

Sexually dimorphic stress responses in rodents, *Drosophila melanogaster* and primates

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Abstract

Stress is expressed in a sexually dimorphic manner. The predominant male stress response is the fight-or-flight response, where males either “fight” or “flight” the stressor. The predominant female stress response is the tend-or-befriend response, where females “tend” to their offspring and “befriend” other females to alleviate stress. Empirical evidence for the tend-and-befriend response is evaluated in *Drosophila melanogaster* and several primate species. These were chosen to represent species that show no parental care, show high maternal care and show some paternal care and to see whether this affects the stress responses displayed. I conclude that females do show tend-and-befriend responses in stressful situations. Certain male primates also show some tend-and-befriend responses following stress. More research on sexually dimorphic stress responses should be done, especially in species that show high paternal care, to improve treatment opportunities of stress-related disorders.

Introduction

Stress is a cause of heart problems (Headrick *et al.*, 2017) in both men and women, but men are around two times more likely to get a myocardial infarction than females (Bucholz *et al.*, 2014). This implies that the effect of stress is sexually dimorphic. Two factors can explain this: men and women are exposed to different stressors or they have different stress responses to the same stressors.

Stress is a state caused by a real or perceived threat to homeostasis; aversive stimuli like the presence of a predator or hypo-thermic temperatures (Smith & Vale, 2006; Chrousos, 2009). These stressors cause behavioural stress responses, for example rises in vigilance and attention (Cannon, 1932). Cannon (1932) proposed that if the individual were to think it could overcome the stressor, it would enter “fight mode” and try to beat it, whereas if the contrary were true, it would enter “flight mode” and try to flee it. Therefore, he named it the “fight-or-flight” response.

Mediation of the stress response is mostly by the hypothalamic-pituitary-adrenal (HPA) axis (Smith & Vale, 2006). This axis for the stress response consists of the paraventricular nucleus (PVN) of the hypothalamus, the anterior lobe of the pituitary gland and the adrenal gland. Neurons in the PVN produce corticotropin-releasing factor (CRF) and vasopressin (AVP). When stress is induced, CRF is released and binds to CRF type-1 receptors (CRFR1) on the anterior lobe of the pituitary gland. This activates cyclic adenosine monophosphate (cAMP) pathway events, which induce the release of adrenocorticotrophic hormone (ACTH). AVP causes synergistic effects on ACTH release when CRF is near. This is mediated by the V_{1b} receptor, which binds AVP. When ACTH reaches the adrenal cortex, it binds to melanocortin type-2 receptors (MC2-Rs). This binding stimulates the production and secretion of glucocorticoids. The main glucocorticoid in humans is cortisol (Kudielka & Kirschbaum, 2005). Glucocorticoids regulate the physiological events associated with stress and inhibit further HPA axis activation. For a schematic overview, see Figure 1 (Smith & Vale, 2006).

However, this system does not take into account sex differences. This is a problem, because research into the fight-or-flight response was, at the time, primarily conducted on males (Taylor *et al.*, 2000). Females, especially female rats, were often excluded from studies due to their greater hormonal fluctuations caused by the reproductive cycle. The research that was done on females shows inconsistent evidence for a fight-or-flight response. This gap in female stress response research and inconsistent evidence led to building a theory. What if the fight-or-flight response was not the predominant stress response in females?

Taylor *et al.* (2000) suggested that another stress response, the “tend-and-befriend” response, was dominant in females. The fight-or-flight response would then be mainly a male response. The function of this female-specific response is based on females “tending” to their offspring and “befriending” other females for protection. They came up with a theoretical model, which would explain the evolution of the tend-and-befriend response. They reasoned that, firstly, successful responses to stress would have been passed on to future generations through natural selection. They also reasoned that because the parental investment of females in most species is high, responses to threats that were passed on were most likely those which successfully protected their offspring and their own lives. This leads to the suggestion that there should be selection for a stress response which preserves the health of the female and her offspring, maximising the odds of their survival. This is where the “tending” part comes in. Tending, which they described as “quieting and caring for offspring and blending into the environment”, could be an effective way to address several threats. Showing a fight-or-flight response instead would jeopardise the female and her offspring. Should she choose to fight, she could get hurt or even die, minimising the fitness of her and her offspring. Flight would also be a suboptimal option. If she were to be pregnant, nursing her offspring or be responsible for them in any other way, fleeing would jeopardise their health and safety. Both fighting and fleeing would not

be ideal in this case. Therefore, according to Taylor *et al.* (2000), it would seem that other behavioural responses are likely to have been evolved in females.

