Imperial College London

Final-Year Research Project Cover Sheet

Name of Student: Sorrell Cowen

Degree Stream: Biological Sciences

Date: 05/05/2020

Word Count: 7506

Project Title:

The Effect of Social Structure on Homosexual Behaviour in Male Rhesus' Macaques

Type of Project:

Practical Project Data Project (10 weeks) – DP1/DP2

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ABSTRACT

Homosexual activity persists across many primate species, with several current competing explanations as to why it exists. The social structure of primate populations is a factor that may affect the sexual behaviour of individuals. Two theories of homosexual activity that involve the structure of the population are firstly, the theory of affiliation, and secondly, the theory of access to reproductive opportunity. The theory of affiliation states that same-sex mounting occurs to reinforce social bonds. The theory of access to reproductive opportunity states that individuals are more likely to engage in same-sex mounting if they have limited access to the opposite sex due to the individual's position within the population's structure. For this study, the population observed was the group of free-ranging rhesus' macaques on the island of Cayo Santiago, and the investigation looked at spatial proximity count data, as a proxy measure of social structure, and male sexual mounting to analyse these two theories. It was found that subadult males engaged, on average, in a significantly higher frequency of homosexual mounts than adult males, and subadult males were found in close proximity to a significantly lower average number of females than adult males. This study provides evidence that homosexual activity could be used as an affiliative mechanism in the formation of novel same-sex social bonds as subadult males develop. Furthermore, a significant relationship was found between male proximity to females and homosexual mount involvement. Males that were observed in close proximity to fewer females participated in a higher proportion of homosexual mounts. This suggests males with limited access to females engaged more frequently in same-sex sexual behaviour. With these results, it is clear that the social structure of rhesus' macaques does influence a male's likelihood to participate in homosexual mounts, but it is through a multitude of factors, of which male social affiliation and male reproductive opportunity access are only part of the explanation. This study of male rhesus' macaques will contribute to a developing database that offers insight into the fundamental mechanisms of primate homosexual behaviour.

INTRODUCTION

Primates are highly sociable mammals and have complex relationships formed from great cognitive understanding (Cheney, Seyfarth & Smuts, 1986). The existence of sociality has been an extensively researched topic, to investigate causes of intricate social behaviour within the order Primates (Seyfarth & Cheney, 2012). This investigation specifically focuses on how the social structure of rhesus' macaques can influence male homosexual activity. Homosexual behaviour in rhesus' macaques is poorly understood, even though the Old-World monkey is one of the most intensively studied species in socio-biology (Agar & Mitchell, 1975). Understanding convoluted primate behaviour such as homosexual activity could even improve knowledge about how humans act, and why certain primate social interactions occur (Raichlen & Polk, 2013).

The structure of a species' population is a crucial variable in understanding its behaviour (McGrew, Marchant & Nishida, 1996). The largest range of vertebrate social structures known is found in Primates (Janson, 2017). This range consists of examples such as monogamous pairing in gibbons, or one-male groups in colobus monkeys (Dunbar, 1988). Primate social systems may also have temporal instability, seen in fission-fusion societies among macaque species (Sueur, Petit & Deneubourg, 2010). A fission-fusion system consists of the constant movement of subgroups and individuals between larger groups. The differences in primate group structure can signify differences in behaviour and how individuals interact with one another (Hinde, 1976). For a multi-male multi-female grouped species such as macaques (Rawlins & Kessler, 1986), their behaviour around others is notably different from species such as orangutans, who exist as a semi-solitary species (Hanazuka et al., 2013). Macaques have much higher frequencies and a greater variation of playful interactions than orangutans (Yanagi & Berman, 2014). This is evidence of the direct effect the social system can have on a species' behaviour.

