping is random rather than dyad-specific. To determine expected values, I used the function “randomizeMatrix” in the R (version 3.4.3: R Core Team 2013) package “picante” (Kembel et al. 2010) to shuffle the observed parties, while keeping the number of observations of each individual the same, using 100,000 iterations to produce a randomized dataset. This approach allowed me to create simulated scenarios in which individuals varied in their frequency of being observed, controlling for varying group size (Mitani et al. 2002), and joined parties without reference to existing members. So that values above and below expectation would have equal weight, I log-transformed my final observed/expected ratios (Mitani et al. 2002) to create the final PAI.

This measure of measuring affinity assumes that males with several offspring do not associate with one at the expense of others. There is no reason to assume that, if males were providing care to their infants, parties would not consist of multiple offspring of a single male. Therefore a male having multiple offspring concurrently will not have affected the analysis. Family groups could be formed actively by both mothers and fathers. Mothers should seek out males if they are offering some form of paternal care and if males benefit from having their infants close by they could control those infants' mothers' movements with the goal of encouraging formation of particular parties in the same way they do while escorting females on consortship (Tutin 1979).

I distinguished between three infant-age categories: <1 yr; 1 – < 2 yrs; 2 – < 3 yrs. These age categories were the narrowest that my sample size would allow, but reasonable for the purposes of this study. If paternal care is linked to infanticide prevention, as suggested by Murray et al. (2016), there should be significant benefits for males in killing infants at least up to one year old in a species in which the average interbirth interval is around six years (Emery Thompson, Jones, et al. 2007b). In order to be included in my analyses, fathers had to be observed for a minimum of 20 hours during the period in which their infant fitted within the age category. Some infants were observed while they were in more than one age category and, since some males fathered more than a single infant, they are also represented in multiple categories. Across both study periods, there were seven mothers and five fathers who had infants (n = seven) in age category one (<1 yr), seven mothers and four fathers who had infants (n = seven) in age category two (1 – < 2 yrs), and seven mothers and five fathers who had infants (n = seven) in age category three (2 – < 3 yrs). This represents ten different mothers, seven different fathers, 13 different infants and 59 mother-father dyads.

I calculated the rate of aggression directed by every adult male against every adult female (aggressive interactions/time in association). For mothers of young infants (<= three yrs old), I calculated the rate of aggression directed towards them from each male when their infants were in each of the three age categories (0 – one yr, one – two yrs, two – thee yrs). For all other females, I calculated the rate of aggression directed towards them by each male across the whole of each study period.

I used linear mixed models implemented in the R package “lme4” (Bates et al. 2015) to analyse these data. In all models, I included the identities of both the mother and the male as random effects. In model1, testing whether paternity and age/sex of the mother’s infant influenced male-mother affinity indices, I set the PAI of each dyad as the response variable, with whether or not the male in question was the father (Y/N), infant-age category, and infant sex as predictors. I also looked at the interaction between father (Y/N), and both infant-age category and infant sex. The sample size in this model was 59, the total number of mother-father dyads. In model two, testing whether mothers were subjected to differential rates of aggression compared to other adult females, I set dyadic rate of aggression as the response, and whether or not the female in question was a mother of a young infant (Y/N) as the predictor. The sample size for model two was 297, the total number of male-female dyads. In model three, testing whether paternity affected the rate of aggression within a mother-male dyad, I again set the dyadic rate of aggression as the response variable, with whether or not the male in question was the father (Y/N) and infant-age category, and the interaction between the two, as predictors. The sample size for model three was 153, the total number of male-mother dyads. Play between adult males and infants was too infrequent to analyse (three incidences of fathers of young infants playing with infants under three yrs in study period two; not observed in study period one). I used likelihood ratio tests to assess the significance of variables in my models.

Results

PAIs of males and mothers range from -1.52 to 1.09 (median 0.12). PAIs generally clustered around 0 (random association: see Figure 6.1), with 40% indicating some level of avoidance and 60% indicating some preferential association. Overall it appears as though the majority of dyads did not exhibit a strong preference either way. Of the 23 dyads whose PAIs were below 0 (avoidance), 10 were mother-infant-father triads and of the 36 triads whose PAIs were above 0 (preferential association), 8 were mother-infant-father triads. Both the most frequently and most rarely associating triads were mother-infant-non-father. PAIs varied significantly by individual. Mean PAIs of males varied from -0.84 to 0.25 (median 0.13). Mean PAIs of mothers varied from -0.44 to 0.29 (median 0.12). Forty-three percent of males had an average PAI indicating avoidance of or by females (less than 0), while only 30% of females had an average PAI indicating avoidance of or by males.

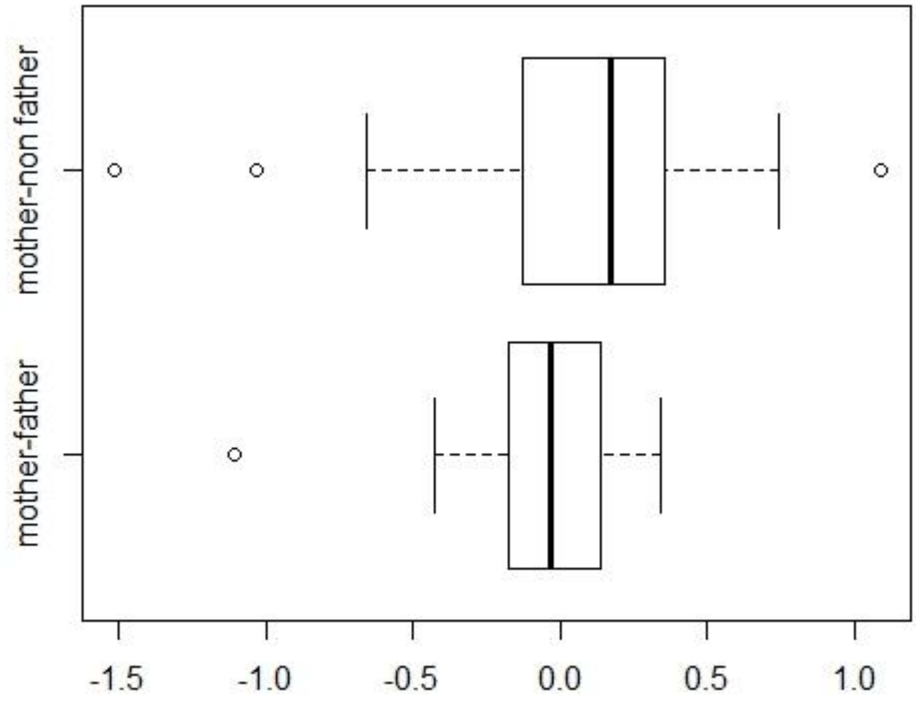
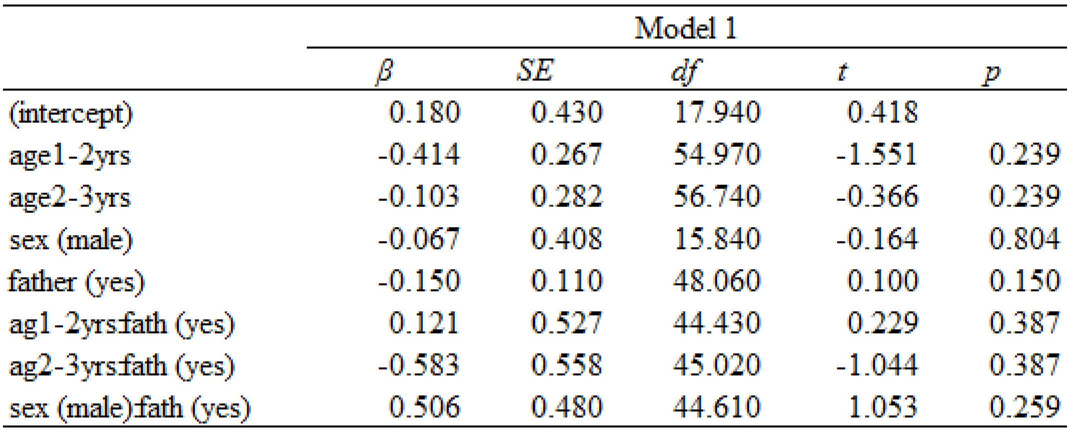


Figure 6.1. *Boxplot showing distribution, mean and inter-quartile range of PAIs of mother-male dyads.*

The majority of male to female aggression consisted of threats, rather than physical aggression (564 out of 592 incidences were non-contact) and aggression towards females was not particularly frequent. Male to mother dyadic aggression rates ranged from 0 to 0.54 interactions h^{-1}, with a median of 0.00. For non-mothers, the range was 0 to three interactions h^{-1} with a median of 0.01. Fathers directed aggression towards mothers of their infants between 0 and 0.04 times h^{-1}, with a median of 0.00. For mother non-father dyads, the range was 0 to 0.54 interactions h^{-1} with a median of 0.00. Overall fathers were aggressive marginally less frequently towards mothers than were non-fathers (average rate of 0.04 and 0.05 interactions per hour, respectively). Not all males were equally aggressive: 7 of 16 males were never recorded directing aggression towards an adult female. Similarly, the rate of aggression received varied notably between females with two females never observed as victims of male aggression during the study periods.

LMM analysis found no influence of paternity on the PAI values of mother-infant-male triads (Model one: $\beta \pm SE = -0.15 \pm 0.11$, $p = 0.15$), nor any significant interactions between paternity and infant sex or age. Mothers of young infants did receive less male aggression compared to other females (Model two: $\beta \pm SE = -0.07 \pm 0.03$, $p = 0.01$, Table 6.2), although a reduction in 0.07 aggressive interactions per hour is small. Neither paternity (Model three: $\beta \pm SE = -0.01 \pm 0.01$, $p = 0.61$, Table 6.3), infant age (Model three: $\beta \pm SE = 0.01 \pm 0.01$, $p = 0.30$), or the interaction between the two (Model three: $\beta \pm SE = -0.01 \pm 0.02$, $p = 0.70$) had a significant effect on the rate of aggression directed by males towards mothers of young infants. That is, fathers were not less aggressive to the mothers of their infants than they were to adult females in general.

Table 6.1. *Mixed model results from Model 1 showing how PAIs are predicted by whether the male dyad partner is the father of the female's infant, as well as age and sex of the infant.*



	Model 1				
	β	*SE*	*df*	*t*	*p*
(intercept)	0.180	0.430	17.940	0.418	
age1-2yrs	-0.414	0.267	54.970	-1.551	0.239
age2-3yrs	-0.103	0.282	56.740	-0.366	0.239
sex (male)	-0.067	0.408	15.840	-0.164	0.804
father (yes)	-0.150	0.110	48.060	0.100	0.150
ag1-2yrs:fath (yes)	0.121	0.527	44.430	0.229	0.387
ag2-3yrs:fath (yes)	-0.583	0.558	45.020	-1.044	0.387
sex (male):fath (yes)	0.506	0.480	44.610	1.053	0.259

Table 6.2. *Mixed model results from Model 2 showing how dyadic rates of male-female aggression vary depending on the female's reproductive state (mother/non-mother).*

	Model 2				
	β	*SE*	*df*	*t*	*p*
(intercept)	0.085	0.024	21.430	3.475	
mother (yes)	-0.069	0.026	27.689	-2.619	**0.013**

Table 6.3. *Mixed model results from Model 2 showing how dyadic rates of male-female aggression vary depending on whether the aggressor is the father of the female's infant.*

	Model 3				
	β	*SE*	*df*	*t*	*p*
(intercept)	0.002	0.012	55.740	0.146	
father (yes)	-0.007	0.014	135.530	-0.514	0.605
age category	0.006	0.005	61.620	1.079	0.296
father (yes) : age category	-0.006	0.016	137.760	-0.379	0.700

As well as there being no overall pattern of kin biased behaviour, a specific male identified as a possible protector previously (Chapter Four) did not associate with his own offspring more than unrelated infants, and instead had a marginally higher PAI with mothers of unrelated infants (0.04) than mothers of his own infants (-0.09).

Discussion

These results show that, in this community of chimpanzees, paternity has no effect on adult males' association with young infants and their mothers. This is consistent with Lehmann et al. (2006)'s findings from western chimpanzees of the Taï forest, but contrary to the findings of Murray et al. (2016)'s study of eastern chimpanzees from Gombe National Park. Further, and in contrast to findings from both Taï and Gombe (Lehmann et al. 2006; Murray et al. 2016), I found that Sonso-males directed aggression as frequently towards mothers of their own infants as towards those of unrelated infants. This was despite males being less aggressive to mothers in general. Lower levels of aggression towards mothers of young infants (in comparison to other females) are not in themselves indicative of paternal care: this pattern could be a consequence of sexually coercive aggression directed towards cycling females (Muller et al. 2011) rather than a reduction in aggression towards mothers, and sexual coercion has been shown to be a viable strategy for males of my study community (Stefano S K Kaburu & Newton-Fisher 2015). Thus, males of the Sonso community do not show any bias in their behaviour towards their own infants – they show no paternal care – and the fact that they attack mothers of their own infants as frequently as mothers of unrelated infants suggests further that Sonso fathers do not recognise their infants, since attacking one's own infant and/or its mother – on whom the infant is nutritionally and socially dependent – would be maladaptive. Conclusions that chimpanzee fathers provide direct paternal care, and that this is evidence of kin recognition seem premature. At best, existing studies show a diversity in the degree of kin-biasing of behaviour across different communities, and if paternal investment is an adaptive strategy, such diversity could reflect significant variation in social or ecological pressures between these study sites.

If wild chimpanzees are not able to recognise their own non-maternal kin, how can I account for the biases in behaviour reported for other communities? Theoretically, strongly rank-skewed paternity would result in rank being an effective proxy for paternity, but even an alpha-male chimpanzee only achieves between 30-50% of paternities (Boesch et al. 2006; Newton-Fisher et al. 2010; Wroblewski et al. 2009; Inoue et al. 2008), with the consequence that if top-ranked males invested in all infants sired during their tenure (i.e. used rank as a proxy), 70-50% of that investment would be directed towards non-kin. Alternatively, information about mating history may provide information about paternity. Male chimpanzees at Taï and Gombe may be more effective at mate-guarding, or engage in more consortships, than the Sonso males. This information, rather than direct matching (kin recognition), may then result in males biasing their behaviour towards their own infants.

While a lack of paternal care – or biasing – does not necessarily mean a lack of recognition, and I cannot rule out the presence of paternal kin recognition in my study population, or for chimpanzees as a whole, I find no evidence to support a conclusion of kin recognition. Although chimpanzees can identify mother-offspring and father-offspring pairs using phenotypic matching under experimental conditions (Parr et al. 2010), it is not clear how well this mechanism would work in the wild since such matching is visual, and wild chimpanzees cannot know what they themselves look like. Phenotypic matching of offspring by fathers could only be accomplished by matching those infants with maternal kin (mothers and half siblings) rather than themselves, an extra genealogical step that increases the complexity of the problem and has not been demonstrated. There is also evidence that chimpanzees may be able to use olfaction to discriminate between kin (Henkel & Setchell 2018), suggesting that kin recognition may be possible in this species, even if it is not evident from paternal behaviour.

Even if male chimpanzees could identify their own offspring, I question whether paternal investment would offer significant enough returns to be a viable strategy. A lack of paternal care is what is predicted in a highly promiscuous species. Even when paternal care could improve their offspring’s prospects, males should in general still derive greater benefits from investing in further mating opportunities: under a wide range of conditions, simulated male strategies are shaped more by mating than parenting (Hawkes et al. 1995). This is particularly applicable for chimpanzees, for whom male social rank is an important factor in achieving access to fertile females and, consequently, paternity (Boesch et al. 2006; Newton-Fisher et al. 2010; Wroblewski et al. 2009; Inoue et al. 2008). Aside from opportunities for play which may be beneficial for infant development (Poirier & Smith 1974), it is not immediately obvious what measurable benefit fathers might provide by their presence. The most valuable form of paternal care is arguably infanticide protection, which has been observed or inferred in several species (Borries, Launhardt, Epplen, Jörg T Epplen, et al. 1999; Watts 1989a; Parmigiani et al. 1994). Since infanticide is well documented in chimpanzees (Murray et al. 2007b; Townsend et al. 2007; Wilson et al. 2014, Chapter Three), protecting infants from lethal aggression could theoretically provide significant fitness returns for fathers. However, despite this being posited as a potential benefit of paternal care by chimpanzees (Murray et al. 2016), male defence of infants is extremely rare at Sonso and I am unaware of any published accounts of it elsewhere. Of 33 attempted infanticides (both successful and unsuccessful) in my study community between 1993 – 2017, there were only two recorded incidences of a male intervening, one of whom was the son of the mother being attacked (Chapter Three). In addition, I found no evidence here from association patterns that would indicate that fathers are pursuing such a strategy. While my relatively small sample size might account for the lack of a statistically significant relationship between male-female association and paternity, for paternal care to be of biological significance, it would need to be a strong effect, detectible from two years of detailed observation. This should be particularly true if fathers are protecting their offspring from infanticide. Since any investment in protecting infants is lost if that infant is killed, fathers would have to associate almost constantly with their offspring to ensure that the time and opportunity costs incurred were not wasted. Given that infanticide is far more frequent at Sonso than at any other community (Chapter Three; Wilson et al. 2014), if fathers are providing protection as a counterstrategy, this should be a strong effect and the relationship between association and paternity in my data, as well as being statistically insignificant, is a negative one. This is meaningful in that it is a contrast to the effect I would expect were there some form of paternal care in this community but my sample size was too small to identify it statistically (i.e. a small but statistically insignificant positive effect).