Maximising your own fitness and that of your offspring is not the easiest task. This task would be better manageable when getting help from the outside. Effectively making use of your social group would therefore be more successful and lead to a higher fitness. Selection would then lead to this behaviour becoming the norm, rather than the exception. Therefore they suggested that females may affiliate with other females during stressful situations, ultimately “befriending” one another. Here they defined befriending as “the creation of networks of associations that provide resources and protection for the female and her offspring under the conditions of stress”. This would eventually increase the chances of survival for the females and their offspring, because they would help each other when faced with a threat.

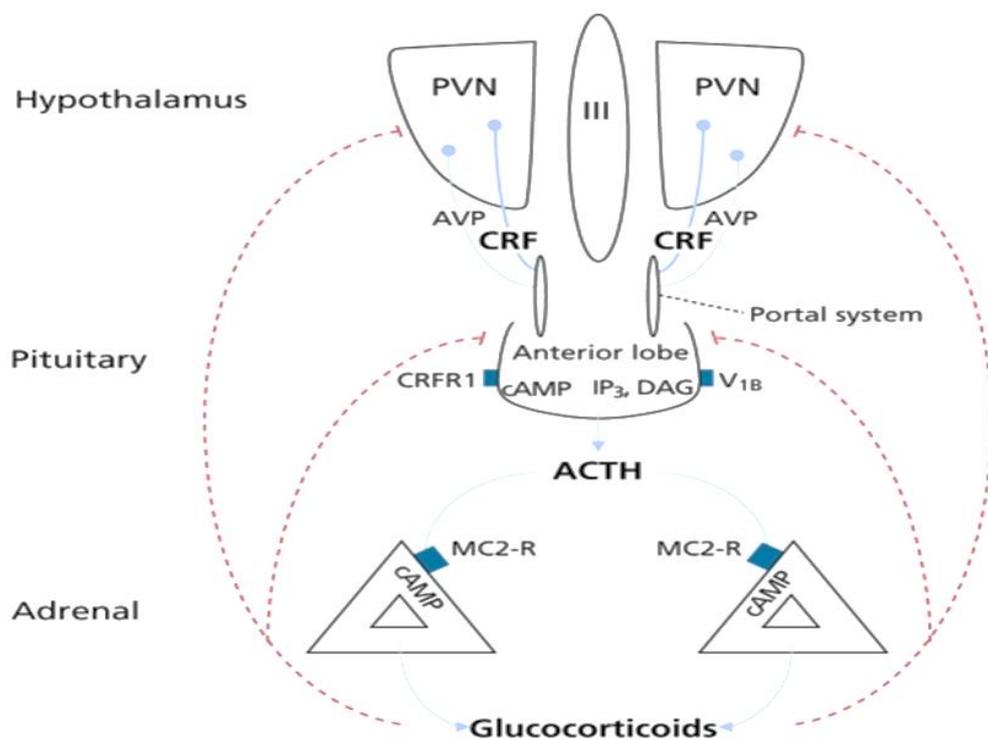


Figure 1: A schematic overview of the hypothalamic-pituitary-adrenal (HPA) axis. Red dotted lines indicate inhibitory effects. Blue lines indicate promoting effects. PVN=paraventricular nucleus; CRF=corticotropin releasing factor; AVP=vasopressin; CRFR1=CRF type 1 receptor; cAMP=cyclic adenosine monophosphate; ACTH=adrenocorticotrophic hormone; MC2-R=melanocortin type 2 receptor; IP3=inositol triphosphate; DAG=diacylglycerol (Smith & Vale, 2006).