There are many strategies available to attempt to measure primate social structure. For example, social network analysis (SNA) is an approach that provides an in-depth analysis of all interactions that

occur within a social structure, by looking at a population as a network of nodes linked together in a visual representation of how individuals are a part of the overall system (Kasper & Voelkl, 2009). This method is precise but carries spatial and temporal limitations. A social network analysis can only reflect a population at a point in time (Wey et al., 2008), so other methods are required to measure structure over longer periods less exhaustively. Dominance ranking can help measure population structure in certain primate species where interaction frequency is high (Bayly, Evans & Taylor, 2006). A dominance hierarchy is a complete measure of how a society is organised, and this can be correlated with behaviour under certain conditions (De Vries, 1998). However, methods involving dominance have shortcomings when applied to highly dynamic primate societies (Neumann et al., 2011). This method also has drawbacks when considering demographics such as juveniles, who may not be structured in society by dominance (Janson, 2017). Alternatively, spatial proximity counts are a simple yet effective way to measure a population's structure (Zhang et al., 2012). It involves observations of the distance between individuals, as well as how often individuals are seen in close proximity to one another. These distances give general patterns of how an individual is embedded within its population's social structure. These proximity measures are important simply because primates are more likely to interact with each other when in close spatial proximity (Zhang et al., 2012). However, proximity is a proxy measure of social structure and interaction. This is because distance is quantitative and easily measured, whereas behaviour is qualitative and much more complex.

Using social proximity counts is one way that could be used to understand homosexual activity within a group. Homosexual activity is an apparent evolutionary paradox, though there are competing explanations for its persistence in numerous species (Poiani, 2010). Despite these explanations, homosexual activity seems to undermine the mechanism of sexual reproduction, which is essential for a species to survive and evolve. A priority of non-reproductive sexual activity over reproductive sexual activity would be detrimental to an organism's fitness, as it would decrease the chance of offspring production (Kirkpatrick et al., 2000). However, homosexual activity continues to exist in many species, such as humans and tortoises (Bonnet et al., 2016), and it has also been observed in certain species of

beetles (Poiani, 2010). To explain homosexual activity as an evolutionary paradox has its flaws, as the fitness costs of homosexual activity are still largely unknown (Savolainen & Hodgson, 2016).

There are several hypotheses as to why homosexual behaviour exists so abundantly throughout different lineages (Sommer & Vasey, 2006). Using measures of social proximity can help explain how social structure affects such an apparent paradoxical behaviour. Social proximity in this case can be a proxy measure of affiliative social bonds or skews in male reproductive access to females, both of which are theories explaining the existence of homosexual activity (Sommer & Vasey, 2006). In some cases of nonhuman primates, homosexual activity can be a behaviour used to form alliances (Fairbanks, McGuire & Kerber, 1977). In other cases, it occurs to express dominance, as seen in female stumptail macaques (Chevalier-Skolnikoff, 1976). However, display of dominance and homosexual activity show no consistent relationship in many studies (Rendall & Taylor, 1991). Using proximity data, the hypothesis of affiliation can be tested, where homosexual activity could be a behaviour associated with reinforcing social bonds, as seen in female chimpanzees (Anestis, 2004). Furthermore, proximity data can be used as a proxy for access to reproductive opportunity, allowing an examination of the hypothesis that links high levels of homosexual activity to an individual's limited access to the opposite sex (Dunbar, 1988).

For this study, the focus is on homosexual activity in male rhesus' macaques. Both male and female rhesus' macaques exhibit homosexual activity (Vasey, 1995), but this investigation will solely focus on males and the impact of social structure on this behaviour. Homosexual activity is expected to be inversely linked to female access, measured using the proxy of proximity. The same pattern has been seen in female rhesus' macaque homosexual behaviour, when observing male access (Wolfe, 1986). Male homosexual behaviour is also expected to be linked with the social bonding of males with other males (Oi, 1990), again using proximity counts to measure the affiliation of individuals.