On the other hand, while paternal investment may not provide sufficiently significant returns for fathers, association with (or at the very least, a reduction in avoidance of) fathers might offer some benefits for mothers. Aggression records from the Sonso community for the study periods do not contain any accounts of active protection of adult females by adult males and longer term records only show one case of an unrelated male protecting an infant (Chapter Three), but there are occasional instances of females approaching high ranking males when threatened (details in Chapter Four). This suggests that some males may act as a deterrent: male presence reduces the risk of female-female aggression (Kahlenberg et al. 2008), while old males seek refuge with higher-ranking males when threatened (Simpson 1973, Newton-Fisher, personal observations). If male presence also deters aggression from potentially infanticidal males, mothers may benefit from association with certain males but this need not be linked to paternity. I have previously identified a potential “protector” male who associated with younger and therefore more vulnerable infants during a time of elevated infanticide risk (Chapter Four). However, here I found no evidence that this male was associating more with his own infants rather than unrelated ones. I suggested earlier (Chapter Four) that this “protector” male may be sought out by mothers because he functions as a deterrent to other, potentially infanticidal males because of his high aggression rate, rather than his chance of having fathered infants, since more aggressive males might be more likely to deter potentially infanticidal males from mounting any kind of attack in their presence for fear of retaliation.

Since paternity has no influence on association patterns at Sonso, I can assert that mothers are not seeking out fathers (or vice versa), for protection or otherwise in this community. My finding that adult males direct aggression towards the mothers of their own offspring as frequently as they do towards other mothers strongly suggests that male chimpanzees cannot recognise their infants, precluding the possibility of any kin bias in behaviour by fathers in this community. While infanticide is a major risk to infant safety in this community (Chapter Three) and mothers have active counterstrategies (Chapters four and six), fathers do not appear to directly protect their offspring.

7. Discussion

Summary

This thesis has investigated the adaptive function of infanticide and parental counterstrategies in wild eastern chimpanzees. Infanticide is under-reported in this species (38% of intracommunity cases complied by Wilson et al. in their 2014 review were previously unpublished) and information on the nature of this behaviour is therefore patchy. Through a detailed review of intra-community infanticides in the Sonso community of chimpanzees at Budongo from 1993 – 2017, I found that it is predominantly perpetrated by adult males against very young infants and results in a major reduction in inter-birth intervals. This supports the sexual selection hypothesis, according to which, males kill unrelated infants to shorten the amount of time before their mothers are available to mate again (Sommer 1987; Hrdy 1974). The evidence did not support hypotheses that infanticide is predominantly due to female resource competition or meat acquisition (Hrdy 1979), or male mate competition (Takahata 1985; Agoramoorthy and Mohnot 1988). Female committed infanticide was too rare to identify any clear trends and its function in this community therefore remains unclear. Active defence of a mother and targeted infant was very rare. When it did occur, it was almost exclusively by females who defended their kin (sometimes successfully) against attacks by infanticidal males. Sonso appear to be much more infanticidal than other chimpanzee communities (Wilson et al. 2014), which I suggest is due to dynamic variation in male hierarchy steepness and stability. Male rank increases, particularly within the upper ranks, in which paternity is concentrated (Newton-Fisher et al. 2010), creates high infanticide risk and stable male hierarchical relationships should reduce it. It is not clear why Sonso's hierarchy should be different enough from other communities to result in such a comparatively high rate of infanticide, although we know that hierarchy structure does vary between sites (Stefano S.K. Kaburu & Newton-Fisher 2015). Demographic factors are likely to play a role, i.e. if there are lots of adult males of similar ages, and therefore competitive ability, they would be more likely to compete over rank, creating instability than if there were a small number of mature males and several adolescents who are unlikely to be able to mount a challenge for their rank. Deaths of high ranking individuals would create a power vacuum which might also be an important factor.

Having confirmed that the majority of infanticides fit within the framework of the sexual selection hypothesis, I investigated counter-strategies by both mothers and fathers. For a slow breeding species like the chimpanzee, the loss of an infant is a major cost to overall fitness, especially to mothers who will lose ~1.3 years of their reproductive lifespan for an infant killed at birth (Chapter Three). Female promiscuity is considered a counter-strategy to male committed infanticide as it confuses paternity, increasing the costs for males of killing infants (Wolff & Macdonald 2004). However, despite the promiscuous mating system, 23% of Sonso infants have died as a result of confirmed or presumed infanticidal attacks and infanticide is responsible for 63% of infant mortality (Chapter Three), indicating that counter-strategies are not particularly effective. Since promiscuity is constrained by male sexual coercion (Muller et al. 2011), and females are in a poor position to defend against attacks from males due to their smaller size and lower social status (Goodall 1986), I argue that females have little choice but to attempt to reduce the opportunities for infanticide by avoiding high-risk males. This will be a limited strategy, since females cannot ensure that they will never encounter an infanticidal male and will occasionally be forced in encounters with males due to food availability, but it is arguably the lowest risk strategy they have at their disposal. Due to the fission-fusion nature of chimpanzee society (Y Sugiyama 1968), mothers can selectively avoid joining parties containing high-risk individuals (in this case, adult males), and leave parties when such males join. Such avoidance has been proposed as an anti-infanticide strategy, with chimpanzee mothers elsewhere being less gregarious than females without infants (Otali & Gilchrist 2006). However, my initial investigation into maternal avoidance in this community (Chapter Four) found that mothers did not treat all males as if they were dangerous, but only a male who rose rapidly in rank. This implies that not all males, pose a risk to infants. This may be linked to paternity certainty. While promiscuity may hinder paternity certainty, it does not confuse paternity entirely. Males do not have an equal chance of siring a given infant. Rank predicts paternity in chimpanzees (Inoue et al. 2008; Boesch et al. 2006; Newton-Fisher et al. 2010; Wroblewski et al. 2009), so males should be able to use rank as a probabilistic indicator of paternity, even if they cannot identify their own offspring directly. If males change in rank, their likelihood of having fathered existing infants may be different to their chance of siring any infants conceived at their new rank. This should make males who rise in rank particularly high risk to mothers, as these males would benefit from killing current infants and replacing them with those they are more likely to have sired. Conversely, a male whose chance of fathering a new infant is the same as his chance of fathering a current infant would gain no fitness benefit from, and so should have no motivation to commit, infanticide. So mothers need not avoid all males, but should recognise those individuals who pose a high risk to their infants and avoid them selectively. I investigated maternal responses to a male who increased rapidly from rank 5 to rank 2 (Chapter Four), significantly increasing his chance of siring offspring (Newton-Fisher et al. 2010). The evidence supported an avoidance strategy by mothers relating to the transition from low to elevated risk period, but only in relation to the high-risk male. In addition to avoiding this male, mothers associated with a potential protector male during the high risk period. This male was a highly aggressive individual and I suggest that deterring potentially infanticidal individuals may arise as a by-product of the presence of such an individual. These results show that mothers will use avoidance as a counter-strategy to infanticide, but that doing so is sensitive to the risks posed by each adult male, rather than a categorical avoidance of males.

Because my initial investigations into maternal avoidance had indicated that mothers were sensitive to male risk (Chapter Four), I decided to look in more detail at association, this time directly testing whether males or females were initiating close contact. By looking at movements of individuals within parties, rather than party level presence/absence data, I found direct evidence of behavioural decision making and concluded that mothers were indeed avoiding initiating close proximity with males in general, compared to non-mothers.

While the cost of infanticide is higher for mothers than fathers as mothers invest more heavily in reproduction (Trivers 1972), the father's reproductive success is also lowered when an infant dies. Fathers could therefore benefit from offering protection to infants and having identified a possible protector role for one male (Chapter Four), I investigated the possibility of a paternal infant protection strategy (Chapter Six). Although chimpanzees only have probabilistic indications of paternity, there is some evidence that fathers bias behaviour towards their own kin and that this may serve to protect against infanticide (Murray et al. 2016; Lehmann et al. 2006), although the kin recognition mechanism is not clear. I found little evidence for this strategy in the Sonso community, with males only very rarely protecting infants from attacks (Chapter Three). Males confirmed as fathers through genetic analysis never did so. Further, I found no evidence of any preferential association with, or treatment of, own infants or their mothers by fathers (Chapter Six). This is the third study which has addressed the question of paternal care in wild chimpanzees, and the third pattern of behaviour identified. Theoretical models of adaptive infanticide and paternal protection indicate that males can pursue one of two distinct strategies: protecting infants and attempting to gain 100% paternity certainty, or not protecting infants and allowing enough paternity uncertainty that they benefit from reduced infanticide risk (Boyko & Marshall 2009). Partial protection in a system with high levels of paternity uncertainty (as suggested by Murray et al. 2016) does not fit with these models, and I therefore argue that association patterns identified at Gombe do not provide strong evidence of a paternal strategy to protect against infanticide in this species. Spatial relationships (use of overlapping core areas) between males and females have as strong an effect on reproduction as does male rank (Langergraber et al. 2013a). This could be an alternative explanation for mother-infant-father association at Gombe. If mothers seek out male parties when their infants are young in order to acquire socialisation benefits (Murray et al. 2014), they may associate with close-by males (who, because of the relationship between space use and reproduction, are more likely to be fathers) purely because of lower travel costs compared to associating with further-flung individuals.

This alternative explanation also explains why there was not a similar pattern of association at Sonso. The much higher infanticide rate at Sonso would make socialising with males much more risky and this cost could outweigh any socialisation benefits for infants. If mothers do not preferentially associate with males when their infants are young due to heightened risk of infant death, this pattern of males associating with mother-infant pairs would disappear.

In conclusion, this thesis found that infanticide is a significant cause of infant mortality in the Sonso community of chimpanzees and sexually selected infanticide should be considered a major selective force on their behaviour. Mothers avoid initiating close proximity with males when they have infants and are sensitive to the varying risks posed by individual males. There was no evidence of males actively protecting their own infants but there may be a passive male protection effect as mothers seek out certain males as buffers.

Avenues for further research

Counterstrategies by males and females

While this thesis addresses several counterstrategies to infanticide (maternal avoidance of males, active defence during attacks, paternal protection and mothers using males as buffers), it is possible that there are other strategies used by mothers (and perhaps fathers) which are employed to reduce the risk of infanticide. If such strategies are particularly effective, and employed by individuals in communities other than Sonso, this may account for some of the variation in infanticide rates between study sites. However, it is not clear what such counterstrategies might be. While females of some species mate selectively in return for male protection (e.g. gorillas (*G. b. beringei*): Robbins et al. 2013), female chimpanzees cannot easily selectively mate with preferred males (although this would be of dubious benefit anyway in a multi-male society since it would concentrate paternity, making non-sires more dangerous), since male chimpanzees effectively constrain female choice via sexual coercion (Muller et al. 2011). Males limiting female choice not only precludes a selective mating-for-protection strategy, but also limits the effectiveness of promiscuity, concentrating paternity in fewer males, thus increasing infanticide risk (Muller et al. 2009a; Muller et al. 2011; Feldblum et al. 2014). Maternal aggression and territoriality are common defences against infanticide in some other species (e.g. rodents: Wolff 1985, 1993) but not viable as strategies for group living, sexually dimorphic chimpanzees.

Active defence of targeted infants was rare in this community, but deserves further attention. Defence by individuals other than the victim’s mother occurred during 3 of 5 attacks on the infants of natal females in which the attack was clearly seen, and female kin were the most common protectors (Chapter Three). In communities with a larger proportion of breeding natal females (e.g. 50% at Gombe, Tanzania: Constable et al. 2001) and thus higher availability of female kin, such protection may be more frequent.

Three of the four Sonso infants who were protected by an individual other than their mother survived infancy (Chapter Three), suggesting that protection can be successful in preventing infant death and may be an important counter-strategy in communities where natal females remain to breed. In one instance at Sonso (Chapter Three), an adult male attacker was injured by protector females, indicating that the costs of infanticidal aggression are meaningfully increased when individuals other than the mother offer defence. Such costs could be enough of a deterrent to prevent infanticide in some cases. Future research should investigate the possibility of female kin support as a counterstrategy. In a comparable way to Chapter Four, which tested whether mothers of younger (more vulnerable) infants were less likely to associate with dangerous males, it would be valuable to test whether natal females with young infants have heightened association with their female kin. I predict that association with potential protectors will be highest when infants are youngest and most at risk of sexually selected infanticide.

While infanticide rates do not appear to be linked to female emigration patterns (e.g. Mahale: 12 intra-community infanticides 1966 – 2014: Wilson et al. 2014, 90% female emigration: Nishida et al. 2003 vs. Gombe: 16 intra-community infanticides 1965 – 2014: Wilson et al. 2014, 50% female emigration: Constable et al. 2001), such superficial comparisons may be confounded. Rates of infanticide reflect the outcome of an interplay between male and female strategies together with demography. The level of risk is not constant across communities, or across time, as male hierarchical relationships affect infanticide risk (Chapter Four, and see below), while the simultaneous presence of potential victims for infanticide, and potentially infanticidal males, are subject to demographic forces. Females may be more likely to emigrate from their natal community if and when infanticide risk is high, as the risk of losing an infant could be lower elsewhere (despite the absence of potential kin support), although to what extent emigration is a counter to infanticide or a response to resource availability (cf. howler monkeys: Crockett 1984) remains an open question, and options are likely to vary between individual females. Since defence by female kin did not always prevent infanticide, I suggest that defence is likely to be a fall-back strategy and emigrating to a community with low infanticide rates would be preferential. However, primiparous females suffered a heavy infanticide toll in Sonso and only one female secondarily transferred after losing an infant (Chapter Three), suggesting either that infanticide risk is not a major factor in community selection by females or that joining Sonso has other benefits which outweigh the cost of heightened infanticide. Remaining in one's natal community must have costs associated with it, or all females would presumably stay with kin who can offer protection. As well as the potentially detrimental costs of incestuous breeding, male behaviour towards natal females may be a factor. Natal females may be more likely than immigrant females to lose an infant to infanticide (although this was not a significant difference in our small sample size: Chapter Three), and it is feasible that this functions to coerce females into emigrating, infanticidal males may then benefit from weak female-female relationships and subsequent low coalitionary power between females because it reduces the likelihood of defence and therefore the costs of infanticide.

While I found very limited evidence for male defence (no paternal care was evident and an unrelated male protected an infanticide victim only once: Chapters three and five), there are circumstances in which male protection could offer significant returns to males. I have concluded that, even if males can recognise their infants, males should invest time and energy in rank acquisition rather than infant protection as this will offer a greater return on their investment (Chapter Six). However, if a male drops rapidly from a very high rank to a much lower rank, he will have a good chance of having fathered current infants and little chance of fathering new ones. Depending on this male's competitive ability (his likelihood of being able to rise back up in the ranks), it may be adaptive for him to switch to investing in infant care and protection, rather than rankstriving and mate competition. Of course, a male with reduced competitive abilities may be of somewhat limited use as a protector but if he had a very low chance of future reproductive success, protecting infants could be a viable option for him. The behaviour of males, particularly older males, who have dropped in rank should be investigated to test whether they increase their association with mothers and infants.

Risk factors for infanticide

Female committed infanticide: ecological risk factors

If female-committed infanticide is linked to resource competition, then a reduction in fruit availability should lead to increases in the number of female-committed infanticides. Female infanticide makes up a much smaller proportion of the total number of incidents at Budongo than at some other sites (Chapter Three; Wilson et al. 2014). It is possible that this difference is linked to food availability. There is little evidence for food scarcity at Budongo (N. E. Newton-Fisher 1999) and the community's frequent crop-raiding of high energy crops (primarily sugarcane) provides a valuable buffer (Tweheyo & Lye 2005). At Gombe, chimpanzees live too far from farms to raid crops (Goodall 1986) and low ranking females in particular experience persistent food scarcity due to competition with higher ranking females for access to high quality core areas (Murray et al. 2006). At Gombe, 5 of 8 infanticides for which the attackers sex was known were committed by females (Wilson et al. 2014), indicating that food competition might be an important factor. Future research needs to test whether there is a link between food abundance and female committed infanticide frequency. If resource competition is the cause of female infanticide, then periods of scarcity will be associated with spikes in the frequency of infanticide.

Male-committed infanticide: social risk factors

Since changes in male rank affect infanticide risk (Chapter Four), the nature of the male hierarchy will be key to infanticide risk. Stable hierarchical relationships between males, through which individuals maintain their positions for long periods, will rarely give males the opportunity to replace an infant with one they are more likely to have fathered. For killers, the chance to replace an infant with one more likely to be fathered by themselves will be largely contingent on increases in rank post conception of the current infant because higher ranking males sire more offspring (Constable et al. 2001; Newton-Fisher et al. 2010; Wroblewski et al. 2009; Inoue et al. 2008). This means that rank instability should be the primary risk factor for infanticide in chimpanzees. Assuming that paternity skew is at least partly because high ranking males limit the mating access of lower ranked males (e.g. through possessive mating: Constable et al. 2001), then the steeper the male hierarchy, the greater the difference in achieving paternity will be between ranks. In more egalitarian hierarchies made up of more evenly matched males, excluding each other from mating opportunities should be less feasible. Large differences in probability of paternity between close ranks in steeper hierarchies will increase the benefit of infanticide for a male who increases in rank. We know that hierarchy steepness and egalitarianism varies between communities and within communities across time (Stefano S.K. Kaburu & Newton-Fisher 2015), so it seems highly likely that variation in infanticide frequency is largely mediated by the nature of the male dominance hierarchy. Comparative studies which review long term hierarchy stability and egalitarianism in chimpanzees across multiple communities would be very valuable in testing this hypothesis. Communities with steep, unstable hierarchies should experience more infanticide and, within communities, more unstable periods, particularly when combined steep hierarchies should be associated with an increase in infanticide.