Since the model provided by Taylor *et al.* (2000) is theoretical, the question now remains whether there is empirical evidence for tend-and-befriend behaviour in different species. And because the stress response is regulated by the HPA axis, one would expect the HPA axis to act differently in

males and females. To investigate if the tend-and-befriend response is the predominant stress response in females, examples of sexually dimorphic stress responses in different species will be looked at. First, the sexual differences in the HPA axis will be highlighted. Second, the effects of stress on *Drosophila melanogaster*, which show no parental care, will be examined. Third, the effects of stress on maternal care in primates will be discussed. Lastly, paternal efforts in primates will be inspected. They will then be evaluated to see whether these responses are better explained by the fight-or-flight response or by the tend-and-befriend response. It would be expected that females with higher parental care are more prone to show tend-and-befriend behaviour.

HPA axis

Taylor *et al.* (2000) proposed that the behavioural response of tending builds on the attachment-caregiving system. This bio-behavioural mechanism is a stress-related system, which has been explored for its role in maternal bonding and child development. It is thought to be especially activated in response to threats and offspring distress (Bowlby, 1988).

Tending could in this case be a crucial part of the infant attachment mechanism, which is critical for the development of normal biological regulatory systems in offspring (Hofer, 1994). According to a research performed by Liu *et al.* (1997), tending responses are directly linked to stress. In this research, they removed infant rats from their mothers, handled them by a human researcher and subsequently put them back with their mothers. The mothers immediately responded with intense grooming, licking and nursing behaviour. This directly nurtures and soothes the infants.

Thought to be at the core of the tending response are oxytocin and endogenous opioid mechanisms (Panksepp, Nelson & Bekkedal, 1997). Treatment of female rhesus monkeys with naloxone, an opioid antagonist, shows decreased caregiving and protective behaviour towards infants (Martel *et al.*, 1993). Another research in sheep showed that when naltrexone, a long-acting opioid antagonist, was administered, maternal behaviour was inhibited under experimental conditions (Kendrick & Keverne, 1989).

Multiple studies in different animal species show that central administration of oxytocin reduces anxiety and has mildly sedative properties in both males and females (Fahrbach, Morrell & Paff, 1985; Drago *et al.*, 1986; Witt, Carter & Walton, 1990; Carter *et al.*, 1992; McCarthy *et al.*, 1996; Uvnäs-Moberg, 1997a). This response appears to be stronger in females than in males. Other studies have found that intracerebroventricular administration of oxytocin increases maternal behaviour in ewes (Kendrick, Keverne & Baldwin, 1987; Kendrick *et al.*, 1997). This suggests oxytocin might have two roles to play when females are exposed to a threat, namely calming the stressed female and

promoting affiliative behaviour, for example towards their offspring (Taylor *et al.*, 2000). Grooming and nurturing the infants may help quiet them. These effects of oxytocin seem to be bidirectional, since oxytocin enhances affiliative behaviour, which then increases the flow of oxytocin (Uvnäs-Moberg, 1997b).

Several animal studies show the positive effects maternal contact has on offspring during stressful situations. Maternal touching in rats reduces HPA changes in infants, suggesting a weaker stress response (Pihoker *et al.*, 1993; Wang, Bartolome & Schanberg, 1996; Liu *et al.*, 1997). When rat infants are separated from their mothers, their corticosterone levels increase. When the mothers return, these levels decrease (Stanton, Gutierrez & Levine, 1988; Kuhn, Pauk & Schanberg, 1990). In rhesus monkeys, studies have found that after a threatening event, ventral contact between offspring and their mother cause rapid decreases in HPA activity and sympathetic nervous system arousal (Mendoza *et al.*, 1978; Gunnar *et al.*, 1981; Reite *et al.*, 1981).