Rhesus' macaques are known to have a largely multi-sex group structure, but all-male and all-female groups can also exist (Dunbar, 1988). Females usually stay within their natal social troop, whereas

males disperse in the population and exist mostly in non-natal groups (Rawlins & Kessler, 1986). Troop sizes vary within populations of rhesus' macaques (McMillan & Duggleby, 1981).

Homosexual activity within rhesus' macaques occurs at considerably high levels in males, with lower levels still occurring in females (Altmann, 1962). It is understood that homosexual behaviour in this species is multifactorial, with dominance, partner preference, stimulation and past experience all impacting intra-individual variance in the behavioural phenotype (Akers & Conaway, 1979). To better understand homosexual activity in this species, factors associated with social structure dynamics need to be examined as well, for a more extensive overview of male homosexual behaviour in rhesus' macaques.

The main aim of this study is to understand how the social bonds and the social structure of the population will affect homosexual activity in male rhesus' macaques. This paper will explore how proximity is a key factor in determining the structure of primate social systems (Sugiura, 2007), and how this in turn may lead to substantial results about the possible causes of homosexual actions. This involves a discussion of male rhesus macaque behaviour and population structure, as well as a combined analysis of all results. First, looking at general behaviour and proximity counts will be beneficial in understanding how they are linked. The focus will then primarily be on the discussion of the different theories for homosexual activity that are associated with social structure, and which theories can be given the most confidence in populations of free-ranging rhesus' macaques. It will also include a debate about the use of proximity as a proxy measure of social structure, and how this can have a number of caveats. Conclusions can then be made about why the proximity between individuals is important, and how it can link as a general theme in terms of homosexuality in other species (Gadpaille, 1980).

METHODS

The study population of Rhesus' Macaques is found in Cayo Santiago, an island of Puerto Rico. It consists of 1755 individuals (May 2019 Data). This is one of the oldest continuously managed free-ranging populations of rhesus' macaques (Rawlins & Kessler, 1986). On the island, the troop sizes of macaques range from 30 individuals to over 500. Many studies have been carried out on this population, due to their close relation to humans, using the primate species as a model organism (Hernández et al., 2007). Rhesus' macaques were transferred from Northern India to Cayo Santiago in 1938, and now the free ranging population exists in larger numbers on the island (Rawlins and Kessler, 1986). The monkeys are managed by humans, with drinking and feeding points situated around the field centre (Marriott, Roemer & Sultana, 1989). Considering the lack of some ecological pressures, such as predation, the colony is not seen to be significantly different from the ecology of wild populations (Balasubramaniam et al. 2014). The population has continued to reproduce very successfully, with individuals occasionally having to be removed from the site in order to avoid overpopulation (Hernández-Pacheco et al., 2013). Due to the constant management, yet free-ranging nature, this population has characteristics to enable the measure behaviour of primates on a much larger scale than seen in laboratories, while having some control over the area in order to keep results consistent and reliable (Widdig et al., 2016). The sociality of this species of Old-World monkey in particular means it is an ideal population to study, due to their communal nature and repeated frequent interactions (Balasubramaniam et al., 2014).

With an extremely active population, different approaches were needed to collect the data. Two techniques were carried out simultaneously within the timeframe. The observation protocol was chosen as a combination of ad libitum sampling and scan sampling (Dawkins, 2007). Data collection occurred between 05/03/2019 and 31/05/2019 inclusive. All observations were recorded on smartphone hardware using behavioural and demographic databases, built on HanDBase (DDH

Software 2011). The data was collected by Jackson Clive, a research postgraduate at Imperial College London.