Male mating strategies vary between individuals in chimpanzees and include possessive and opportunistic mating behaviour (Constable et al. 2001; Tutin 1979). The proportion of infants born as a result of each type of strategy varies between populations but also within populations across time. Early studies at Gombe argued that consortships were the dominant mating pattern and had high success rates (Tutin 1979) but more recent work from the same site has found that only 3 of 12 study subjects were conceived during a consortship (Constable et al. 2001). At Mahale, 7% of copulations were categorised at "restrictive" (a combination of possessive mating and consortships) and only one infant was likely to have been conceived during a consortship (Hasegawa & Hiraiwa-Hasegawa 1983). Variation in male mating strategies between communities is important because the mating strategy under which an infant was conceived may affect its likelihood of being victim of an infanticidal attack. For instance, highly effective mate-guarding and consortships may increase paternity certainty for the sire, but increase risk of infanticide by males who have a similarly increased certainty of not being the father. It would therefore be valuable to test the extent to which an infant's risk of death depends on the circumstances in which it was conceived. Infants born following restrictive mating will have more certain paternity (and therefore be more at risk) than those born after highly promiscuous mating by the mother. Even if males do not change in rank (and therefore do not have a different chance of siring a new infant vs the current one), it could still be adaptive to kill an infant if the chance of paternity is close to 0 (as could be the case if it were born after an extended consortship with another male).

Chapter Three established that some females are more at risk than others, with primiparous females most likely to lose an infant to infanticide. However, there may be other factors which make mothers and their infants vulnerable. It is possible that the infants of rarely seen peripheral females are more likely to be killed, for example. These infants and their mothers range close to the edge of the territory and therefore they might be more likely to have extra-group fathers (although the rate of extra-group paternity is low in chimpanzees, at around 0 – 7%: Constable et al. 2001; Newton-Fisher et al. 2010). Mothers who are rarely seen and/or range close to the territory edge could be more likely to lose infants to infanticide if males use mating history as an indicator of paternity, as occurs in other primates (reviewed in: Widdig 2007). Future research could test whether ranging behaviour and sociality of females is linked to infanticide history. If mating history is used to provide clues to paternity, females who spend less time with males (particularly if they are absent for multiple menstrual cycles or spend time alone when maximally swollen) and those who range close to the community boundaries should be at a higher risk from intra-group infanticide as there is an increased chance of extra-group-paternity. Since Chapter Six suggested that males could not identify their offspring and Chapter Four indicated that they may instead use a probabilistic indicator of paternity based on rank, this would also be valuable in testing the extent to which Sonso males also use mating history as an indicator of paternity.

Conclusions

For chimpanzee females, considering the infant mortality rate of 49% (Chapter Three), keeping infants alive will be probably the most important factor in determining their reproductive success. If 63% of infant deaths and disappearances are due to infanticide (Chapter Three) then infanticide is one of the most significant concerns for chimpanzee mothers, and accordingly should shape their behaviour. As a major selective force on behaviour in the Sonso community, infanticide has had far reaching implications for the ways in which adults interact with each other. A key feature of eastern chimpanzee social structure is weak inter-sexual relationships (Zarin P Machanda et al. 2013) If adult males pose a serious threat to females and their infants and a key counter-strategy is maternal avoidance, this will be a significant factor in shaping female gregariousness and intersexual relationships (or the lack of them). Infanticide risk is arguably the most important factor mediating adult inter-sexual relationships in chimpanzees and should be factored in to any consideration of chimpanzee sociality.

Sonso is the most infanticidal community of chimpanzees on record. In Chapter Three, I report 24 lethal attacks on infants by community members over a 24-year study period, a rate of one per year. The next most infanticidal site is Gombe, which reports 16 across two communities over a 49 year study period (Wilson et al. 2014), a rate of 0.33 per year, meaning that Sonso chimpanzees are three times as infanticidal as the community with the second highest rate (even before taking into account the fact that the Gombe attacks are spread over two communities). At the other end of the spectrum, there has only been one reported instance of infanticide in the Kanyawara community of Kibale since observation began in 1988, a rate 1/25th that of Sonso. (Wilson et al. 2014; Wilson et al. 2012). This variation between communities in the prevalence of infanticide indicates important differences in social structure and inter-individual relationships and begs for comparative work to investigate the underlying causes of infanticide in chimpanzees.

References

Agoramoorthy, G. & Mohnot, S.M., 1988. Infanticide and juvenilicide in hanuman langurs (presbytis entellus) around jodhpur, india. *Human Evolution*, 3, pp.279–296.

Akesson, A. & Henricson, B., 1972. Embryonic death in pigs caused by unbalanced karyotype. *Acta Veterinaria Scandinavica*, 13, p.151.

Alexander, R.D., 1974. The evolution of social behaviour. *Annual Review of Ecology and Systematics*, 5, pp.324–383.

Altmann, J., 1974. Observational study of behavior: sampling methods. *Animal Behaviour*, 49, pp.227–266.

Altmann, J. & Samuels, A., 1992. Costs of maternal care: infant-carrying in baboons. *Behavioral Ecology and Sociobiology*, 29, pp.391–398.

Angelier, F., 2006. Kidnapping of chicks in emperor penguins: a hormonal by-product? *Journal of Experimental Biology*, 209, pp.1413–1420.

Arcadi, A.C. & Wrangham, R.W., 1999. Infanticide in chimpanzees: review of cases and a new within-group observation from the kanyawara study group in kibale national park. *Primates*, 40, pp.337–351.

Asdell, S.A., 1946. *Patterns of Mammalian Reproduction*, Ithaca, New York: Comstock Publishing Co. Inc.

Asensio, N. et al., 2008. Intragroup aggression, fission-fusion dynamics and feeding competition in spider monkeys. *Behaviour*, 145, pp.983–1001.

Aureli, F. et al., 2008. Fission-fusion ddynamics. *Current Anthropology*, 49, pp.627–654.

Author, R. et al., 1995. Wanderers between harems and bachelor bands: male hanuman langurs (*Presbytis entellus*) at Jodhpur in Rajasthan. *Behaviour*, 132, pp.255–299.

Awmack, C.S. & Leather, S.R., 2002. Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology*, 47, pp.817–844.

Bădescu, I. et al., 2017a. A novel fecal stable isotope approach to determine the timing of age-related feeding transitions in wild infant chimpanzees. *American Journal of Physical Anthropology*, 162, pp.285–299.

Bădescu, I. et al., 2017b. A novel fecal stable isotope approach to determine the timing of age-related feeding transitions in wild infant chimpanzees. *American Journal of Physical Anthropology*, 162, pp.285–299.

Baniel, A., Cowlishaw, G. & Huchard, E., 2017. Male violence and sexual intimidation in a wild primate society. *Current Biology*, 27, p.2163–2168.e3.

Banks, E.M. et al., 1979. Social rank and priority of access to resources in domestic fowl. *Behavioural Processes*, 4, pp.197–209.

Bateman, A.J., 1948. Intra-sexual selection in *drosophila*. *Heredity*, pp.349–368.

Bates, D. et al., 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, pp.1–48.

Bean, A., 1999. Ecology of sex differences in great ape foraging. In Phyllis Lee, ed.

Comparative Primate Socioecology. Cambridge: Cambridge University Press, pp. 399–362.

Bellemain, E., Swenson, J.E. & Taberlet, P., 2006. Mating strategies in relation to sexually selected infanticide in a non-social carnivore: the brown bear. *Ethology*, 112, pp.238–246.

Black, J., 1996. Introduction: pair bonds and partnerships. In J. Black, ed. *Partnerships in birds: The study of monogamy: The study of monogamy*. Oxford: Oxford University Press, pp. 3–20.

Blumer, L.S., 1979. Male parental care in the bony fishes. *The Quarterly Reivew of Biology*, 54, pp.149–161.

Blumstein, D.T., 2000. The evolution of infanticide in rodents: a comparative analysis. In C. P. van Schaik & C. H. Janson, eds. *Infanticide by males and its implications*. Cambridge: Cambridge University Press, pp. 178–197.

Boesch, C. et al., 2006. Male competition and paternity in wild chimpanzees of the Taï forest. *American Journal of Physical Anthropology*, 130, pp.103–15.

Boesch, C. & Boesch-Achermann, H., 2000. *The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution*, USA: Oxford University Press.

Boesch, C. & Boesch, H., 1989. Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology*, 78, pp.547–573.

Boklage, C.E., 1990. Survival probability of human conceptions from fertilization to term. *International Journal of Fertility*, 35, pp.75–94.

Bongaarts, J., 1980. Does malnutrition affect fecundity? a summary of evidence. *Science*, 208, pp.564–569.

Borries, C., Launhardt, K., Epplen, C., Epplen, J.T., et al., 1999. DNA analyses support the hypothesis that infanticide is adaptive in langur monkeys. *Proceedings of the Royal Society of London B: Biological Sciences*, 266, pp.901–904.

Borries, C., 1997. Infanticide in seasonally breeding multimale groups of hanuman langurs (*Presbytis entellus*) in Ramnagar (South Nepal). *Behavioral Ecology and Sociobiology*, 41, pp.139–150.

Borries, C., Launhardt, K., Epplen, C., Epplen, J.T., et al., 1999. Males as infant protectors in hanuman langurs (*Presbytis entellus*) living in multimale groups - defence pattern, paternity and sexual behaviour. *Behavioral Ecology and Sociobiology*, 46, pp.350–356.

Bortolotti, G.R., Wiebe, K.L. & Iko, W.M., 1991. Cannibalism of nestling American kestrels by their parents and siblings. *Canadian Journal of Zoology*, 69, pp.1447–1453.

Bosch, O.J., 2013. Maternal aggression in rodents: brain oxytocin and vasopressin mediate pup defence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368, p.20130085.

Bourliere, F., Hunkeler, C. & M, B., 1970. Ecology and behavior of Lowe’s guenon (*Cercopithecus campbelli lowei*) in the ivory coast. In J. R. Napier & P. H. Napier, eds. *Old World Monkeys*. New York: Academic Press, pp. 297–350.

Boyko, R.H. & Marshall, A.J., 2009. The willing cuckold: optimal paternity allocation, infanticide and male reproductive strategies in mammals. *Animal Behaviour*, 77, pp.1397–1407.

Brennan, K., 2002. Evidence of infanticide and exposure in antiquity: tolerated social practice, uncontrolled phenomenon or regulated custom. *University College Dublin Law Review*, 2, p.92.

Broom, M., Borries, C. & Koenig, A., 2004. Infanticide and infant defence by males - modelling the conditions in primate multi-male groups. *Journal of Theoretical Biology*, 231, pp.261–270.

Bruce, H.M., 1959. An exteroceptive block to pregnancy in the mouse. *Nature*, 184, p.105.

Buchan, J.C. et al., 2003. True paternal care in a multi-male primate society. *Nature*, 425, pp.179–181.

Bustnes, J.O. & Erikstad, K.E., 1991. Parental care in the common eider (*Somateria mollissima*): factors affecting abandonment and adoption of young. *Canadian Journal of Zoology*, 69, pp.1538–1545.

Bygott, J.D., Bertram, B.C.R. & Hanby, J.P., 1979. Male lions in large coalitions gain reproductive advantages. *Nature*, 282, pp.839–841.

Calhoun, J.B., 1962. Population density and social pathology. *Scientific American*, 206, pp.139–149.

Campbell, C.J., 2006. Lethal intragroup aggression by adult male spider monkeys *(Ateles geoffroyi)*. *American Journal of Primatology*, 68, pp.1197–1201.

Cant, M.A., 2003. Patterns of helping effort in co-operatively breeding banded mongooses (*Mungos mungo*). *Journal of Zoology*, 259, pp.115–121.

Caro, S.M. et al., 2016. Unpredictable environments lead to the evolution of parental neglect in birds. *Nature Communications*, 7, p.10985.

Carter, K.D. et al., 2013. Fission-fusion dynamics in wild giraffes may be driven by kinship, spatial overlap and individual social preferences. *Animal Behaviour*, 85, pp.385–394.

Charpentier, M.J.E. et al., 2007. Kin discrimination in juvenile mandrills, *Mandrillus sphinx*. *Animal Behaviour*, 73, pp.37–45.

Clifton, K.E., 1990. The costs and benefits of territory sharing for the caribbean coral reef fish, *Scarus iserti*. *Behavioral Ecology and Sociobiology*, 26, pp.139–147.

Clutton-Brock, T., 1991. *The Evolution of Parental Care*, Princeton: Princeton University Press.

Clutton-Brock, T.H. et al., 1998. Infanticide and expulsion of females in a cooperative mammal. *Proceedings of the Royal Society of London B: Biological Sciences*, 265, pp.2291–2295.

Clutton-Brock, T.H., 1991. Parental care in ectotherms. In T. H. Clutton Brock & J. R. Krebs, eds. *The evolution of parental care*. New Jersey: Princeton University Press, pp. 100–129.

Cockburn, A., 2006. Patterns of parental care in birds , together with their phylogeny and geographic region. *Proceedings of the Royal Society of London B*, 273, pp.1–281.

Collet, J.M. et al., 2014. The measure and significance of Bateman’s principles. *Proceedings. Biological Sciences*, 281, p.20132973.

Collins, D.A., Busse, C.D. & Goodall, J., 1984. Infanticide in two populations of savanna baboons. In G. Hausfater & S. B. Hrdy, eds. *Infanticide: Comparative and Evolutionary Perspectives*. New York: Aldine, pp. 193–125.

Connor, R. et al., 2000. The bottlenose dolphin: social relationships in a fission fusion society. In J. Mann et al., eds. *Cetacean Societies: Field Studies of Dolphins and Whales*. Chicago: University of Chicago Press.

Constable, J.L. et al., 2001. Noninvasive paternity assignment in Gombe chimpanzees. *Molecular Ecology*, 10, pp.1279–1300.

Corbett, L.K., 1988. Social dynamics of a captive dingo pack: population regulation by dominant female infanticide. *Ethology*, 78, pp.177–198.

Cortés-Avizanda, A. et al., 2009. Carcasses increase the probability of predation of ground-nesting birds: a caveat regarding the conservation value of vulture restaurants. *Animal Conservation*, 12, pp.85–88.

Creel, S. et al., 1992. Behavioural and endocrine mechanisms of reproductive suppression in serenge dwarf mongooses. *Animal Behaviour*, 43, pp.231–245.

Crockett, C.M., 1984. Emigration by female red howler monkeys and the case for female competition. In Meredith Small, ed. *Female Primates: Studies by Women Primatologists*. New York: Alan R Liss, pp. 159–173.

Crockett, C.M. & Janson, C.H., 2000. Infanticide in red howlers: female group size, male membership, and a possible link to folivory. In *Infanticide by Males and its Implications*. pp. 75–98.

Crockett, C.M. & Rudran, R., 1987. Red howler monkey birth data ii: interannual, habitat, and sex comparisons. *American Journal of Primatology*, 13, pp.369–384.

Crockford, C. et al., 2013. Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, 280, p.20122765.

Crump, M.L., 1996. Parental care among the amphibia. *Advances in the Study of Behavior*, 25, pp.109–144.

Culot, L. et al., 2011. Reproductive failure, possible maternal infanticide, and cannibalism in wild moustached tamarins, *Saguinus mystax*. *Primates*, 52, pp.179–186.

Curtin, R. & Dolhinow, P., 1978. Primate social behavior in a changing world. *American Scientist*, 66, pp.468–475.

Daly, M. & Wilson, M., 1984. A sociobiological analysis of human infanticide. In G. Hausfater & S. B. Hrdy, eds. *Infanticide: Comparative and Evolutionary Perspectives*. New York: Aldine, pp. 487–502.

Deag, J.M. & Crook, J.H., 1971. Social behaviour and 'agonistic buffering' in the wild barbary macaque *Macaca sylvana Folia Primatologica*, 15, pp.183–200.

Deschner, T. et al., 2004. Female sexual swelling size, timing of ovulation, and male behavior in wild west african chimpanzees. *Hormones and Behavior*, 46, pp.204–215.

Deschner, T. et al., 2003. Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees (*Pan troglodytes verus*). *Animal Behaviour*, 66, pp.551–560.

Dias, P.A.D., Rangel-Negrín, A. & Canales-Espinosa, D., 2011. Effects of lactation on the time-budgets and foraging patterns of female black howlers (*Alouatta pigra*).

American Journal of Physical Anthropology, 145, pp.137–146.

Digby, L., 1995. Infant care, infanticide, and female reproductive strategies in polygynous groups of common marmosets (*Callithrix jacchus*). *Behavioral Ecology and Sociobiology*, 37, pp.51–61.

Dittus, O.P.J., 1977. The social regulation of population density and age-sex distribution in the toque monkey. *Behaviour*, 63, pp.281–322.

Drickamer, L.C., 1974. A ten-year summary of reproductive data for free-ranging M*acaca mulatta*. *Folia Primatologica*, 21, pp.81–80.

Duffy, K.G., Wrangham, R.W. & Silk, J.B., 2007. Male chimpanzees exchange political support for mating opportunities. *Current Biology*, 17, pp.R586–R587.

Dunbar, R.I.M., 1984. Infant-use by male gelada in agonistic contexts: agonistic buffering, progeny protection or soliciting support? *Primates*, 25, pp.28–35.

Ebensperger, L. & Blumstein, D., 2007. Nonparental infanticide. In J. Wolff & P. Sherman, eds. *Rodent societies: an ecological and evolutionary perspective*. Chicago: University of Chicago Press, p. 267 279.

Ebensperger, L.A., 1998. Strategies and counterstrategies to infanticide in mammals. *Biological Reviews*, 73, pp.321–346.

Eccard, J.A., Dammhahn, M. & Ylönen, H., 2017. The bruce effect revisited: is pregnancy termination in female rodents an adaptation to ensure breeding success after male turnover in low densities? *Oecologia*, 185, pp.81–94.

Eckardt, W., Fawcett, K. & Fletcher, A.W., 2016. Weaned age variation in the virunga mountain gorillas (*Gorilla Beringei beringei*): influential factors. *Behavioral Ecology and Sociobiology*, 70, pp.493–507.

Eggeling, W.J., 1947. Observations on the ecology of the Budongo Rain Forest, Uganda. *Journal of Ecology*, 34, pp.20–87.

Ekman, J.B. & Askenmo, C.E.H., 1984. Social rank and habitat use in willow tit groups. *Animal Behaviour*, 32, pp.508–514.