Besides reducing stress, oxytocin might also enhance affiliation in stressful situations. In oestrogen-treated female prairie voles for example, central administration of oxytocin led to diminished aggression and enhanced social contact (Witt, Carter & Walton, 1990). Furthermore, exogenous administration of oxytocin in rats led to an increase in social contact and in grooming (Argiolas & Gessa, 1991; Witt, Winslow & Insel, 1992; Carter, DeVries & Getz, 1995). Research has also reported that animals prefer to spend time with animals with which they have previously experienced high brain oxytocin and endogenous opioid activities (Panksepp, 1998). Additionally, contact with a friend or a supportive person during stressful periods downregulates sympathetic and neuroendocrine responses to stress in humans. It also facilitates recovery from the physiological effects of acute stress (Kamarck, Manuck & Jennings, 1990; Gerin *et al.*, 1992; Lepore, Allen & Evans, 1993; Sheffield & Carroll, 1994; Gerin *et al.*, 1995; Kirschbaum *et al.*, 1995; Christenfield *et al.*, 1997; Kors, Linden & Gerin, 1997; Roy, Steptoe & Kirschbaum, 1998; Thorsteinsson, James & Gregg, 1998; Fontana *et al.*, 1999; Glynn, Christenfield & Gerin, 1999). Though both sexes experience the stress-regulatory benefits of social support, women seek such contact more often. Besides that, the stress-reducing benefits are more consistent when support is provided by a female rather than a male (Gerin *et al.*, 1995).

That females show more desire for social contact than males during stress might be modulated by endogenous opioid mechanisms. The endogenous opioid peptides released during stress are believed to influence social interactions (Benton, 1988; Jalowiec, Calcagnetti & Fanselow 1989). Animal studies suggest that when endogenous opioid levels are high, levels of social interaction and maternal behaviour increase as well. In the previously discussed research by Martel *et al.* (1993), besides showing reduced maternal behaviour when administered with naloxone, female rhesus monkeys also showed reduced social grooming of other females. Jamner *et al.* (1998) also found that administration of naltrexone increased women's time spent alone, decreased their time spent with friends and

Stress responses in *Drosophila melanogaster*

Drosophila melanogaster is an interesting example for a species without parental care. *Drosophila melanogaster* show several social behaviours, including courtship, aggression, mating, oviposition and social learning (Mery *et al.*, 2009; Sarin & Dukas, 2009; Fernandez *et al.*, 2010; Sokolowski, 2010; Dahunakar & Ray, 2011; Gorter *et al.*, 2016; Laturney & Billeter, 2016; Pasquaretta *et al.*, 2016; Schneider, Atallah & Levin, 2017). When stress research is being done on *Drosophila melanogaster*, stress is often induced by heat or electric stimuli (Fasolo & Krebs, 2004; Yang *et al.*, 2013; Rauschenbach *et al.*, 2014; Batsching, Wolf & Heisenberg, 2016; Ostrowski *et al.*, 2018). The research of Ostrowski *et al.* (2018) showed that when acute stress was applied for thirty seconds, by heat or electric shock, the stress response consisted out of two parts. The *Drosophila* first increase their activity during the shock. Afterwards, for up to five hours after the shock, they show a decrease in activity. Yang *et al.* (2013) suggested that the effect of the heat shock might be different in males and females. It has also been shown that individual or group rearing affects the stress response to electric shocks (Batsching, Wolf & Heisenberg, 2016).

A research performed by Lamers, Soto-Padilla & Billeter (2018) aimed to look at the effect of social interactions on stress in *Drosophila melanogaster*. Here heat was used as an external stressor. They divided the *Drosophila* in groups that were either individually reared or reared in a group of three flies. They also separated the males from the females. In the tests, they first let the *Drosophila* acclimatise to the arena for seven minutes at 16°C. Afterwards, the temperature was increased every minute by 2°C, stopping at 46°C. They determined that 36°C is the temperature in which activity is the highest in *Drosophila*. All *Drosophila* were tested individually and in a group. During the acclimatisation phase at 16°C, females showed no significant differences in activity between flies reared and tested individually or in a group. Males that were group reared however, showed a significant increase in activity compared to individual reared males. This also shows that there is a significant interaction between rearing group and sex, since the females showed no increase in activity when reared in a group.