The scan sampling was important to this investigation in particular, as it measured specific behavioural states and the proximity of different demographics to the individual carrying out the particular activity. The time of study was from 7am to 2pm each day. The states observed were Resting, Travelling, Socialising, Chow Feeding and Foraging/Other Feeding. Scans were conducted at 10-minute intervals, with adult males and subadult males the focal subjects of the recording. The different demographics were classed into Male (5+ yr), Female (3+ yr), Subadult Male (3.5-5 yr) and Juvenile (< 3 yr). The number of each demographic within 2m of the Male/Subadult Male carrying out the specific activity was recorded. The only Animal Identification (ID) noted was the ID of the focal male. The ID of a macaque was recognisable by the observer prior to the start of the data collection. All focal males within the line of sight of the observer were recorded at every interval, with each having their own demographic proximity measures. This investigation focuses on how overall proximity to males' changes, broken down into specific age and gender categories. The scan data is used to understand patterns in the social structure of the population. This can then be linked to the ad libitum data in order to explore how distance between individuals- the proxy for social structure- may influence sexual behaviour.

Ad libitum sampling can be used to measure homosexual activity (Martin, Bateson & Bateson, 1993). This technique involved recording every event observed that was part of a prepared ethogram that defined sexual interactions. The time and period of data collection was the same as the scan data. The definition of sexual activity was defined as mounting alone. Using mounts as the measure of sexuality is considered a more robust definition, as it excludes behaviour that could be purely social, such as embracing. The hypothesis being tested requires homosexual behaviour to be measured quantifiably, and the volume of mounting data was sufficient to be able to reach valid conclusions. Mounting is a key process of sexual behaviour in rhesus' macaques and can also be observed easily during data

collection (Maestripieri & Wallen, 1997), allowing for a definitive, albeit simplistic, measure of homosexual activity. The ID of both the actor and recipient in a mounting event was recorded. If the mount was heterosexual, the recipient ID was recorded as an Unknown Female (FUN) to avoid confusion and clearly separate heterosexuality from homosexuality. The number of females observed within 10m of the mounting event was also recorded. This was key in identifying any proximity patterns associated with individual occurrences of mounting.

Census data was provided by the Cayo Santiago research centre. It included the Animal ID, sex, age, and status of each monkey. The status was a note of whether the monkey was currently In Cayo Santiago, Dead, or Removed from the island. The census was crucial into determining the sex of each monkey in particular, to confirm that all homosexual mounts consisted of two males. It was also key in defining whether an identified monkey was an adult male or a subadult male. This was important in order to analyse any effect male age may have on social structure, which could cause differences in homosexual activity between the two age categories.

The software used to analyse the data collected was RStudio Version 1.2.1335 (R Core Team, 2019). This investigation focuses primarily on the analysis of homosexual activity, but the analysis of general underlying proximity patterns between individuals was key to first determine the social structure of the Cayo Santiago Rhesus' Macaques. This was also so proximity counts could be confirmed as a valid proxy measure of social structure. The analysis commenced with the assessment of proximity measures to identify patterns that represented the structure of the population (Ryder et al., 2012). This involved specifically looking at the proximity of different demographics to males across all behaviour. The main approach was to analyse male and female proximity, as this aspect of social structure could then be linked to sexual activity. Two-sampled T tests were the analysis of choice to compare the mean number of each demographic in close proximity to males. This was a representative test for the exploration of assumptions about a male's interactions within its population's social structure (Barton, Byrne & Whiten, 1996). Adult males and subadult males were then assessed in

terms of proximity differences to females, and differences in involvement of homosexual activity. This allows for the analysis of the affect age and male affiliation may have on homosexual behaviour.