Ellison, P.T., 2008. Energetics, reproductive ecology, and human evolution. *PaleoAnthropology*, pp.172–200.

Emery Thompson, M., Jones, J.H., et al., 2007a. Aging and fertility patterns in wild chimpanzees provide insights into the evolution of menopause. *Current Biology*, 17, pp.2150–2156.

Emery Thompson, M., Jones, J.H., et al., 2007b. Aging and fertility patterns in wild chimpanzees provide insights into the evolution of menopause. *Current Biology*, 17, pp.2150–2156.

Emery Thompson, M., Kahlenberg, S.M., et al., 2007. Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. *Animal Behaviour*, 73, pp.501–512.

Emery Thompson, M., 2013. Reproductive ecology of female chimpanzees. *American Journal of Primatology*, 75, pp.222–37.

Fahy, G.E. et al., 2014. Stable nitrogen isotope analysis of dentine serial sections elucidate sex differences in weaning patterns of wild chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology*, 153, pp.635–42.

Feldblum, J.T. et al., 2014. Sexually coercive male chimpanzees sire more offspring.

Current Biology : CB, 24, pp.2855–60.

Gargett, V., 1978. Sibling aggression in the black eagle in the Matopos, Rhodesia. *Ostrich*, 49, pp.57–63.

Ghiglieri, M.P., 1984. *The Chimpanzees of the Kibale Forest*, New York: Columbia University Press.

Gilby, I.C. & Wrangham, R.W., 2007. Risk-prone hunting by chimpanzees (P*an troglodytes schweinfurthii*) increases during periods of high diet quality. *Behavioral Ecology and Sociobiology*, 61, pp.1771–1779.

Goldberg, T.L. & Wrangham, R.W., 1997. Genetic correlates of social behaviour in wild chimpanzees: evidence from mitochondrial dna. *Animal Behaviour*, 54, pp.559–570.

Goodall, J., 1989. *Glossary of Chimpanzee Behaviors.*, Tucson: Jane Goodall Institure.

Goodall, J., 1977. Infant killing and cannibalism in free-living chimpanzees. *Folia Primatologica*, 28, pp.259–282.

Goodall, J., 1983. Order without law. In M. Gruter & P. Bohannan, eds. *Law, Biology and Culture: the Evolution of Law*. Santa Barbara: Ross-Erikson, pp. 50–62.

Goodall, J., 1986. *The Chimpanzees of Gombe: Patterns of Behavior*, Cambridge, MA: Belknap Press of Harvard University Press.

Graziani, L., 1995. Infanticide in the alpine marmot (*Marmota marmota*). *Ethology Ecology and Evolution*, 7, pp.191–194.

Grether, W.F. & Yerkes, R.M., 1940. Weight norms and relations for chimpanzee. *American Journal of Physical Anthropology*, 27, pp.181–197.

Gubernick, D.J. & Teferi, T., 2000. Adaptive significance of male parental care in a monogamous mammal. *The Royal Society*, 267, pp.147–150.

Gustafsson, L. et al., 1994. Infectious diseases, reproductive effort and the cost of reproduction in birds. *Philosophical Transactions - Royal Society of London, B*, 346, pp.323–331.

Hackländer, K. & Arnold, W., 1999. Male-caused failure of female reproduction and its adaptive value in alpine marmots (*Marmota marmota*). *Behavioral Ecology*, 10, pp.592–597.

Hackländer, K., Möstl, E. & Arnold, W., 2003. Reproductive suppression in female alpine marmots, *Marmota marmota*. *Animal Behaviour*, 65, pp.1–8.

Hamilton, W.D., 1971. Geometry for the selfish herd. *Journal of Theoretical Biology*, 31, pp.295–311.

Harley, D., 1985. Birth spacing in langur monkeys (*Presbytis entellus*). *International Journal of Primatology*, 6, pp.227–242.

Harlow, H.F. et al., 1966. Maternal behavior of rhesus monkeys deprived of mothering and peer associations in infancy. *Proceedings of the American Philosophical Society*, 110, pp.58–66.

Hasegawa, T. & Hiraiwa-Hasegawa, M., 1983. Opportunistic and restrictive mating among wild chimpanzees in the mahale mountains, tanzania. *Journal of Ethology*, 1, pp.75–85.

Hass, C.C. & Valenzuela, D., 2002. Anti-predator benefits of group living in white-nosed coatis (*Nasua narica*). *Behavioral Ecology and Sociobiology*, 51, pp.570–

578.

Hawkes, K., Rogers, A.R. & Charnov, E.L., 1995. The male’s dilemma: increased offspring production is more paternity to steal. *Evolutionary Ecology*, 9, pp.662–677.

Heinsohn, R., Legge, S. & Barry, S., 1997. Extreme bias in sex allocation in eclectus parrots. *Proceedings of the Royal Society B: Biological Sciences*, 264, pp.1325–1329.

Heithaus, M.R. & Dill, L.M., 2002. Food availability and tiger shark predations risk influence bottlenose dolphin habitat use. *Behavioral Ecology*, 83, pp.480–491.

Henkel, S. & Setchell, J.M., 2018. Group and kin recognition via olfactory cues in chimpanzees (*Pan troglodytes*). *Proceedings of the Royal Society B: Biological Sciences*, 285, p.20181527.

Hiraiwa-Hasegawa, M. & Hasegawa, T., 1994. Infanticide in nonhuman primates: sexual selection and local resource competition. In S. Parmigiani & F. S. vom Saal, eds. *Infanticide and Parental Care*. Chur, Switzerland: Harwood Academic Publishers, pp. 137–154.

Hobaiter, C. et al., 2017. Variation in hunting behaviour in neighbouring chimpanzee communities in the Budongo Forest, Uganda K. A. Bard, ed. *PLoS ONE*, 12, p.e0178065.

Hoogland, J., 1995. *The Black-Tailed Prairie Dog: Social Life of a Burrowing Mammal*, Chicago: University of Chicago Press.

van Hook, L.R., 1920. The exposure of children at Athens. *Transactions and Proceedings of the American Philological Association*, 51, pp.134–145.

Horvat, J.R. & Kraemer, H.C., 1981. Infant socialization and maternal influence in chimpanzees. *Folia Primatologica*, 36, pp.99–110.

Hosaka, K. et al., 2001. Predation of mammals by the chimpanzees of the Mahale Mountains, Tanzania. *All Apes Great and Small, Vol. I.*, pp.107–130.

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

Hrdy, S.B., 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, 1, pp.13–40.

Hrdy, S.B., 1974. Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatologica*, 22, pp.19–58.

Hrdy, S.B., 1981. *The Woman That Never Evolved. , Cambridge, Massachusetts*, Cambridge, MA: Harvard University Press.

Huchard, E. et al., 2013. Paternal effects on access to resources in a promiscuous primate society. *Behavioral Ecology*, 24, pp.229–236.

Huck, U.W. & Banks, E.M., 1982. Male dominance status, female choice and mating success in the brown lemming, *Lemmus trimucronatus*. *Animal Behaviour*, 30, pp.665–675.

Humle, T. & Matsuzawa, T., 2001. Behavioural diversity among the wild chimpanzee populations of Bossou and neighbouring areas, Guinea and Côte D’ivoire, West Africa: a preliminary report. *Folia Primatologica*, 72, pp.57–68.

Hunt, S.M., Gamache, K.M. & Lockard, J.S., 1978. Babysitting behavior by age/sex classification in squirrel monkeys (*Saimiri sciureus*). *Primates*, 19, pp.179–186.

Inoue, E. et al., 2008. Relatedness in wild chimpanzees: influence of paternity, male philopatry, and demographic factors. *American Journal of Physical Anthropology*, 137, pp.256–262.

Janicke, T., David, P. & Chapuis, E., Environment-dependent sexual selection: bateman's parameters under varying levels of food availability.

Janson, C., 1985. Aggresive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology*, 18, pp.125–138.

Jasienska, G. & Ellison, P.T., 1998. Physical work causes suppression of ovarian function in women. *Proceedings of the Royal Society B: Biological Sciences*, 265, p.1847.

Jindal, S. et al., 2017. A test of male infanticide as a reproductive tactic in a cichlid fish. *Royal Society Open Science*, 4, p.160891.

Johnson, L.K. & Hubbell, S.P., 1974. Aggression and competition among stingless bees: field studies. *Ecology*, 55, pp.120–127.

Jones, J.H., 2011. Primates and the evolution of long, slow life histories. *Current Biology : CB*, 21, pp.R708-17.

Jones, R.B. & Nowell, N.W., 1973. *Aversive and Aggression-Promoting Properties of Urine from Dominant and Subordinate Male Mice*,

Jouventin, P., Barbraud, C. & Rubin, M., 1995. Adoption in the emperor penguin, *Aptenodytes forsteri*. *Animal Behaviour*, 50, pp.1023–1029.

Kaburu, S.S.K. & Newton-Fisher, N., 2015. Egalitarian despots: hierarchy steepness, reciprocity and the grooming-trade model in wild chimpanzees, *Pan troglodytes*. *Animal Behaviour*, 99, pp.61–71.

Kaburu, S.S.K. & Newton-Fisher, N., 2015. Trading or coercion? variation in male mating strategies between two communities of East African chimpanzees. *Behavioral Ecology and Sociobiology*, 69, pp.1039–1052.

Kahlenberg, S.M. et al., 2008. Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal Behaviour*, 76, pp.1497–1509.

Kappeler, P, M. & Pereira, M, E., 2003. *Primate Life Histories and Socioecology*, Chicago, Illinois: University of Chicago Press.

Kembel, S.W. et al., 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, pp.1463–1464.

Kerth, G. & König, B., 1999. Fission, fusion and nonrandom associations in female bechstein's bats (*Myotis bechsteinii*). *Behaviour*, 136, pp.1187–1202.

Kingdon, J., 1997. *The Kingdon Field Guide to African Mammals*, London: Academic Press.

Kirchhoff, C.A. et al., 2018. Infanticide in chimpanzees: taphonomic case studies from Gombe. *American Journal of Physical Anthropology*, 165, pp.108–122.

Kleiman, D.G. & Malcolm, J.R., 1981. The evolution of male parental investment in mammals. In D. J. Gubernick & P. H. Klopfer, eds. *Parental Care in Mammals*.

Ann Arbor: Plenum Press, pp. 347–387.

Klosowski, G., Klosowski, T. & Zielinski, P., 2002. A case of parental infanticide in the black stork *Ciconia nigra*. *Avian Science*, 2, pp.1–4.

Knörnschild, M. et al., 2011. Sexually selected infanticide in a polygynous bat B. Fenton, ed. *PLoS ONE*, 6, p.e25001.

Knott, C.D. et al., 2010. Female reproductive strategies in orangutans, evidence for female choice and counterstrategies to infanticide in a species with frequent sexual coercion. *Proceedings of the Royal Society B: Biological Sciences*, 277, pp.105–113.

Krebs, J.R. & Davies, N.B., 1987. *An Introduction to Behavioural Ecology* Second., Oxford: Blackwell Scientific Publications.

Kuester, J. & Paul, A., 1986. Male-infant relationships in semifree-ranging barbary macaques (M*acaca sylvanus*) of affenberg salem/frg: testing the “male care” hypothesis. *American Journal of Primatology*, 10, pp.315–327.

Kummer, H., 1971. *Primate Societies: Group Techniques of Ecological Adatpations*, Chicago, Illinois: Aldine-Atherton Publishers.

Kummer, H., 1968. *Social Organization of Hamadryas Baboons*, Chicago: University of Chicago Press.

Kümmerli, R., 2004. Patterns of infant carriage by barbary *Macaques macaca sylvanus* in gibraltar. In *Proceedings of the 18th Congress of the International Primatological Society. Vol. 1*.

Langergraber, K.E. et al., 2013a. Male-female socio-spatial relationships and reproduction in wild chimpanzees. *Behavioral Ecology and Sociobiology*, 67, pp.861–873.

Langergraber, K.E. et al., 2013b. Male–female socio-spatial relationships and reproduction in wild chimpanzees. *Behavioral Ecology and Sociobiology*, 67, pp.861–873.

Langergraber, K.E., Mitani, J.C. & Vigilant, L., 2007. The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America*, 104, pp.7786–90.

Langos, D. et al., 2013. The impact of paternity on male-infant association in a primate with low paternity certainty. *Molecular Ecology*, 22, pp.3638–3651.

Lappan, S., 2008. Male care of infants in a siamang (*Symphalangus syndactylus)* population including socially monogamous and polyandrous groups. *Behavioral Ecology and Sociobiology*, 62, pp.1307–1317.

LeBoeuf, B.J. & Campagna, C., 1994. Protection and abuse of young in pinnipeds. In S. Parmigiani & F. S. vom Saal, eds. *Infanticide and Parental Care,*. Chur: Harwood Academic Publishers, pp. 257–76.

Lehmann, J., Boesch, C. & Fickenscher, G., 2006. Kin biased investment in wild chimpanzees. *Behaviour*, 143, pp.931–955.

Lourdais, O. et al., 2005. Adaptive maternal cannibalism in snakes (*Epicrates cenchria maurus, boidae*). *Biological Journal of the Linnean Society*, 84, pp.767–774.

Lukas, D. & Clutton-Brock, T.H., 2013. The evolution of social monogamy in mammals. *Science*, 341, pp.526–530.

Lukas, D. & Huchard, E., 2014. The evolution of infanticide by males in mammalian societies. *Science*, 346, pp.841–844.

Lydersen, C. & Kovacs, K.M., 1996. Energetics of lactation in harp seals (*Phoca groenlandica*) from the gulf of st. lawrence, canada. *Journal of Comparative Physiology - B Biochemical, Systemic, and Environmental Physiology*, 166, pp.295–304.

Machanda, Z.P., Gilby, I.C. & Wrangham, R.W., 2013. Male-female association patterns among free-ranging chimpanzees (*Pan troglodytes schweinfurthii*). *International Journal of Primatology*, 34, pp.917–938.

Machanda, Z.P., Gilby, I.C. & Wrangham, R.W., 2013. Male – female association patterns among free-ranging chimpanzees (*Pan troglodytes schweinfurthii).* *International Journal of Primatology*, 34, pp.917–938.

Maestripieri, D., 1992. Functional aspects of maternal aggression in mammals. *Canadian Journal of Zoology*, 70, pp.1069–1077.

Matsumoto-Oda, A., Hosaka, K. & Huffman, M. a, 1998. Factors affecting party size in chimpanzees of the Mahale Mountains. *International Journal of Primatology*, 19, pp.999–1011.

McCarthy, M.M. & Vom Saal, F.S., 1985. The influence of reproductive state on infanticide by wild female house mice (*Mus musculus*). *Physiology and Behavior*, 35, pp.843–849.

McLellan, B.N., 2005. Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival. *Ursus*, 16, pp.141–156.

McNeilly, A.S., Tay, C.C.K. & Glasier, A., 1994. Physiological mechanisms underlying lactational amenorrhea. *Annals of the New York Academy of Sciences*, 709, pp.145–155.

Mennella, J.A. & Moltz, H., 1988. Infanticide in rats: male strategy and female counter-strategy. *Physiology and Behavior*, 42, pp.19–28.

Mitani, J.C. et al., 2002. Demographic and social constraints on male chimpanzee behaviour. *Animal Behaviour*, 64, pp.727–737.

Mitani, J.C. & Watts, D.P., 2001. Why do chimpanzees hunt and share meat? *Animal Behaviour*, 61, pp.915–924.

Moller, A.P. & Birkhead, T.R., 1993. Certainty of paternity covariates with parental care in birds. *Behavioral Ecology and Sociobiology*, 33, pp.261–268.

Moller, A.P. & Cuervo, J.J., 2000. The evolution of paternity and paternal care in birds. *Behavioral Ecology*, 11, pp.472–485.

Molvar, E.M. & Bowyer, R.T., 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *Journal of Mammalogy*, 75, pp.621–630.

Mori, A., Iwamoto, T. & Bekele, A., 1997. A case of infanticide in a recently found gelada population in Arsi, Ethiopia. *Primates*, 38, pp.79–88.

Muller, M.N. et al., 2007. Male coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of the Royal Society of London B: Biological Sciences*, 274, pp.1009–14.

Muller, M.N. et al., 2011. Sexual coercion by male chimpanzees shows that female choice may be more apparent than real. *Behavioral Ecology and Sociobiology*, 65, pp.921–933.

Muller, M.N., Kahlenberg, S.M. & Wrangham, R.W., 2009a. Male aggression against females and sexual coercion in chimpanzees. In M. N. Muller & R. W. Wrangham, eds. *Sexual coercion in primates and mammals*. Cambridge, MA: Harvard University Press, pp. 184–217.

Muller, M.N., Kahlenberg, S.M. & Wrangham, R.W., 2009b. Male aggression and sexual coercion of females in primates. In M. N. Muller & R. W. Wrangham, eds. *Sexual coercion in primates and humans*. Cambridge, MA: Harvard University Press, pp. 3–22.

Muller, M.N., Thompson, M.E. & Wrangham, R.W., 2006. Male chimpanzees prefer mating with old females. *Current Biology*, 16, pp.2234–2238.

Muller, M.N. & Wrangham, R.W., 2004. Dominance, aggression and testosterone in wild chimpanzees: a test of the 'challenge hypothesis.' *Animal Behaviour*, 67, pp.113–123.

Mumme, R.L., Koenig, W.D. & Pitelka, F.A., 1983. Mate guarding in the acorn woodpecker: within-group reproductive competition in a cooperative breeder. *Animal Behaviour*, 31, pp.1094–1106.

Murray, C.M. et al., 2016. Chimpanzee fathers bias their behaviour towards their offspring. *Royal Society Open Science*, 3, p.160441.

Murray, C.M. et al., 2014a. Early social exposure in wild chimpanzees: mothers with sons are more gregarious than mothers with daughters. *Proceedings of the National Academy of Sciences*, 111, pp.18189–18194.