When looking at the highest activity level at 36°C in females, there was also no significant difference between flies reared and tested individually or in a group. Males showed a significant increase in activity when tested as a group compared to when tested individually. This is true for both rearing conditions. In this case, the interaction between testing condition and sex is significant. These results show that rearing conditions only influence the initial activity in males and have no effect on the stress response created by increased temperature. They also suggest that the stress response increases in males when tested in groups.

To determine whether female *Drosophila* need to be able to sense other females to not increase their maximum activity in response to the increase in temperature, they also looked at the effects of pheromones. It has previously been shown that *Drosophila* have a sexually dimorphic pheromone profile (Billeter *et al.*, 2009). They use this to detect the sex of the flies around them. Females can be given a masculinised pheromone profile. When these masculinised females were tested in groups, they showed a significant increase in maximum activity levels compared to those individually tested at 36°C. The grouped masculinised females also showed increased maximum activity compared to grouped control females. By repeating the same test again with *Drosophila* that had knockouts for each of the five senses (except for vision, where they were tested in the dark), they determined that the sense touch is necessary to not increase activity in a group. This might suggest that females use touch to calm each other down when stress is induced by increasing temperatures.

Stress responses in female primates

As an example of species with high maternal care, primates will be studied. Several researches have been done on the effects of stress in primates, though mostly on groups of males. More stress research on wild female primates would be beneficial, however, as it offers a good model for human stress. For starters, wild female primates usually live in large social groups that consist of kin and nonkin. Both competitive and cooperative relationships are maintained in these populations. This allows for increased social stress and opportunities for its alleviation to be observed. Secondly, wild female primates are confronted with several environmental stressors and traumatic events. These present a challenge to their reproduction and survival, but can also damage an individual's social relationships (Cheney & Seyfarth, 2009).

Female-female relationships in primates are typically characterised by frequent grooming, close spatial proximity and acts of obtaining coalitionary support (Silk, Seyfarth & Cheney, 1999; Silk, Alberts & Altmann, 2003). Grooming has been shown to dampen elevated stress responses in female rhesus macaques (Gust *et al.*, 1994). These social relationships are hypothesised to be valuable to adult females because they enhance the prospects of obtaining coalitionary support in within-group contests (Sterck, Watts & Schaik, 1997) or increase tolerance from stronger group members (Henazi & Barret, 1999). Furthermore, social relationships between females may provide a benign environment for raising and socialising their offspring (Cheney & Seyfarth, 2009). Social relationships with adult males may also be valuable to females due to male associates protecting females from harassment (Smuts, 1985) and support their offspring in agonistic interactions (Buchan *et al.*, 2003). In some

populations, males also protect the females' infants from predators and infanticidal attacks (Palombit, 1999).

The effects of these social interactions have been studied in wild savannah baboons, *Papio cynocephalus*. These baboons are very sociable and live in large mixed-sex groups. The females remain in their natal group throughout life, whereas the males disperse when they mature (Melnick & Pearl, 1987). Silk, Alberts & Altmann (2003) compared the sociality of females in several well-habituated baboon groups to the survival of their offspring. Relative offspring survival per female was measured by tracking the proportion of offspring that survived their first year of life. Females who were measured to have high sociality scores had offspring with relatively higher survival than those of females who were measured to have low sociality scores. While high dominance is associated with high values of both sociality scores and relative infant survival, the relationship between sociality and infant survival remained significant after accounting for dominance rank statistically.

In a research performed on a group of free-ranging chacma baboons (*Papio cynocephalus ursinus*), the strength of social bonds and offspring survival were compared. In this research, offspring survival was measured by tracking the proportion of offspring that survived the first five years of their life. They found that females who formed strong social bonds with other females lived significantly longer than the offspring of females with weaker social bonds. Furthermore, offspring survival was not affected by their mothers' dominance rank or their own sex. Offspring survival was especially higher in females who had stronger bonds with their mothers and adult daughters (Silk *et al.*, 2009).