Homosexual activity and the link with social structure was examined using a combined analysis of the ad libitum and scan data. The relationship between the frequency of mounting events and the proximity of females to mounting events was assessed first. Then, the average proximity of females to identified males across all behaviour was calculated. Each individual male observed had its own female proximity measure, obtained from the scan data. The sexual activity of these males was then modelled against their average female proximity measures using a linear regression analysis . Sexual activity was split into four measures: the individual male frequency of involvement in a homosexual mount, the individual male frequency of being the mounter (the actor) in a homosexual mount, the individual male frequency of involvement in a heterosexual mount, and the individual homosexual activity ratio of the male involvement in mounts (Homosexual Mounts : Total Mounts). For the measure of an individual's ratio, the classification of involvement was chosen as the events when the individual was the actor in the mount. This was chosen for accuracy, as a male was only ever seen as the actor in a heterosexual mount. The only variable is the recipient of the mount, with homosexual and heterosexual mounts often indistinguishable otherwise (Vasey, 1995). Individual ratios represented the activity of acting in a sexual mount. This is different to the individual's frequency of involvement in a homosexual mount, as these frequency measures included the times when the male was mounted (the recipient) as well, with recipient data included to make a comparison between overall homosexual mount involvement and solely being the actor in a homosexual mount. Actor mount data was the most reliable to use however, for a valid comparison between homosexual and heterosexual mount data.

RESULTS

To begin assessment of the link between social structure and general behaviour, the difference in the mean number of other macaques within 2m of males for each of the five behavioural states observed

in the scan data was analysed. Determined by a one-way Analysis of Variance (ANOVA), there was a statistically significant difference in the group means ($F(3,77858)=103.6$, $p=<0.001$). Therefore, the proximity of other demographics to males significantly differs for each behavioural state identified.

The next step was to analyse specific demographic proximities. Across all behavioural states, the number of adult males within 2m of males (mean (M)=0.050) was significantly lower than the number of females within 2m of males (M=0.071), ($t=-6.80$, $df=33710$, $p=<0.001$). Similar statistical results were obtained for the average number of subadult males in close proximity to males compared to females in close proximity to males. The number of subadult males within 2m of males (M=0.025) was significantly lower than the number of females within 2m of males (M=0.071), ($t=-16.39$, $df=29278$, $p<0.001$). Males, on average, were found in close proximity to females significantly more often than to other males.

The next analysis tested the effect of social structure and age on behaviour. The number of females within 2m of adult males (M=0.117) was significantly higher than the number of females within 2m of subadult males (M=0.060), ($t=7.43$, $df=4149$, $p<0.001$). When comparing the frequency of homosexual activity between age groups, the average frequency of homosexual mount involvement per adult male (M=1.37) was significantly lower than the average frequency of homosexual mount involvement per subadult male (M=3.53), ($t=-2.46$, $df=75.9$, $p=0.0164$). Only males observed as an actor or recipient in at least one same-sex mount were included.

Exploring homosexual activity further required the assessment of the relationship between the male proximity of females and male mounting events. Figure 1 shows a general decrease in the frequency of mounts as the number of females in close proximity to the individuals mounting increased. The main difference is that a much larger number of homosexual mounts occurred when there were no females within 10m of the mount compared to heterosexual mount frequency. Another observation is the small spike of mount frequency on both plots when the number of females within 10m of the mount is 15+. The number of females within 10m of a homosexual mount (M=2.16) was significantly

lower than the number of females within 10m of a heterosexual mount (M=3.62), (t=-6.09, df=1127, p<0.001). The character value 15+ was adjusted to be the numerical value of 15 in the statistical comparison of means.