Murray, C.M. et al., 2014b. Early social exposure in wild chimpanzees: mothers with sons are more gregarious than mothers with daughters. *Proceedings of the National Academy of Sciences*, 111, pp.18189–18194.

Murray, C.M. et al., 2009. Reproductive energetics in free-living female chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology*, 20, pp.1211–1216.

Murray, C.M., Eberly, L.E. & Pusey, A.E., 2006. Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). *Behavioral Ecology*, 17, pp.1020–1028.

Murray, C.M., Mane, S. V. & Pusey, A.E., 2007. Dominance rank influences female space use in wild chimpanzees, *Pan troglodytes*: towards an ideal despotic distribution. *Animal Behaviour*, 74, pp.1795–1804.

Murray, C.M., Wroblewski, E. & Pusey, A.E., 2007. New case of intragroup infanticide in the chimpanzees of Gombe National Park. *International Journal of Primatology*, 28, pp.23–37.

Newton-Fisher, N., 1999a. Association by male chimpanzees: a social tactic? *Behaviour*, 136, pp.705–730.

Newton-Fisher, N., 2006. Female coalitions against male aggression in wild chimpanzees of the Budongo Forest. *International Journal of Primatology*, 27, pp.1589–1599.

Newton-Fisher, N., 2004. Hierarchy and social status in Budongo chimpanzees. *Primates*, 45, pp.81–7.

Newton-Fisher, N., 1999b. Infant killers of Budongo. *Folia Primatologica*, 70, pp.167–169.

Newton-Fisher, N., 2017. Modeling social dominance : elo-ratings, prior history, and the intensity of aggression. *International Journal of Primatology*, p.DOI 10.1007/s10764-017-9952-2.

Newton-Fisher, N. et al., 2010. Paternity and social rank in wild chimpanzees (*Pan troglodytes*) from the budongo forest, uganda. *American Journal of Physical Anthropology*, 142, pp.417–428.

Newton-Fisher, N., 2002. Ranging patterns of male chimpanzees in the budongo forest: range structure and individual differences. In C. S. Harcourt & B. R. Sherwood, eds. *New Perspectives in Primate Evolution and Behaviour*. Westbury Scientific Publishing, pp. 287–308.

Newton-Fisher, N., 1997. *Tactical Behaviour & Decision Making in Wild Chimpanzees (Doctoral Dissertation)*. Cambridge, UK: University of Cambridge.

Newton-Fisher, N. & Emery Thompson, M., 2012. Comparative evolutionary perspectives on violence. In T. Shackleford & V. Weekes-Shackelford, eds. *The Oxford Handbook of Evolutionary Perspectives on Violence, Homicide, and War*. New York: Oxford University Press, pp. 41–60.

Newton-Fisher, N., Reynolds, V. & Plumptre, A.J., 2000. Food supply and chimpanzee (*Pan troglodytes schweinfurthii*) party size in the budongo forest reserve, uganda. *International Journal of Primatology*, 21, pp.613–628.

Newton-Fisher, N.E., 1999. The diet of chimpanzees in the Budongo Forest Reserve, uganda. *African Journal of Ecology*, 37, pp.344–354.

Newton-Fisher, N.E., 2003. The home range of the Sonso community of chimpanzees from the Budongo Forest, Uganda. *African Journal of Ecology*, 41, pp.150–156.

Newton-Fisher, N.E., 2015. The hunting behavior and carnivory of wild chimpanzees. In *Handbook of Paleoanthropology*. Berlin, Heidelberg: Springer Berlin Heidelberg, pp. 1661–1691.

Newton-Fisher, N.E. & Kaburu, S.S.K., 2017. Grooming decisions under structural despotism: the impact of social rank and bystanders among wild male chimpanzees. *Animal Behaviour*, 128, pp.153–164.

Newton-Fisher, N.E., Notman, H. & Reynolds, V., 2002. Hunting of mammalian prey by Budongo Forest chimpanzees. *Folia Primatologica*, 73, pp.281–283.

Nishida, T., 1983. Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Primates*, 24, pp.318–336.

Nishida, T. et al., 2003. Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *American Journal of Primatology*, 59, pp.99–121.

Nishida, T., 1990. *The Chimpanzees of the Mahale Mountains*, Tokyo: University of Tokyo Press.

Nishida, T., 1968. The social group of wild chimpanzees in the Mahale Mountains. *Primates*, 9, pp.167–224.

Nishida, T. & Hosaka, 1996. Coalition strategies among adult male chimpanzees of the Mahale Mountians, Tanzania. In W. McGrew, L. Marchant, & T. Nishida, eds. *Great Ape Societies*. Cambridge: Cambridge University Press.

Nishida, T. & Kawanaka, K., 1985. Within-group cannibalism by adult male chimpanzees. *Primates*, 26, pp.274–284.

Nishida, T., Takasaki, H. & Takahata, Y., 1990. Demography and reproductive profiles.

In T. Nishida, ed. *The chimpanzees of the Mahale Mountains*. Toyko: University of Tokyo Press, pp. 63–97.

Nishie, H. & Nakamura, M., 2018. A newborn infant chimpanzee snatched and cannibalized immediately after birth: implications for “maternity leave” in wild chimpanzee. *American Journal of Physical Anthropology*, 165, pp.194–199.

O’Connor, D.E. & Shine, R., 2004. Parental care protects against infanticide in the lizard *Egernia saxatilis* (Scincidae). *Animal Behaviour*, 68, pp.1361–1369.

Ogada, D.L. et al., 2012. Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. *Conservation Biology*, 26, pp.453–460.

Opie, C. et al., 2013. Male infanticide leads to social monogamy in primates. *Proceedings of the National Academy of Sciences of the United States of America*, 110, pp.13328–32.

Ostermeyer, M., 1983. Maternal aggression. In R. W. Elwood, ed. *Parental Behaviour in Rodents*. Chichester, New York: John Wiley & Sons Ltd, pp. 151–179.

Ostfeld, R.S., 1990. The ecology of territoriality in small mammals. *Trends in Ecology and Evolution*, 5, pp.411–415.

Otali, E. & Gilchrist, J.S., 2006. Why chimpanzee (*Pan troglodytes schweinfurthii*) mothers are less gregarious than nonmothers and males: the infant safety hypothesis. *Behavioral Ecology and Sociobiology*, 59, pp.561–570.

Packer, C. & Pusey, A.E., 1983. Adaptations of female lions to infanticide by incoming males. *The American Naturalist*, 121, pp.716 – 728.

Palombit, R. et al., 2000. Male infanticide and defence of infants in chacma baboons. In C. van Schaik, Carel, Janson, ed. *Infanticide by Males and its Implications*. Cambridge: Cambridge University Press, pp. 123–152.

Palombit, R. a., Seyfarth, R.M. & Cheney, D.L., 1997. The adaptive value of “friendships” to female baboons: experimental and observational evidence. *Animal Behaviour*, 54, pp.599–614.

Palombit, R.A., 2015. Infanticide as sexual conflict: coevolution of male strategies and female counterstrategies. *Perspectives in Biology*, 7, pp.1–31.

Parmigiani, S. et al., 1994. Infanticide and protection of young in house mice (*Mus domesticus*): female and male strategies. In S. Parmigiani & F. S. vom Saal, eds. *Infanticide and Parental Care*. Chur: Harwood Academic Publishers, pp. 341–364.

Parmigiani, S., Palanza, P. & Brain, P.F., 2010. Intraspecific maternal aggression in the house mouse (*Mus domesticus*): a counterstrategy to infanticide by males? *Ethology Ecology & Evolution*, 1, pp.341–352.

Parra, G.J., Corkeron, P.J. & Arnold, P., 2011. Grouping and fission-fusion dynamics in Australian snubfin and Indo-Pacific humpback dolphins. *Animal Behaviour*, 82, pp.1423–1433.

Patris, B. & Baudoin, C., 2000. A comparative study of parental care between two rodent species: implications for the mating system of the mound-building mouse *Mus spicilegus*. *Behavioural Processes*, 51, pp.35–43.

Patterson, C., 1985. “Not worth rearing”: the causes of infant exposure in ancient greece. *Transactions of the American Philological Association (1974-)*, 115, pp.103–123.

Patterson, I.A.P. et al., 1998. Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises? *Proceedings of the Royal Society B: Biological Sciences*, 265, pp.1167–1170.

Pepper, J.W., Mitani, J.C. & Watts, D.P., 1999. General gregariousness and specific social preferences among wild chimpanzees. *International Journal of Primatology*, 20, pp.613–632.

Pereira, M.E. & Weiss, M.L., 1991. Female mate choice, male migration, and the treath of infanticide in ringtailed lemurs. *Behavioral Ecology and Sociobiology*, 28, pp.141–152.

Perera, B.M.A.O., 2011. Reproductive cycles of buffalo. *Animal Reproduction Science*, 124, pp.194–9.

Plumptre, A.J., 1996. Changes following 60 years of selective timber harvesting in the Budongo Forest Reserve, Uganda. *Forest Ecology and Management*, 89, pp.101–113.

Plumptre, A.J., Cox, D. & Mugume, S., 2003. *The Status of Chimpanzees in Uganda*,

Plumptre, A.J. & Reynolds, V., 1996. Censusing chimpanzees in the Budongo Forest, Uganda. *International Journal of Primatology*, 17, pp.85–99.

Plumptre, A.J. & Reynolds, V., 1994. The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. *The Journal of Applied Ecology*, 31, p.631.

Poirier, F.E. & Smith, E.O., 1974. Socializing functions of primate play. *Integrative and Comparative Biology*, 14, pp.275–287.

Pond, C.M., 1977. The significance of lactation in the evolution of mammals. *Evolution*, 31, pp.177–199.

Post, D.G., Hausfater, G. & McCuskey, S.A., 1980. Feeding behavior of yellow baboons (*Papio cynocephalus*): relationship to age, gender and dominance rank. *Folia Primatologica; International Journal of Primatology*, 34, pp.170–195.

Potts, K.B., Watts, D.P. & Wrangham, R.W., 2011. Comparative feeding ecology of two communities of chimpanzees (*Pan troglodytes*) in Kibale National Park, Uganda. *International Journal of Primatology*, 32, pp.669–690.

Pride, R.E., 2005. Optimal group size and seasonal stress in ring-tailed lemurs *(Lemur catta)*. *Behavioral Ecology*, 16, pp.550–560.

Pruetz, J.D. & Bertolani, P., 2007. Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Current Biology*, 17, pp.412–417.

Pusey, A.E., 1983. Mother-offspring relationships in chimpanzees after weaning. *Animal Behaviour*, 31, pp.363–377.

Pusey, A.E. & Packer, C., 1987. The evolution of sex-biased dispersal in lions. *Behaviour*, 101, pp.275–310.

Quiatt, D., 1979. Aunts and mothers - adaptive implications of allomaternal behavior of nonhuman-primates. *American Anthropologist*, 81, pp.310–319.

Reynolds, V. et al., 1998. Condensed tannins and sugars in the diet of chimpanzees (*Pan troglodytes schweinfurthii)* in the Budongo Forest, Uganda. *Oecologia*, 115, pp.331–336.

Reynolds, V., 2005. *The Chimpanzees of the Budongo Forest : Ecology, Behaviour, and*

Conservation: Ecology, Behaviour, and Conservation, OUP Oxford.

Reynolds, V. & Reynolds, F., 1965. Chimpanzees of the Budongo Forest. In I. DeVore, ed. *Primate behavior: field studies of monkeys and apes*. New York: Holt, Rinehart and Winston, pp. 368–462.

Rhodes, M., 2007. Roost fidelity and fission–fusion dynamics of white-striped free-tailed bats (*Tadarida australis*). *Journal of Mammalogy*, 88, pp.1252–1260.

Robbins, A.M. et al., 2013. Impact of male infanticide on the social structure of mountain gorillas. *PLoS ONE*, 8, p.e78256.

Roberts, E.K. et al., 2012. A bruce effect in wild geladas. *Science*, 335, pp.1222–1225.

Robertson, R.J., 1990. Tactics and counter-tactics of sexually selected infanticide in tree swallows. In J. Blondel et al., eds. *Population Biology of Passerine Birds*. Berlin, Heidelberg: Springer, pp. 381–390.

Rose, L., 2015. *Massacre of the Innocents*, London: Routledge.

Rubio, C. et al., 2003. Chromosomal abnormalities and embryo development in recurrent miscarriage couples. *Human Reproduction*, 18, pp.182–188.

vom Saal, F.S., 1985. Time-contingent change in infanticide and parental behavior induced by ejaculation in male mice. *Physiology and Behavior*, 34, pp.7–15.

Samuni, L. et al., 2014. Socially learned habituation to human observers in wild chimpanzees. *Animal Cognition*, 17, pp.997–1005.

Sanders, W.J., Trapani, J. & Mitani, J.C., 2003. Taphonomic aspects of crowned hawk-eagle predation on monkeys. *Journal of Human Evolution*, 44, pp.87–105.

van Schaik, C., 2000a. Infanticide by male primates: the sexual selection hypothesis revisited. In C. van Schaik & C. Janson, eds. *Infanticide by males and its implications*. Cambridge: Cambridge University Press, pp. 27–60.

van Schaik, C., 2000b. Social counterstrategies against infanticide by males in primates and other mammals. In Peter Kappeler, ed. *Primate Males: Causes and Consequences of Variation in Group Composition*. Cambridge: Cambridge University Press, pp. 34 – 54.

van Schaik, C.P., 2000a. Infanticide by male primates – the sexual selection hypothesis revisited. In *Infanticide and Parental Care*. pp. 27–60.

van Schaik, C.P., 2000b. Vulnerability to infanticide by males: patterns among mammals. In C. P. van Schaik & C. Janson, eds. *Infanticide by males and its implications*. Cambridge: Cambridge University Press, pp. 61–71.

van Schaik, C.P., 2000c. Vulnerability to infanticide by males: patterns among mammals. In *Infanticide by males and its implications*. pp. 61–71.

Schel, A.M. & Zuberbühler, K., 2009. Responses to leopards are independent of experience in guereza colobus monkeys. *Behaviour*, 146, pp.1709–1737.

Schreiner, C.A. & Hoornbeek, F.K., 1973. Developmental aspects of sirenomelia in the mouse. *Journal of Morphology*, 141, pp.345–357.

Sharpe, F. & Rosell, F., 2003. Time budgets and sex differences in the eurasian beaver. *Animal Behaviour*, 66, pp.1059–1067.

Sherman, P., 1976. *Natural Selection among Some Group-Living Organisms*. University of Michigan.

Shopland, J.M., 1982. An intergroup encounter with fatal consequences in yellow baboons (*Papio cynocephalus*). *American Journal of Primatology*, 3, pp.263–266.

Shopland, J.M. & Altmann, J., 1987. Fatal intragroup kidnapping in yellow baboons. *American Journal of Primatology*, 13, pp.61–65.

Silk, J.B. et al., 1981. Differential reproductive success and facultative adjustment of sex ratios among captive female bonnet macaques (*Macaca radiata*). *Animal Behaviour*, 29, pp.1106–1120.

Simpson, M.J.A., 1973. Social displays and the recognition of individuals. In *Perspectives in Ethology*. Boston, MA: Springer US, pp. 225–279.

Singh, R. et al., 2014. Strategy of female tigers to avoid infanticide. *Current Science*, 107, pp.1595–1597.

Smith, J.E. et al., 2008. Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. *Animal Behaviour*, 76, pp.619–636.

Smolker, R.A. et al., 1992. Sex differences in patterns of association among indian ocean bottlenose dolphins. *Behaviour*, 123, pp.38–69.

Smuts, B., 1985. *Sex and Friendship in Baboons*, New York: Aldine.

Smuts, B. & Smuts, R., 1993. Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior*, 22, pp.1–63.

Soltis, J. et al., 2000. Infanticide by resident males and female counter-strategies in wild japanese macaques (*Macaca fuscata*). *Behavioral Ecology and Sociobiology*, 48, pp.195–202.

Sommer, V., 1989. Infant mistreatment in langur monkeys - sociobiology tackled from the wrong end. In A. Rasa, C. Vogel, & E. Voland, eds. *The sociobiology of social and reproductive strategies*. London: Chapman and Hall, pp. 110–127.

Sommer, V., 1987. Infanticide among free-ranging langurs (*Presbytis entellus*) at Jodhpur (Rajasthan/India): recent observations and a reconsideration of hypotheses. *Primates*, 28, pp.163–197.

Sommer, V., 2000. The holy wars about infanticide. which side are you on? and why? In C. van Schaik & C. Janson, eds. *Infanticide by Males and its Implications*. Cambridge: Cambridge University Press, pp. 9–26.

Sommer, V. & Mohnot, S.M., 1985. New observations on infanticides among hanuman langurs (*Presbytis entellus*) near Jodhpur (Rajasthan India). *Behavioral Ecology and Sociobiology*, 16, pp.245–248.

Stanford, C.B. et al., 1994. Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, 1982–1991. *American Journal of Physical Anthropology*, 94, pp.213–228.

Struhsaker, T.T. & Leland, L., 1985. Infanticide in a patrilineal society of red colobus monkeys. *Zeitschrift Für Tierpsychologie*, 69, pp.89–132.

Stumpf, R.M. & Boesch, C., 2005. Does promiscuous mating preclude female choice? female sexual strategies in chimpanzees (*Pan troglodytes verus*) of the Taï National Park, Côte D'Ivoire. *Behavioral Ecology and Sociobiology*, 57, pp.511–524.

Stumpf, R.M. & Boesch, C., 2006. The efficacy of female choice in chimpanzees of the Taï Forest, Côte D’Ivoire. *Behavioral Ecology and Sociobiology*, 60, pp.749–765.

Sueur, C. et al., 2011. Collective decision-making and fission-fusion dynamics: a conceptual framework. *Oikos*, 120, pp.1608–1617.

Sugiyama, Y., 1965. On the social change of hanuman langurs (*Presbytis entellus*) in their natural condition. *Primates*, 6, pp.381–418.