Another research that focused on free-ranging female chacma baboons (*Papio hamadryas ursinus*) looked at the effects of predation. Females that lost a close relative experienced significant increases in glucocorticoid (GC) levels. The increases remained for weeks after the death of their relative. These females increased their grooming rate and grooming partners after the relative's death. It appeared that females compensate for their loss by broadening and strengthening their grooming networks. The GC levels soon returned to baseline, perhaps as a result of their increased grooming (Engh *et al.*, 2005).

Wittig *et al.* (2008) observed the effect of social instability in a group of baboons from the Okavango Delta in Botswana. After an eight-month period of relative social stability, the resident alpha male was challenged by a potentially infanticidal male. The resident alpha male disappeared afterwards and the male immigrated into the group. This caused the GC levels to rise significantly in all females, indicating elevated stress. A faster decrease of GC levels was observed in females who were at lower risk of infanticide however. Three factors were observed which suggest that females rely on a focused grooming network as a coping mechanism to alleviate stress. First, the grooming networks of all females became less diverse in the weeks after the arrival of the male. For most females, these focused grooming networks consisted of close relatives. Second, the females that already had a

focused grooming network showed a less dramatic rise in GC levels than females that had a more diverse grooming network. Third, females that contracted their grooming network the most experienced a faster decrease in GC levels the following week. This leads to believe that strong bonds with a few preferred partners allow female baboons to alleviate stress induced by social instability (Wittig *et al.*, 2008).

An explanation for why strong social bonds lead to high offspring survival might be that females with stronger social bonds are less spatially separated. This causes the offspring to be less vulnerable for predators when they are feeding during the day and sleeping in trees at night (Silk *et al.*, 2009). Another reason might be that females with strong social bonds may be better shielded from social conflicts, allowing them to feed more efficiently (Silk *et al.*, 2003). A third explanation, as just discussed, is that females who have more focused social networks experience lower GC levels than other females (Wittig *et al.*, 2008).

The effects of stress on paternal care

The effects of stress on males that provide paternal care are not fully clear (Wynne-Edwards & Timonin, 2007). Some relationships between stress hormones and paternal efforts have been found. For example, some studies found a correlation between faecal GC (fGC) level increases and paternal effort in meerkats (*Suricata suricatta*) (Carlson *et al.*, 2006) and prairie voles (*Microtus ochrogaster*) (Bales *et al.*, 2006). This effect is less clearly seen in monogamous primates (Nunes *et al.*, 2001; Cavanaugh & French 2013). In male Barbary macaques (*Macaca Sylvanus*), time spent with infants is associated with increased levels of fGC. However, the interactions of males with infants tend to function primarily to facilitate social bonds among males, not for protection (Henkel *et al.*, 2010).

In polygynous species, for example baboons, males tend to invest less care in offspring than males in monogamous or cooperatively breeding species. Paternal care is not entirely absent however. Paternal care might be shown through indirect acts, for example when a male defends the territorial integrity of his social group. Paternal care can also be shown directly, when a male defends offspring against predation or an infanticidal conspecific (Clutton-Brock, 1991). Investment in offspring for males is costly however.

Baboons are a great example for the potential costs of mating and paternal efforts in a polygynous species. Male baboons compete with each other through aggressive threat displays and escalated fights (Kitchen *et al.*, 2003, 2005). Furthermore, access to females is skewed towards dominant males (Bulger, 1993; Weingrill *et al.*, 2000; Alberts *et al.*, 2006). Males do show paternal care, however, by forming 'friendships' with lactating females. These friendships serve to protect