Sugiyama, Y., 1968. Social organisation of chimpanzees in the Budongo Forest, Uganda. *Primates*, 92, pp.225–258.

Sugiyama, Y., 1968. Social organisation of chimpanzees in the Budongo Forest, Uganda. *Primates*, 92, pp.225–258.

Sussman, R., Cheverud, J. & Barlett, T., 1995. Infant killing as an evolutionary strategy: reality or myth? *Evolutionary Anthropology*, 3, pp.149–151.

Symington, M.M., 1990a. Fission-fusion social organization in *Ateles* and *Pan. International Journal of Primatology*, 11, pp.47–61.

Symington, M.M., 1990b. Fission-fusion social organization in *Ateles* and *Pan. International Journal of Primatology*, 11, pp.47–61.

Takahata, Y., 1985. Adult male chimpanzees kill and eat a male newborn infant: newly observed intragroup infanticide and cannibalism in Mahale National Park, Tanzania. *Folia Primatologica*, 44, pp.161–170.

Tardif, S.D., Layne, D.G. & Smucny, D.A., 2002. Can marmoset mothers count to three? effect of litter size on mother-infant interactions. *Ethology*, 108, pp.825–836.

Tennie, C., Gilby, I.C. & Mundry, R., 2009. The meat-scrap hypothesis: small quantities of meat may promote cooperative hunting in wild chimpanzees (*Pan troglodytes*). *Behavioral Ecology and Sociobiology*, 63, pp.421–431.

Thompson, M.E., Muller, M.N. & Wrangham, R.W., 2012. The energetics of lactation and the return to fecundity in wild chimpanzees. *Behavioral Ecology*, 23, pp.1234–1241.

Townsend, S.W., Slocombe, K.E., Emery Thompson, M., et al., 2007. Female-led infanticide in wild chimpanzees. *Current Biology*, 17, pp.R355–R356.

Townsend, S.W., Slocombe, K.E. & Thompson, M.E., 2007. Infanticide in wild chimpanzees. *Current Biology*, 17, pp.R355–R356.

Treves, A., Drescher, A. & Snowdon, C.T., 2003. Maternal watchfulness in black howler monkeys (A*louatta pigra*). *Ethology*, 109, pp.135–146.

Trivers, R.L.L., 1972. Parental investment and sexual selection. *Sexual Selection and the Descent of Man*, pp.136–179.

Tutin, C.E.G., 1979. Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, 6, pp.29–38.

Tweheyo, M. & Lye, K.A., 2005. Patterns of frugivory of the Budongo Forest chimpanzees, Uganda. In *African Journal of Ecology*. pp. 282–290.

Viazzo, P.P., Bortolotto, M. & Zanotto, A., 2000. Five centuries of foundling history in florence: changing patterns of abandonment, care and mortality. In C. Panter-Brick & M. T. Smith, eds. *Abandoned children*. Cambridge University Press, pp. 70–91.

Walker, C.S. et al., 2018. Morphological identification of hair recovered from feces for detection of cannibalism in eastern chimpanzees. *Folia Primatologica*, 89, pp.240–

250.

Wallis, J., 1997a. A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *Journal of Reproduction and Fertility*, 109, pp.297–307.

Wallis, J., 1997b. A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *Reproduction*, 109, pp.297–307.

Watts, David, P. et al., 2006. Lethal intergroup aggression by chimpanzees in Kibale National Park , Uganda. *American Journal of Primatology*, 68, pp.161–180.

Watts, D.P., 1998. Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, 44, pp.43–55.

Watts, D.P., 1996. Comparative socio-ecology of gorillas. *Great Ape Societies*, pp.16–28.

Watts, D.P., 1989a. Infanticide in mountain gorillas: new cases and a reconsideration of the evidence. *Ethology*, 81, pp.1–18.

Watts, D.P., 1989b. Infanticide in mountain gorillas: new cases and a reconsideration of the evidence. *Ethology*, 81, pp.1–18.

Watts, D.P. & Mitani, J.C., 2001. Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, 138, pp.299–327.

Watts, D.P. & Mitani, J.C., 2002. Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, 23, pp.1–28.

Watts, D.P. & Mitani, J.C., 2000. Infanticide and cannibalism by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Primates*, 41, pp.357–365.

Wells, R.S., Scott, M.D. & Irvine, A.B., 1987. The social structure of free-ranging bottlenose dolphins. *Current Mammalogy*, pp.247–305.

White, P.A., 2005. Maternal rank is not correlated with cub survival in the spotted hyena, *Crocuta crocuta*. *Behavioral Ecology*, 16, pp.606–613.

Whiten, A. et al., 1999. Cultures in chimpanzees. *Nature*, 399, pp.682–685.

Whiten, A. & Rumsey, T.J., 1973. “Agonistic buffering” in the wild barbary macaque, *Macaca sylvanus*. *Primates*, 14, pp.421–425.

Wickham, H., 2016. Ggplot2: elegant graphics for data analysis.

Widdig, A., 2007. Paternal kin discrimination: the evidence and likely mechanisms. *Biological Reviews*, 82, pp.319–334.

Wiebe, K.L. & Martin, K., 1998. Costs and benefits of nest cover for ptarmigan: changes within and between years. *Animal Behaviour*, 56, pp.1137–1144.

Wilkinson, I.S. et al., 2000. Infanticide and cannibalism in the new zealand sea lion, *Phocarctos hookeri*. *Marine Mammal Science*, 16, pp.494–500.

William Huck, U., Soltis, R.L. & Coopersmith, C.B., 1982. Infanticide in male laboratory mice: effects of social status, prior sexual experience, and basis for discrimination between related and unrelated young. *Animal Behaviour*, 30, pp.1158–1165.

Williams, G.C., 1966. Natural selection, the costs of reproduction, and a refinement of lack’s principle. *The American Naturalist*, 100, pp.687–690.

Williams, J.M. et al., 2002. Female competition and male territorial behaviour influence female chimpanzees’ ranging patterns. *Animal Behaviour*, 63, pp.347–360.

Wilson, A., 1989. Illegitimacy and its implications in mid-eighteenth-century london: the evidence of the foundling hospital. *Continuity and Change*, 4, pp.103–164.

Wilson, M.L. et al., 2012. Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. *Animal Behaviour*, 83, pp.263–268.

Wilson, M.L. et al., 2014. Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts. *Nature*, 513, pp.414–429.

Wilson, M.L., Wallauer, W.R. & Pusey, A.E., 2004. New cases of intergroup violence among chimpanzees in Gombe National Park, Tanzania. *International Journal of Primatology*, 25, pp.523–549.

Wittig, R.M. et al., 2014. Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, 281, pp.20133096–20133096.

Wolff, J.O., 1985. Maternal aggression as a deterrent to infanticide in P*eromyscus leucopus* and P. *maniculatus*. *Animal Behaviour*, 33, pp.117–123.

Wolff, J.O., 1993. Why are female small mammals territorial? *Oikos*, 68, p.364.

Wolff, J.O. & Cicirello, D.M., 1989. Field evidence for sexual selection and resource competition infanticide in white-footed mice. *Animal Behaviour*, 38, pp.637–642.

Wolff, J.O. & Macdonald, D.W., 2004. Promiscuous females protect their offspring. *Trends in Ecology & Evolution*, 19, pp.127–34.

Wolff, J.O. & Peterson, J.A., 1998. An offspring-defense hypothesis for territoriality in female mammals. *Ethology Ecology and Evolution*, 10, pp.227–239.

Woodroffe, R. & Vincent, A., 1994. Mother's little helpers: patterns of male care in mammals. *Trends in Ecology and Evolution*, 9, pp.294–297.

Wrangham, R., 2000. Why are male chimpanzees more gregarious than mothers? a scramble competition hypothesis. In P. M. Kappeler, ed. *Primate Males: Causes and Consequences of Variation in Group Composition*. Cambridge: Cambridge University Press, pp. 248–258.

Wrangham, R. & White, F.J., 1988. Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behaviour*, 105, pp.148–164.

Wrangham, R.W., 2010. An ecological model of female-bonded primate groups. *Strategies*, 75, pp.262–300.

Wrangham, R.W. & Smuts, B., 1980. Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility*, 28, pp.13–31.

Wright, H.W.Y., 2006. Paternal den attendance is the best predictor of offspring survival in the socially monogamous bat-eared fox. *Animal Behaviour*, 71, pp.503–510.

Wroblewski, E. et al., 2009. Male dominance rank and reproductive success in chimpanzees (*Pan troglodytes schweinfurthii*). *Animal Behaviour*, 77, pp.873–885.

Yamagiwa, J., Kahekwa, J. & Basabose, A.K., 2009. Infanticide and social flexibility in the genus *Gorilla*. *Primates*, 50, pp.293–303.

Zipple, M.N. et al., 2017. Conditional fetal and infant killing by male baboons.

Proceedings of the Royal Society B: Biological Sciences, 284, p.20162561.

Zuur, A.F. & Ieno, E.N., 2016. A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution*, 7, pp.636–645.

Appendix I – Publication

Received: 13 December 2017 | Revised: 6 June 2018 | Accepted: 11 September 2018
DOI: 10.1002/ajpa.23723

RESEARCH ARTICLE

Countering infanticide: Chimpanzee mothers are sensitive to the relative risks posed by males on differing rank trajectories

Adriana E. Lowe[1] | Catherine Hobaiter[2] | Nicholas E. Newton-Fisher[1]

[1] Living Primates Research Group, School of Anthropology & Conservation, University of Kent, Canterbury, United Kingdom

[2] Centre for Social Learning & Cognitive Evolution, School of Psychology & Neuroscience, University of St Andrews, St Andrews, United Kingdom

Correspondence
Adriana E. Lowe, School of Anthropology and Conservation, Marlowe Building, University of Kent, Canterbury, CT2 7NR, United Kingdom.
Email: ael22@kent.ac.uk
and
Nicholas E. Newton-Fisher, School of Anthropology and Conservation, Marlowe Building, University of Kent, Canterbury, CT2 7NR, United Kingdom.
Email: n.e.newton-fisher@kent.ac.uk

Funding information
University of Kent, Grant/Award Number: Vice Chancellor's 50th Anniversary Scholarship; Harry Frank Guggenheim Foundation

Abstract

Objectives: Infanticide by males is common in mammals. According to the sexual selection hypothesis, the risk is inversely related to infant age because the older the infant, the less infanticide can shorten lactational amenorrhea; risk is also predicted to increase when an infanticidal male's chance of siring the replacement infant is high. Infanticide occurs in chimpanzees (*Pan troglodytes*), a species in which male dominance rank predicts paternity skew. Infanticidal male chimpanzees (if low-ranking) are unlikely to kill their own offspring, whereas those who are currently rising in rank, particularly when this rise is dramatic, have an increased likelihood of fathering potential future infants relative to any existing ones. Given that mothers should behave in ways that reduce infanticide risk, we predicted that female chimpanzees, and specifically those with younger, more vulnerable infants, would attempt to adjust the exposure of their infants to potentially infanticidal males. Specifically, mothers of young infants should reduce their association with adult males in general, and to a greater extent, with both low-ranking males and those rising in rank from a position where paternity of current infants was unlikely, to a rank where the probability of siring the next infant is significantly higher. We also investigated the alternative possibility that rather than avoiding all adult males, mothers would increase association with males of stable high rank on the basis that such males could offer protection against infanticide.

Materials and methods: We examined data on female association patterns collected from the Budongo Forest, Uganda, during a period encompassing both relative stability in the male hierarchy and a period of instability with a mid-ranking male rising rapidly in rank.

Results: Using linear mixed models, we found that mothers reduced their association with the rank-rising male, contingent on infant age, during the period of instability. We also found evidence that females preferentially associated with a potential protector male during the high-risk period.

Discussion: Our results support the sexually selected hypothesis for infanticide and demonstrate that female chimpanzees are sensitive to the relative risks posed by adult males.

KEYWORDS
aggression, association, Budongo, counter-strategy, *Pan troglodytes*

1 | INTRODUCTION

Infanticide by males is common in mammals (Lukas & Huchard, 2014). According to the sexually selected infanticide hypothesis (Hrdy, 1979; Sommer, 1987), the risk of infanticide increases when (a) males can kill unrelated infants; (b) infanticide reduces the interbirth interval of the targeted infant's mother; and (c) infanticide increases the male's likelihood of achieving paternity (i.e., the chance of siring the replacement infant relative to the infant killed). Infanticide should generate significant selective pressure, and therefore, females are expected to use counterstrategies, such as promiscuity and post-conceptive swellings to confuse paternity, as well as maternal vigilance and aggression

(Hrdy, 1979; Parmigiani, Palanza, & Brain, 2010; Treves, Drescher, & Snowdon, 2003; van Schaik, 2000a; Wolff & Macdonald, 2004).

Infanticide occurs in multiple communities of East African chimpanzees, with most cases perpetrated by males (*Pan troglodytes schweinfurthii*: Arcadi & Wrangham, 1999; Newton-Fisher, 1999; Murray, Wroblewski, & Pusey, 2007; Newton-Fisher & Emery, 2012). Female promiscuity is conventionally interpreted as a strategy aimed at confusing paternity and protecting against male-committed infanticide (Hrdy, 1981). However, adult males may be able to track variation in the size of female sexual swellings, suggesting that ovulation is not entirely concealed (Deschner, Heistermann, Hodges, & Boesch, 2003), and in some communities, male coercive aggression may place restrictions on females' ability to determine the males with whom they mate (Feldblum et al., 2014; Muller, Kahlenberg, Emery Thompson, & Wrangham, 2007), although the use of coercion varies between sites (Kaburu & Newton-Fisher, 2015a). More critically, however, male dominance rank typically predicts paternity across multiple communities, including our study group (Boesch, Kohou, Néné, & Vigilant, 2006; Langergraber, Mitani, Watts, & Vigilant, 2013; Newton-Fisher, Thompson, Reynolds, Boesch, & Vigilant, 2010; Wroblewski et al., 2009). This raises a particular problem for females; although promiscuity might reduce rank-related paternity skew (and might be responsible for the relatively moderate degree of skew: 60% of paternities achieved by males of Ranks 1–3 in our study community; Newton-Fisher et al., 2010), it cannot protect fully against infanticide by confusing paternity. Infanticide becomes an adaptive strategy where the chances of a male having sired an existing infant are low, and when changes in social dominance rank increase the probability of him siring a replacement infant (the value of *p* in van Schaik's (2000a) model of adaptive infanticide). As a consequence of the probabilistic relationship between rank and paternity, males who use infanticide as a strategy contingent on their relative dominance rank (and recent changes thereof) will do so, on average, in an adaptive fashion. At a proximate level, tracking outcomes of recent agonistic interactions with other males and thus relative rank is likely to be less challenging than tracking mating history or estimating likelihood of paternity, under a fission–fusion social system with promiscuously mating females. Although such a reliance on rank as a proxy may in some cases be negated by specific mating strategies such as consortships (in which mating is restricted and paternity certainty is potentially high), the existence of a statistical relationship between rank and paternity, itself the outcome of the interplay of male and female mating strategies, will in most cases provide males with a reliable cue (at least considered from the perspective of the evolution of the strategy) which females cannot directly counter. The proposed female strategy of concentrating mating efforts, when most likely to conceive, on preferred males (Stumpf & Boesch, 2005) will only worsen this problem if these preferred males are high-ranking, as it will reinforce or exacerbate the rank-related skew in paternity. If females cannot fully reduce paternity skew through promiscuous and frequent copulation, either because they cannot overcome male coercive aggression (Muller et al., 2007; Muller, Thompson, Kahlenberg, & Wrangham, 2011) or because they seek high quality mates (Stumpf & Boesch, 2005, 2006; Tutin, 1979), additional or alternative strategies will be needed to counter the risk of infanticide.

A consequence of this link between male rank and paternity skew is the correlated link between male rank and infanticide risk. Although low-ranked males generally have a low likelihood of siring any given infant and would have less to lose by pursuing an infanticidal strategy, the greatest risk to females comes from males who rise in rank, all other factors being equal (cf. *Macaca fuscata*: Soltis, Thomsen, Matsubayashi, & Takenaka, 2000). In particular, those males who rise from a rank at which paternity was unlikely when an infant was conceived to a sufficiently high rank that the probability of siring the next infant is non-negligible have both little to lose and a lot to gain (van Schaik, 2000b). Female chimpanzees, who are 20–25% lighter than males (Bean, 1999; Goodall, 1986) and socially subordinate (Goldberg & Wrangham, 1997; Goodall, 1986), are in a poor position to defend their infants directly from attacks by males, although in some cases, they may receive coalitionary support (Kahlenberg, Thompson, Muller, & Wrangham, 2008; Newton-Fisher, 2006).

These arguments assume that male chimpanzees are not able to identify paternity directly, and although recent studies of chimpanzees from communities in both Taï and Gombe (Lehmann, Boesch, & Fickenscher, 2006; Murray, Stanton, Lonsdorf, Wroblewski, & Pusey, 2016) have shown that male chimpanzees bias socially positive interactions toward their offspring, these studies did not explore males' knowledge of paternity. The statistical dependency between rank and paternity, which we argue allows males to be adaptively infanticidal, may allow males to provide paternal investment without offspring recognition by biasing behavior according to their expected probability of paternity according to rank, although other factors, such as previous association with the mother, may also be involved (Langergraber et al., 2013). Furthermore, the nature of this paternal biasing differs between Taï and Gombe; although males at both sites bias social behavior (play, reduced aggression) toward their own infants and those infants' mothers, only males at Gombe preferentially associate with their own infants (Lehmann et al., 2006; Murray et al., 2016). Preliminary data from our study community suggest a different pattern again, with paternity having no effect on either association or aggression rates, with adult male–infant play too infrequent to be analyzed (Lowe & Newton-Fisher, in prep). The preferential association of male chimpanzees with maternal, but not paternal, siblings (Langergraber, Mitani, & Vigilant, 2007) further questions direct recognition of kin; paternal siblings may be valuable coalition partners rather than reproductive rivals. We suggest, therefore, that it is premature to assume that male chimpanzees have direct knowledge of paternity.