infants against harassment and potential infanticide. Infanticidal attacks are aggressively defended by these males, which sometimes leads to injuries (Palombit *et al.*, 1997, 2000; Kitchen *et al.*, 2005). Most of these male friends are long-time residents who are likely or actually the fathers of the infants they are protecting (Seyfarth, 1978; Smuts, 1985; Palmobit *et al.*, 1997; Palombit *et al.*, 2000; Weingrill, 2000; Buchan *et al.*, 2003; Clarke *et al.*, 2009; Nguyen *et al.*, 2009; Huchard *et al.*, 2010; Moscovice *et al.*, 2010; Onyango *et al.*, 2013). These friendships appear to function mostly to reduce the threat of infanticide and harassment to females. Currently, no evidence supports the notion that friendships function as a male strategy to improve future mating opportunities (Palombit *et al.*, 2000; Weingrill *et al.*, 2000; Nguyen *et al.*, 2009; Moscovice *et al.*, 2010). Whether friendships constrain a male's mating opportunity is also not known.

In chacma baboons (*Papio hamadryas ursinus*), infanticide occurs at relatively high rates (Cheney *et al.*, 2004). Friendships also appear to be strong. Observation and playback research has shown that male chacma baboons react strongly to the distress calls of their female friends and their offspring (Palombit *et al.*, 1997; Moscovice *et al.*, 2009). As mentioned previously, friendships are potentially costly to males due to the increased risk of injury during infanticidal attacks (Kitchen *et al.*, 2005). Besides physical injury, the threat of infanticide after immigration of a dominant male can lead to costs in the form of increased stress levels. The fGC levels of lactating and pregnant females are increased when a potentially infanticidal male immigrates into their group, even though they are not at a physical risk (Beehner *et al.*, 2004; Engh *et al.*, 2005; Wittig *et al.*, 2008). When females had male friends however, they showed significantly lower fGC levels than females without friends. This might reflect the reduced threat to their infants (Beehner *et al.*, 2004; Engh *et al.*, 2005). For males however, it might be the other way around. A study that investigated the relation between friendship status and fGC levels in males found a non-significant trend for males that befriended females to show higher fGC levels than males that did not befriend females after the arrival of an immigrant male (Bergman *et al.*, 2005). This suggests that there is a cost to paternal care.

The absence of additional data on the amount of costs males face in polygynous mammals lead Cheney *et al.* (2015) to attempt to extend these previous findings in male chacma baboons. They found, in contrast to Bergman *et al.* (2005), that unstable periods (i.e. high rates of (attempted) infanticide) were not marked by higher rates of aggression among males. The observed rates of aggression in unstable months suggested that there were lower rates of male-male aggression than in stable months. Cheney *et al.* (2015) also found that, while both males with and without friends showed an increase in fGC levels during unstable periods, males with friends showed a two-fold increase over males without friends. A significant interaction between dominance rank and friendship status seemed to suggest that lower-ranking male friends tended to have higher fGC levels than higher-ranking friends.

Cheney *et al.* (2015) additionally found a likewise correlation between unstable periods and consort status. As with the males with and without friends, both consorting males and non-consorting males had elevated levels of fGC during unstable periods. Here, the consorting males had a greater increase in fGC levels than non-consorting males. A significant interaction between dominance rank and consort status indicated that lower-ranking males had higher fGC levels than higher-ranking males engaged in sexual consortships.

Furthermore, they examined whether having a friendship during unstable periods might have constrained a male's ability to form consortships. They examined the proportion of days that each male in a group of consorted males was observed in a consortship, while also engaged in a friendship. This was observed in both unstable and stable periods. All observed males spent a smaller proportion of days in consortship during unstable periods (Cheney *et al.*, 2015).

When looking at only the dominance ranks, it was shown that high-ranking males exhibit higher fGC levels than low-ranking males. However, during stable periods, no relation was found between dominance rank and fGC levels, except for alpha males. Their fGC levels were higher than those of beta males in stable periods (Cheney *et al.*, 2015). This might be due to the stress of maintaining the alpha male rank, which is subject to frequent challenges. This was shown to be the case in yellow baboons (Gesquiere *et al.*, 2011).