Chimpanzees have a social system characterized by high fission–fusion dynamics, whereby individuals associate with one another in subgroups ("parties;" Sugiyama, 1968) of variable composition and duration (Boesch & Boesch-Achermann, 2000; Goodall, 1986). Fission–fusion grouping is thought to be a response to managing feeding competition across dispersed patches, particularly of ripe fruit (Symington, 1990), but it also provides individuals with opportunities to adjust their social environment (Murray et al., 2014; Newton-Fisher, 1999; Pepper, Mitani, & Watts, 1999), subject to the conditions that others may do likewise, and that individuals must satisfy their foraging demands. We suggest that females may make use of this flexibility to counter infanticide risk, as the association of dependent infants with other community members is the direct consequence of decisions made by their mothers to join or leave parties.

We consider three nonexclusive possibilities for female counterstrategies to infanticide risk: (a) that females seek protection from high-ranking males who generally have a greater likelihood of having sired their infants (the *male protector hypothesis*: (Borries, Launhardt, Epplen, Epplen, & Winkler, 1999; Kahlenberg et al., 2008; Palombit et al., 2000); (b) that females adjust the exposure of their infants to potentially infanticidal males; specifically, that they reduce association with low-ranking and males who are currently rising in rank, contingent on infant age, as vulnerability and desirability as targets are inversely related to infant age (the *risky-male-avoidance hypothesis*); and (c) that females seek protection for their infants by associating with other mothers (potentially benefiting from both dilution and selfish herd effects; Hamilton, 1971). We also consider the *infant safety hypothesis* (Otali & Gilchrist, 2006), which proposes that low female gregariousness is because of females avoiding association with males in general, because of their potential for aggression. To test these hypotheses, we take advantage of prior work identifying the link between paternity and rank in our study community (Newton-Fisher et al., 2010) and the rapid rise in rank of one of the adult males (NK) in June 2004, from mid to low ranking (Rank 5 of eight adult males) to Rank 2 within 1 month (Newton-Fisher, 2017). As paternity in this community is concentrated in the top three ranks, and rare below Rank 5, this increase in rank represents a significant shift in the likelihood of siring infants, as well as in the level of infanticide risk. Intracommunity infanticide is well documented for this community, with 10 recorded incidents between 2004 and 2013 (Wilson et al., 2014). Of the four infanticides for which the attacker's identity was confirmed, two were committed by males, one by females, and one involved both sexes.

2 | METHODS

2.1 | Data collection

We used data on the Sonso community of chimpanzees from the Budongo Forest, Uganda, collected between October 2003 and January 2005. This community inhabits around 7 km^2 (Newton-Fisher, 2002) of the 428 km^2 semi-deciduous tropical forest within the reserve (Eggeling, 1947; Plumptre, 1996; Reynolds, 2005) and has been studied continuously since 1994 (Newton-Fisher, 1997; Reynolds, 2005). During data collection, the community consisted of 63 individuals, including 8 adult males (by definition, ≥16 years old), 6 adolescent males (ranging from 9 to 14 years old), and 21 adult females (≥14 years old). Age categories follow Goodall (1986). Seven of these females had infants younger than 1 year of age during the study period; these mothers are our focal mothers. Infants of this age are always in the presence of their mothers (Boesch & Boesch-Achermann, 2000). Of these seven females (ID codes: BN, KG, KU, ML, NB, RH, and ZM), two (KU and ZM) had male infants, whereas five females (BN, KG, ML, NB, and RH) had female infants. All focal mothers were multiparous, with between one and four known prior infants. Two infants were of unknown paternity; of the remaining five, adult male BK was the father of three, whereas MA and BB were fathers of one each (all adult males are listed in Figure 1). Data were recorded by Nicholas Newton-Fisher and field assistants using a focal-behavior sampling regime; parties were followed for as long as possible from first encounter until nesting, with preselected focal animals followed when parties fissioned. If contact with chimpanzees was lost because of terrain and/or chimpanzee movement patterns, data were collected from the next party encountered that contained one of the predetermined focal animals. We defined a party following Newton-Fisher's (1999) operational definition: "a collection of independently associating individuals showing coordination in behavior; a cluster of individuals with a radius of around 35m." Party composition was recorded using 5-min-interval instantaneous scan sampling. Given that a chimpanzee could travel >240 m between scan samples (assuming an average travel speed of 2.95 km/h; Newton-Fisher 2003, calculated from data in Wrangham, 1977) and easily leave a party in less than 1 min, an individual's presence in consecutive scans of the same party is not because they are unable to leave within the 5-min period, and therefore, represents an active decision to remain in the same party (e.g., when a party leaves a feeding patch and travels together without changes in membership). All occurrence sampling was used to record aggressive interactions within the focal party (Kaburu & Newton-Fisher, 2015b; Newton-Fisher, 2017).

Our research complied with regulations set by the Ethics Committee of the University of Kent, the protocols of the Budongo Forest Project (now BCFS), and the legal requirements of Uganda. In addition, it complied with the American Association of Physical Anthropologists Code of Ethics as it pertains to living human and nonhuman subjects.

2.2 | Data analysis

We distinguished a new party whenever one or more individuals joined and/or left a party (i.e., at each change in party composition). For the purposes of analysis, we accorded each of the 1,040 parties a unique identifier. This was used to control for multiple observations of the same party. The duration for which party composition remained unchanged was highly variable, with parties lasting between 1 and 47 scans (mean = 2.82 ± 4.07 scans, median = 2). To generate a cardinal measure of social rank, we constructed Elo-ratings from wins and losses of directed aggressive interactions (Newton-Fisher, 2017). We identified several categories of aggression: static threats, approach threats, charging displays, chases and attacks, and scaling the impact that these had on Elo-ratings (for further details, see Newton-Fisher (2017). We used these Elo-ratings (Figure 1) to identify two consecutive 8-month periods in our dataset; the first, when adult male ranks were relatively stable (October 2003 to May 2004) and the second, when a mid-ranking (Rank 5 of eight adult males), adult male (NK) rose rapidly and held high (second) rank (June 2004 to January 2005). NK then remained high-ranking, holding the alpha position from 2006 until 2013. We considered Ranks 1–3 to be "high," 4 and 5 to be "mid," and 6–8 to be "low." Predicted infanticide risk was low during the stable period and higher during the unstable period. We also calculated aggression rates for each male: (a) aggressive interactions per hour toward all members of the community and (b) aggressive interactions per hour toward our focal mothers.

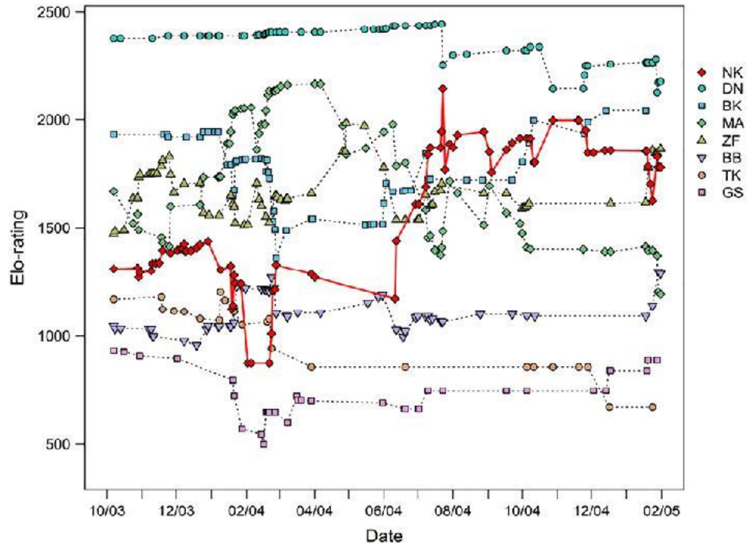


FIGURE 1 Elo-rating derived dominance hierarchy of all adult males (indicated by 2-letter ID codes) throughout the study period. The individual NK is depicted by thick red line with diamond points [Color figure can be viewed at wileyonlinelibrary.com]

Because infant age is a proxy for infanticide risk (Hrdy, 1979), and mothers should be sensitive to this, we looked at the relationship between the age of the focal's infant and party composition. This process allowed us to investigate whether female decisions to participate in parties, based on the composition of those parties, varied as a function of infant age. Given that 86% of chimpanzee infanticide victims with confirmed male attackers were younger than 1 year of age (Wilson et al., 2014), we restricted our analysis to the behavior of mothers with infants younger than 1 year. We used linear mixed-model (LMM) analyses to test our predictions, using the function “lmer” from the R package “lme4” (Bates, Mächler, Bolker, & Walker, 2015) to constructed. We used mixed models with REML and random intercepts to see how the presence of particular individuals related to the age of the focal mother's infant. We produced two models. In Model 1, age of the focal mother's infant was the dependent variable, with the number of adult males and number of mothers of infants younger than 1 year of age in the party as the predictors. This model was designed to show whether mothers of younger (i.e., more vulnerable) infants spent time in parties with more/fewer adult males and other mothers. In Model 2, we again set the age of the focal mother's infant as the dependent variable, this time with the presence (Y/N) of each adult male and time period (low/elevated risk) as predictors, along with an interaction between these. This model, specifically the interaction between male presence and low/elevated risk, was designed to show whether, after taking into account the fact that infants will necessarily be older in the second of these two periods, younger (more vulnerable) infants were more or less likely to be in the presence of particular males in the unstable versus the stable period. We included, as random effects, the ID of the focal mother to account for repeated observations and possible idiosyncratic variation in behavior, and party ID to account for multiple samples from the same parties. We tested the significance of the predictors on the dependent variable by using the “drop1” function to compute a likelihood ratio test.

Age of the focal mother's infant was calculated at each scan sample from either a known birth date or otherwise the midpoint of an estimated date range. Birthdate estimated ranges were 0–14 days, mean: 5.6 days, *SD*: 6.2.

3 | RESULTS

Our focal mothers spent the majority of their time (52.3% of scans) in parties with no adult males, whereas one male was present in 19.6% of scans, two males in 9.5%, and three to seven males in 18.6% of scans. Mothers were alone, except for their dependent infants for 28.9% of scans. The proportion of time which our focal mothers spent in parties with other mothers of infants younger than 1 year of age was similar to that spent with males. They were with no other mothers of young infants in 58.0% of scans, one other mother in 21.8% of scans, two other mothers in 13.9% of scans, and three to six other mothers in 6.3% of scans. We recognize that these percentages may underestimate the total time mothers spend alone, as following lone individuals, in particular females, is typically harder than following larger parties (personal observations). Therefore, time spent with other individuals, or in small all-female parties, may be overrepresented in the data. The mean number of adults in a party was 3 (*SD*: 4), with a mean of one male (*SD*: 2), and two females (*SD*: 2). On average, one of these two females (mean: 1, *SD*: 1) was the mother of an infant younger than 1 year of age.

During the study period, we recorded a mean rate per male of 0.4 (*SD*: 0.2) aggressive interactions per hour (hr^{-1}), but these ranged from 0.1 to 0.7 (median =). Our three lowest ranking males (GS, TK, and BB) were the least aggressive overall, initiating aggressive interactions at rates of 0.1, 0.1, and 0.3 times per hour of observation, respectively. NK was the most aggressive, directing aggression toward other individuals at a rate of 0.7 hr^{-1}. The second most aggressive male was BK, who spent the majority of the study period at either Rank 2 or 3, with a rate of 0.6 hr^{-1}. The other mid- to high-ranking males (Ranks 1–5) had rates between 0.3 hr^{-1} and 0.4 hr^{-1}.

When considering just aggression toward our focal mothers, two low-ranking males (TK and GS) were, again, the least aggressive, with rates of 0.004 hr^{-1} and 0.005 hr^{-1}, respectively. MA, ZF, and BB (high-, mid-, and low-ranking males) had mid-range aggression rates of 0.009 hr^{-1}, 0.2 hr^{-1}, and 0.03 hr^{-1}, respectively. The male most aggressive toward mothers (0.053 hr^{-1}) was the high-ranking BK, followed by NK, our rank-rising male (0.050 hr^{-1}). Aggression rates by the alpha male DN (0.03 hr^{-1}) were lower, comparable to the low-ranking BB.

Male intervention was not observed in any of the 567 recorded attacks or threats toward adult females by other adult males. Two females were observed approaching adult males when threatened and chased by another male, on three separate occasions. On one occasion, this female was a mother; the other two occasions involved the same non-mother. The male aggressor was the rank-rising NK in all three instances, whereas the approached males were all mid- to high-ranking, and in all cases were higher ranking than NK. The mother approached the alpha male, who was not the father of her infant. Approached males did not offer active support in any of the three incidences, and adult males typically ignored aggression directed toward females by other males.

We found no evidence of a relationship between either the number of adult males (Model 1: $\beta \pm \text{SE} = 8.18 \times 10^{-3} \pm 6.51\times 10^{-3}$, $p = .21$) or the number of other mothers of infants younger than 1 year (Model 1: $\beta \pm \text{SE} = 2.29\times 10^{-3} \pm 1.27\times 10^{-3}$, $p = .07$), in the party and the age of the focal mother's infant.

However, we did find (Model 2) statistically significant relationships between the age of the focal's infant and the interaction between the shift from low to elevated infanticide risk and the presence of two of the eight adult males (BK and NK). This reflects which mothers (those with older vs. younger infants) were in the presence of these males. Of the three high-ranking males, there was an effect only for BK, who spent time in parties with mothers of comparatively younger infants during the period of elevated risk than before this period (Model 2: $\beta \pm \text{SE} = -0.12 \pm 0.03$, $p < .0001$). The presence of the male who posed the most likely source of infanticide risk (NK) had the greatest influence; mothers in his presence had infants which were 67.5 days older when risk was elevated compared to the low risk period (Model 2: $\beta \pm \text{SE} = 0.19 \pm 0.03$; $p < .0001$).

4 | DISCUSSION

The *infant safety hypothesis* suggests that adult males, by virtue of being potentially aggressive, are a physical and psychological risk to infants, a risk that is heightened when infants are younger (Otali & Gilchrist, 2006). However, our results suggest that, when considered as a group, male chimpanzees in the Sonso community were not necessarily treated as dangerous by mothers, or at least that any danger posed did not vary with infant age in infants younger than 1 year old.

Instead, mothers of young infants reacted most strongly to the rapid rise in social dominance rank of the male NK, supporting our *risky-male-avoidance hypothesis.* Although we cannot exclude the possibility that our results were the product of this male tending to spend more time with mothers of "older" infants, during and after his rise in rank, we find no convincing explanation why this would be so. It would be difficult to account for such behavior in terms of future mating effort, because all the infants in our dataset are younger than 1 year of age and therefore the mothers of even the oldest are several years away from being sexually receptive; the average interbirth interval (IBI) for chimpanzees, when infants survive, is around 5 years (Goodall, 1986; Kappeler & Pereira, 2003), although the shortest recorded IBI for our study community is 47 months. Furthermore, previous work at Gombe has found that male–female association in chimpanzees does not reflect future mating effort (Murray et al., 2016), although evidence that males may seek out contact with mothers of specific infants was associated with paternity of those infants (Murray et al., 2016). In this study, NK was not the father of any of the five infants younger than 1 year of age for whom paternity was known. By contrast, interpreting these results as attempts by mothers to avoid this male is consistent with the *sexually selected infanticide hypothesis* (Hrdy, 1979; Sommer, 1987). Under this hypothesis, the risk posed by a male depends on the change in his likelihood of achieving paternity with the female's next infant as compared to being the father of her current infant. Risks are greater for younger infants as their death has a greater impact in reducing lactational amenorrhea (Hrdy, 1979; Sommer, 1987; van Schaik, 2000b). An infanticidal male chimpanzee rising in rank will increase his likelihood of achieving future paternities if this rise is postconception and before weaning of the infant(s) at risk. This was precisely the situation for the adult male NK, who was ranked fifth during the first period of our study, only to rise rapidly and sustain high rank in the second period; data from the Sonso community suggest that males of Rank 5 or below have only a low probability of achieving paternity, with most paternity concentrated in males of the top four and particularly the top three ranks (Newton-Fisher et al., 2010). According to the *sexually selected infanticide hypothesis*, NK's rise should have made him the greatest source of infanticide risk, and the male toward whom mothers should therefore respond most strongly. This is precisely what we found.

Our interpretation is supported by our results with respect to males who consistently held high rank; it was the *change* from low to high rank, and thus change in likelihood of achieving paternity, that appeared to be the important factor. Males whose ranks are unchanging between conceptions should not pose an infanticide risk, because without a substantive rise in rank between successive conceptions of a given female, their chance of siring a second infant will be unchanged from that of siring the first, and therefore, they cannot expect to increase their reproductive success through infanticide.

Despite an expectation of higher rates of aggression among high-ranking males (Muller & Wrangham, 2004), and thus the likelihood that infants may be at risk from redirected or unintended violence, we found no evidence that mothers reduced association with higher-ranking males when NK was challenging for high rank. Given that rates of aggression by Sonso community males conform to this general expectation, we would have expected such a reduction if females were concerned primarily about their infants falling victim to inadvertent aggression. Even if high-ranking males were only aggressive when around rank-rising males, this male strategy would result in increased levels of aggression during the second period (when NK was rising in rank), and therefore, we would still expect a reduction in mother–male association as females seek to avoid male aggression, which we did not find. Instead, we found opposite effects for the two most aggressive males; although NK was avoided by mothers of young infants, BK, the second most aggressive male, associated more with younger infants during the unstable period. Danger of misdirected aggression cannot explain these patterns of behavior. We also note that although female chimpanzees will shepherd dependent infants to safety when faced with aggressive males, typically they do not flee from parties under these conditions (personal observations), and it is their older, more independent infants and juveniles who appear to be at most at risk from inadvertent or redirected aggression; the youngest infants—those most vulnerable to infanticide—are more likely to be bodily contact with their mother. Thus, our findings suggest that it is the likelihood of infant-directed attacks, rather than misdirected aggression, to which mothers are sensitive. Given that we find both decreased and increased association with particular males, and no general differences in mothers' associations with adult females compared to their association with adult males, we have no reason to suggest that variation in female association patterns is because of infant socialization (Horvat & Kraemer, 1981). Such patterns may be apparent across the period of infancy (0–5 years), but for infants younger than 1 year, it seems that mothers are attempting to reduce infanticide risk.

We found some support for the *protector male hypothesis* (Borries et al., 1999; Palombit et al., 2000). Of the high-ranking males, the expected effect (an increase in association when infanticide risk was elevated) was seen only for BK, who was father to three of the five infants younger than 1 year old for whom paternity is known. We found no evidence of a "protector" role for the alpha male, although this might have been because the two infants whom he was confirmed to have sired were already over 4 years old at the start of the study period and therefore at low risk of being victims of an infanticidal attack. Although these results are suggestive of a link between paternity and protector male effect, it is not clear why this was not evident for the other fathers in our dataset, unless the effect is small, visible only because of the cumulative effect of multiple infants, or perhaps because BK had higher paternity certainty than might typically be the case because of coercive curtailing of the mother's promiscuity or through fathering an infant during a consortship. Unfortunately, mating history for the relevant period is not available to test these ideas.

Alternatively and perhaps more plausibly, because it does not require identification of paternity, mothers may have been using BK as a shield, regardless of paternity, on the basis that he could deter potentially infanticidal males. Mothers are unlikely to gain active defence—neither BK nor any other male, was observed intervening in an attack by an adult male on an adult female during this study—but may benefit if the presence of aggressive high-ranking males deters aggression from other males. If males interpret aggressive displays from others as rank challenges, this is potentially something that mothers could exploit. However, because BK was also aggressive toward females, such a strategy would be potentially costly, but tolerating high rates of displays, threats, and even contact aggression could be beneficial if linked to protection from infanticidal attacks.

In summary, our results suggest that eastern female chimpanzees in our study community with young infants are sensitive to male rank shifts and respond adaptively to reduce the exposure of their infants to infanticide risk. Mothers reduced their association with (and thus the exposure of their infants to) males who have incentives to commit infanticide, as well as associating with safer, potentially protective males, supporting our risky-male-avoidance hypothesis and, possibly, the male protector hypothesis. We predict that these findings will be generalizable to other chimpanzee communities with rank-based paternity skew, as this generates potential fitness differentials and associated risks of infanticidal behavior. Our findings support the *sexually selected infanticide hypothesis* for within-community infanticide by male eastern chimpanzees.

ACKNOWLEDGMENTS

A.E.L. was supported by a University of Kent Vice Chancellor's Scholarship. Data collection was funded by a grant to NNF from Harry Frank Guggenheim Foundation. Permission to work in Uganda granted by the Uganda National Council for Science and Technology, the President's Office, the Forest Department, and Vernon Reynolds. We are especially grateful to Geresomu Muhumuza and Monday Gideon for assistance in the field.

ORCID

Adriana E. Lowe http://orcid.org/0000-0002-4720-0769
Catherine Hobaiter http://orcid.org/0000-0002-3893-0524
Nicholas E. Newton-Fisher http://orcid.org/0000-0002-7657-2641

REFERENCES

Arcadi, A. C., & Wrangham, R. W. (1999). Infanticide in chimpanzees: Review of cases and a new within-group observation from the Kanyawara study group in Kibale National Park. *Primates*, *40*, 337–351.

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

Bean, A. (1999). Ecology of sex differences in great ape foraging. In P. Lee (Ed.), *Comparative primate socioecology* (pp. 399–362). Cambridge: Cambridge University Press.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï forest: Behavioural ecology and evolution*. USA: Oxford University Press.

Boesch, C., Kohou, G., Néné, H., & Vigilant, L. (2006). Male competition and paternity in wild chimpanzees of the Taï forest. *American Journal of Physical Anthropology*, *130*, 103–115.

Borries, C., Launhardt, K., Epplen, C., Epplen, J. T., & Winkler, P. (1999). Males as infant protectors in hanuman langurs (*Presbytis entellus*) living in multimale groups: Defence pattern, paternity and sexual behaviour. *Behavioral Ecology and Sociobiology*, *46*, 350–356.

Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2003). Timing and probability of ovulation in relation to sex skin swelling in wild west African chimpanzees (*Pan troglodytes verus*). *Animal Behaviour*, *66*, 551–560.

Eggeling, W. J. (1947). Observations on the ecology of the Budongo rain forest, Uganda. *Journal of Ecology*, *34*, 20–87.

Feldblum, J. T., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Paiva, T., Cetinkaya-Rundel, M., … Gilby, I. C. (2014). Sexually coercive male chimpanzees sire more offspring. *Current Biology*, *24*, 2855–2860.

Goldberg, T. L., & Wrangham, R. W. (1997). Genetic correlates of social behaviour in wild chimpanzees: Evidence from mitochondrial DNA. *Animal Behaviour*, *54*, 559–570.

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

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, *31*, 295–311.

Horvat, J. R., & Kraemer, H. C. (1981). Infant socialization and maternal influence in chimpanzees. *Folia Primatologica*, *36*, 99–110.

Hrdy, S. B. (1979). Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, *1*, 13–40.

Hrdy, S. B. (1981). *The woman that never evolved*. Cambridge, MA: Harvard University Press.

Kaburu, S. S. K., & Newton-Fisher, N. (2015a). Trading or coercion? Variation in male mating strategies between two communities of east African chimpanzees. *Behavioral Ecology and Sociobiology*, *69*, 1039–1052.

Kaburu, S. S. K., & Newton-Fisher, N. (2015b). Egalitarian despots: Hierarchy steepness, reciprocity and the grooming-trade model in wild chimpanzees, *Pan troglodytes*. *Animal Behaviour*, *99*, 61–71.

Kahlenberg, S. M., Thompson, M. E., Muller, M. N., & Wrangham, R. W. (2008). Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal Behaviour*, *76*, 1497–1509.

Kappeler, P. M., & Pereira, M. E. (2003). *Primate life histories and socioecology*. Chicago, Illinois: University of Chicago Press.

Langergraber, K. E., Mitani, J. C., & Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 7786–7790.

Langergraber, K. E., Mitani, J. C., Watts, D. P., & Vigilant, L. (2013). Male–female socio-spatial relationships and reproduction in wild chimpanzees. *Behavioral Ecology and Sociobiology*, *67*, 861–873.

Lehmann, J., Boesch, C., & Fickenscher, G. (2006). Kin biased investment in wild chimpanzees. *Behaviour*, *143*, 931–955.

Lukas, D., & Huchard, E. (2014). The evolution of infanticide by males in mammalian societies. *Science*, *346*(80), 841–844.

Muller, M. N., Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2007). Male coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 1009–1014.

Muller, M. N., Thompson, M. E., Kahlenberg, S. M., & Wrangham, R. W. (2011). Sexual coercion by male chimpanzees shows that female choice may be more apparent than real. *Behavioral Ecology and Sociobiology*, *65*, 921–933.

Muller, M. N., & Wrangham, R. W. (2004). Dominance, aggression and testosterone in wild chimpanzees: A test of the 'challenge hypothesis'. *Animal Behaviour*, *67*, 113–123.

Murray, C. M., Lonsdorf, E. V., Stanton, M. A., Wellens, K. R., Miller, J. A., Goodall, J., & Pusey, A. E. (2014). Early social exposure in wild chimpanzees: Mothers with sons are more gregarious than mothers with daughters. *Proceedings of the National Academy of Sciences*, *111*, 18189–18194.

Murray, C. M., Stanton, M. A., Lonsdorf, E. V., Wroblewski, E. E., & Pusey, A. E. (2016). Chimpanzee fathers bias their behaviour towards their offspring. *Royal Society Open Science*, *3*, 160441.

Murray, C. M., Wroblewski, E., & Pusey, A. E. (2007). New case of intragroup infanticide in the chimpanzees of Gombe National Park. *International Journal of Primatology*, *28*, 23–37.

Newton-Fisher, N. (1997). *Tactical behaviour & decision making in wild chimpanzees* (doctoral dissertation), University of Cambridge.

Newton-Fisher, N. (1999). Infant killers of Budongo. *Folia Primatologica*, *70*, 167–169.

Newton-Fisher, N. (2002). Ranging patterns of male chimpanzees in the Budongo forest: Range structure and individual differences. In C. S. Harcourt & B. R. Sherwood (Eds.), *New perspectives in primate evolution and behaviour* (pp. 287–308). Yeadon: Westbury Scientific Publishing.

Newton-Fisher, N. E. (2003). The home range of the Sonso community of chimpanzees from the Budongo Forest. Masindi: Uganda.

Newton-Fisher, N. (2006). Female coalitions against male aggression in wild chimpanzees of the Budongo forest. *International Journal of Primatology*, *27*, 1589–1599.

Newton-Fisher, N. (2017). Modeling social dominance : Elo-ratings, prior history, and the intensity of aggression. *International Journal of Primatology*, *38*, 427–447. https://doi.org/10.1007/s10764-017-9952-2

Newton-Fisher, N., & Emery, T. M. (2012). Comparative evolutionary perspectives on violence. In T. Shackleford & V. Weekes-Shackelford (Eds.), *The Oxford handbook of evolutionary perspectives on violence, homicide, and war* (pp. 41–60). New York: Oxford University Press.

Newton-Fisher, N., Thompson, M. E., Reynolds, V., Boesch, C., & Vigilant, L. (2010). Paternity and social rank in wild chimpanzees (*Pan troglodytes*) from the Budongo forest, Uganda. *American Journal of Physical Anthropology*, *142*, 417–428.

Otali, E., & Gilchrist, J. S. (2006). Why chimpanzee (*Pan troglodytes schweinfurthii*) mothers are less gregarious than nonmothers and males: The infant safety hypothesis. *Behavioral Ecology and Sociobiology*, *59*, 561–570.

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

Parmigiani, S., Palanza, P., & Brain, P. F. (2010). Intraspecific maternal aggression in the house mouse (*Mus domesticus*): A counterstrategy to infanticide by males? *Ethology Ecology and Evolution*, *1*, 341–352.

Pepper, J. W., Mitani, J. C., & Watts, D. P. (1999). General gregariousness and specific social preferences among wild chimpanzees. *International Journal of Primatology*, *20*, 613–632.

Plumptre, A. J. (1996). Changes following 60 years of selective timber harvesting in the Budongo forest reserve, Uganda. *Forest Ecology and Management*, *89*, 101–113.

Reynolds, V. (2005). *The chimpanzees of the Budongo forest: Ecology, behaviour, and conservation*. Oxford: OUP.

Soltis, J., Thomsen, R., Matsubayashi, K., & Takenaka, O. (2000). Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). *Behavioral Ecology and Sociobiology*, *48*, 195–202.

Sommer, V. (1987). Infanticide among free-ranging langurs (*Presbytis entellus*) at Jodhpur (Rajasthan/India): Recent observations and a reconsideration of hypotheses. *Primates*, *28*, 163–197.

Stumpf, R. M., & Boesch, C. (2005). Does promiscuous mating preclude female choice? Female sexual strategies in chimpanzees (*Pan troglodytes verus*) of the Taï National Park, Côte dIvoire. *Behavioral Ecology and Sociobiology*, *57*, 511–524.

Stumpf, R. M., & Boesch, C. (2006). The efficacy of female choice in chimpanzees of the Taï Forest, Côte D'ivoire. *Behavioral Ecology and Sociobiology*, *60*, 749–765.

Sugiyama, Y. (1968). Social organisation of chimpanzees in the Budongo Forest, Uganda. *Primates*, *92*, 225–258.

Symington, M. M. (1990). Fission-fusion social organization in Ateles and Pan. *International Journal of Primatology*, *11*, 47–61.

Treves, A., Drescher, A., & Snowdon, C. T. (2003). Maternal watchfulness in black howler monkeys (*Alouatta pigra*). *Ethology*, *109*, 135–146.

Tutin, C. E. G. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, *6*, 29–38.

van Schaik, C. (2000a). Social counterstrategies against infanticide by males in primates and other mammals. In P. Kappeler (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 34–54). Cambridge: Cambridge University Press.

van Schaik, C. (2000b). Infanticide by male primates: The sexual selection hypothesis revisited. In C. van Schaik & C. Janson (Eds.), *Infanticide by males and its implications* (pp. 27–60). Cambridge: Cambridge University Press.

Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., … Wrangham, R. W. (2014). Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts. *Nature*, *513*, 414–429.

Wolff, J. O., & Macdonald, D. W. (2004). Promiscuous females protect their offspring. *Trends in Ecology & Evolution*, *19*, 127–134.

Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In T. H. Clutton Brock (Ed.), *Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkey and Apes* (502–538). Academic Press. London, New York, San Francisco.

Wroblewski, E., Murray, C., Keele, B., Schumacher-Stankey, J., Hahn, B., & Pusey, A. (2009). Male dominance rank and reproductive success in chimpanzees (*Pan troglodytes schweinfurthii*). *Animal Behaviour*, *77*, 873–885.

How to cite this article: Lowe AE, Hobaiter C, Newton-Fisher NE. Countering infanticide: Chimpanzee mothers are sensitive to the relative risks posed by males on differing rank trajectories. *Am J Phys Anthropol*. 2018;1–7. https://doi.org/10.1002/ajpa.23723

Appendix 2 – Table with details of all intra-community infanticides 1993 – 2017 in Sonso Community

Each row details a single attack (failed or successful infanticide). In two cases there was no “incident” date but the mother was observed without her infant and infanticide was suspected.

Mother ID	Infant DOB	DOB Estimate	Incident Date	Mother Seen Without Infant	Infanticide	Victim Sex	Victim's Age At Attack (Days)	Birth Order of Victim	Mother is Natal?	Mother Visibly Injured?	Attacker Sex	Victim Cannibalised?	Defence By Anyone But The Mother?
KL	27/11/1993	± 1w	27/12/1993		yes	U	30	1	yes	yes	male	no	no
MK	unknown	unknown	15/12/1999		yes	U	N/A	unknown	No	yes	male	no	no
FL	05/03/2004	± 4d	12/03/2004		almost certain	M	7	3	No	yes	suspected females	no	attack not seen
MK	02/07/2006	± 1d	02/07/2006		suspected	U	0	2	No	no	suspected females	unknown	attack not seen
unknown	08/10/2006	± 2w	22/10/2006		suspected	U	14	unknown	N/A	unknown	unknown	unknown	attack not seen
KG	28/10/2008	± 3d	28/10/2008		attempt	F	0	5	No	no	males	N/A	no
MK	11/11/2007	unknown	23/01/2009		attempt	F	439	3	No	yes	male	N/A	no
JL	13/08/2009	± 2w	13/08/2009		yes	M	0	1	No	yes	males and females	yes	no
JL	02/03/2011	± 10d	05/03/2011		attempt	M	3	2	No	yes	males	N/A	no
RS	25/02/2011	± 5d	25/06/2011		attempt	F	120	1	yes	no	male	N/A	no
OK	25/07/2012	exact	25/07/2012		yes	F	0	1	No	yes	males	small piece - not by attackers	no
KL	12/09/2012	exact	13/09/2012		suspected	F	1	6	yes	no	suspected males	no	attack not seen
JN	03/11/2012	± 1d	07/11/2012		almost certain	F	4	4	No	no	suspected female	no	no
KU	15/02/2013	exact	18/02/2013		suspected	U	3	5	No	no	suspected males	no	attack not seen
FL	27/02/2013	± 1d	19/03/2013		attempt	F	20	5	No	no	males	N/A	yes, male
KL	26/07/2013	± 1d	30/07/2013		almost certain	M	4	7	yes	no	suspected male	no	attack not seen
OK	06/09/2013	exact	06/09/2013		yes	M	0	2	No	no	females	yes, but not by attackers	attack not seen
KY	18/09/2013	± 1d	20/09/2013		attempt	F	2	4	yes	no	males	N/A	yes, female kin (offspring)
KY	18/09/2013	± 1d	12/10/2013		suspected	F	24	4	yes	no	suspected males	unknown	attack not seen
RS	08/10/2013	± 2d	20/10/2013		attempt	M	12	2	yes	yes	males	N/A	yes, female kin (mother)
OK	16/09/2014	exact	16/09/2014		attempt	M	0	3	No	yes	males	N/A	yes, male
ML	15/11/2014	exact	17/11/2014		suspected	F	2	5	No	no	suspected males	no	no
KA	29/06/2015	± 1w	12/07/2015		almost certain	U	13	1	Yes	no	suspected males	yes, by potential attacker	attack not seen
CC	05/12/2015	± 1w	06/12/2015		yes	F	1	1	No	no	males	yes, by attackers	no
IN	02/04/2016	exact	08/04/2016		yes	M	6	1	No	no	male	yes, by attacker	no
MK	10/06/2016	± 1w	17/06/2016		yes	U	7	4	No	no	male	unknown	no
DL	25/04/2017	exact	25/04/2017		attempt	U	0	1	No	no	male and female	N/A	no
DL	25/04/2017	exact	26/04/2017		yes	U	1	1	No	no	male	no	no
UP	22/07/2017	± 2d	24/07/2017		yes	F	2	1	No	yes	male	no	attack not seen
MK	16/08/2017	unknown	31/08/2017		suspected	U	15	5	No	no	unknown	no	attack not seen
RM	27/09/2017	exact	27/09/2017		yes	U	0	1	yes	no	male	no	yes, female kin (mother)
JN	02/01/2014	± 4d		04/01/2014	suspected	U	2	5	No	no	unknown	unknown	attack not seen
RS	25/02/2011	± 5d		24/08/2011	suspected	F	180	1	yes	unknown	suspected males	unknown	attack not seen