Discussion

The discussed findings seem to suggest that stress responses are sexually dimorphic in several species. In *Drosophila* for example, males and females were subjected to the same stressors. Females however showed a lower stress response than males in certain situations. When tested in a group while looking at the highest activity level, females showed a lower stress response compared to the group tested males. Since it was shown that touch was the necessary sense for females to not increase their overall activity, this might imply that the females use touch to calm each other down. While the tending part of the tend-and-befriend theory is directed at tending to offspring, perhaps tending to conspecifics might also alleviate stress responses. As previous studies have shown that grooming helps to alleviate stress in several species (Gust *et al.*, 1994; Liu *et al.*, 1997; Uvnäs-Moberg, 1997b; Engh *et al.*, 2005; Wittig *et al.*, 2008), perhaps what was observed here might be a form of grooming as well. Research has shown that *Drosophila* are capable of forming social networks (Ramdya, Schneider & Levine, 2017). Seeing as the rearing situation had no influence on the stress response in females however, it would seem that befriending does not have an influence on the stress responses in female *Drosophila*.

The group tested male *Drosophila* showed higher activity levels than females did during the stress test. Since males were likely to show fleeing behaviour in this situation, it would suggest that they were showing a fight-or-flight response. Vice-versa, it would seem that the female *Drosophila* were showing a tend-or-befriend response, as they alleviated each other's stress response when group tested.

When looking at certain primates, where maternal care was high, it has been shown that females groom other females to alleviate stress. They form social relationships with each other, which increase offspring survivability. The stronger the social bonds, the more likely the offspring are to survive. These are clear examples of tend-and-befriend responses to stress, as befriending other females led to increased offspring survival.

While species that show mostly paternal care have not been discussed, due to stress research on these species being unavailable, paternal efforts in primates have been studied. Besides directly protecting offspring from threats, males also befriend females and form consortships with them. Forming friendships leads to reduced threat of infanticide and harassment of the befriended female. This does come at a cost to the male however, as it increases the risk of injury during infanticidal attacks. Furthermore, befriended males show elevated fGC levels after the arrival of an immigrant male compared to non-befriended males. This suggests that male primates also show tend-and-befriend behaviour, besides fight-or-flight behaviour. The observed decrease in male-male aggression during stressful unstable periods might also be a tend-and-befriend response. Instead of fighting, perhaps the males tended to their offspring in anticipation of infanticidal attacks. On the other hand, it could also be seen as a fleeing response to the new threatful male. Future research could shed a light on this unclarity.

In contrary to the female primates, it seems that tend-and-befriend behaviour elevates stress in males rather than alleviates it. An explanation as to why males engage in these costly behaviours might be to increase their fitness. Protecting their offspring increases the chance of them surviving, thus increasing the fitness of the male. Another explanation might be that because the males that form friendships are not the alpha male, their chances to mate successfully might be limited. Befriending might be a way for the males to ensure successful mating opportunities.

While the effects of stress on males that exhibit paternal efforts have been looked at, this cannot be used to draw conclusions on the effects of stress on males that show high paternal care. Stress research on species that show high paternal care could provide interesting results. Depending on the results found, it might indicate that a tend-and-befriend response is a more suitable stress response for animals that perform most of the parental care. The fact that tend-and-befriend behaviour surfaced in primates that exhibited paternal efforts might support this. The observed stress responses in *Drosophila* seem to counteract this however. Since *Drosophila* do not show parental

behaviour, but females do show a tend-and-befriend response, this might indicate that the stress response is just associated to the sex. To confirm this however, more stress research on sex differences should be done on species which show high paternal care and species which show no parental care.

In this paper, only *Drosophila* and several primates were investigated. This is only a small portion of the species in the world however. To gain a better understanding on sex differences in stress responses, more species should be investigated.

In conclusion, there exists evidence for tend-and-befriend responses in *Drosophila* and several primates. These responses have been shown in females that show no parental care, show high maternal care and in smaller part in males that show paternal efforts. More research should be done on species with high paternal care and on sex differences of stress in general to gain a better understanding of them. This might improve treatment opportunities of stress-related disorders.

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