Figure 1

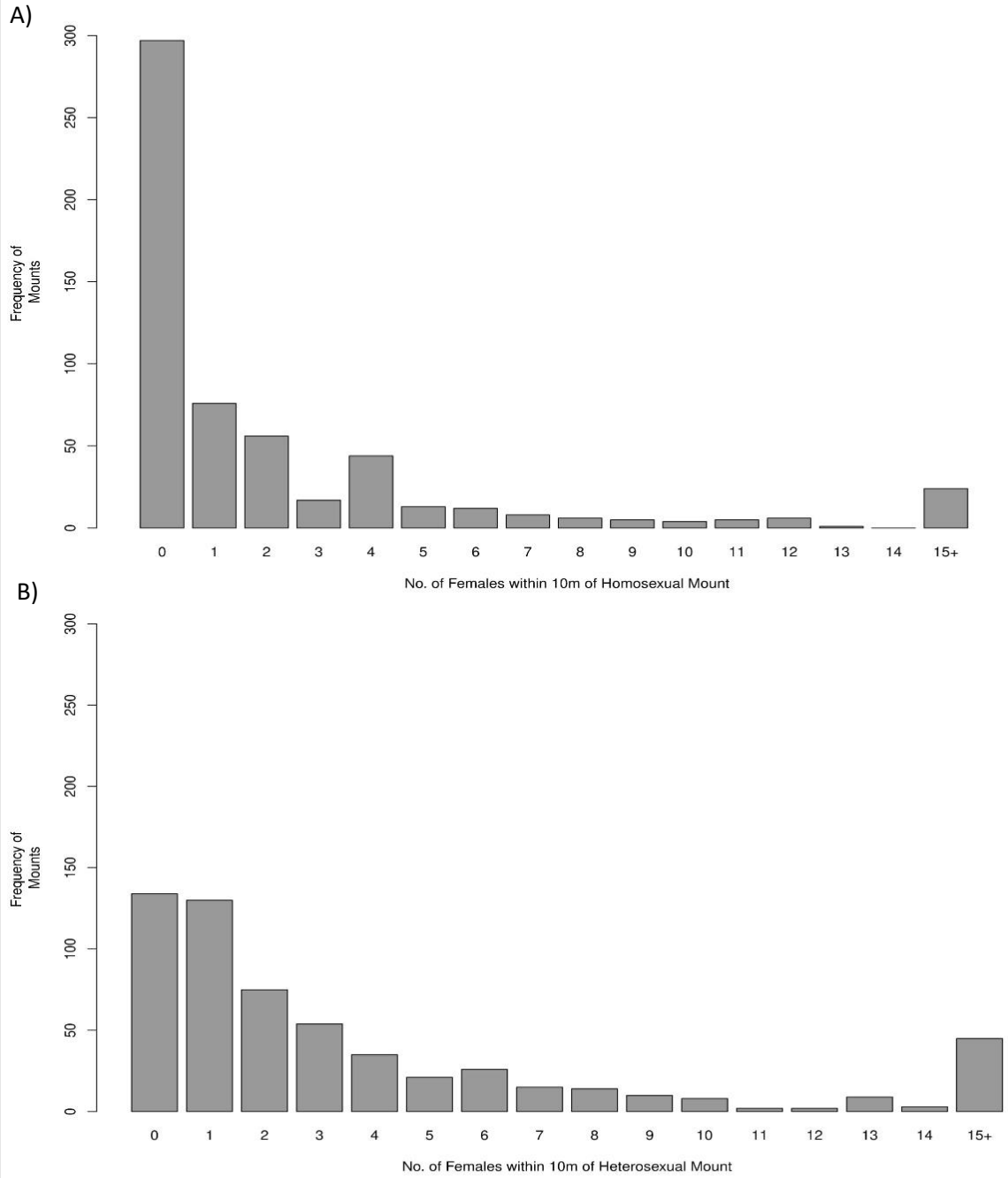

Figure 1. Graphs showing the relationship between the number of females in close proximity to mounting events and the frequency of A) male homosexual mounting events (n=930) and B) male heterosexual mounting events (n=781).

Finally, male sexual activity and its relationship with overall social structure was analysed. Individual males were included if they were observed during the scan sampling. The average number of females within 2m of males across all behaviour ranged from 0 to 0.769.

The first relationship tested was the frequency of male homosexual mount involvement against the average number of females in close proximity to males across all behaviour. The latter is the proxy measure for the social structure of males and females. A non-significant regression equation was found (R^2 =0.017, p=0.056), (see Figure S1). The individual mount frequency counts included events where the male was an actor and a recipient.

Figure 2 shows the relationship between the frequency of being the actor in a homosexual mount and the proxy measure of social structure. This was carried out for a reliable comparison between homosexual and heterosexual activity, as males were only actors in heterosexual mounts.

Figure 2

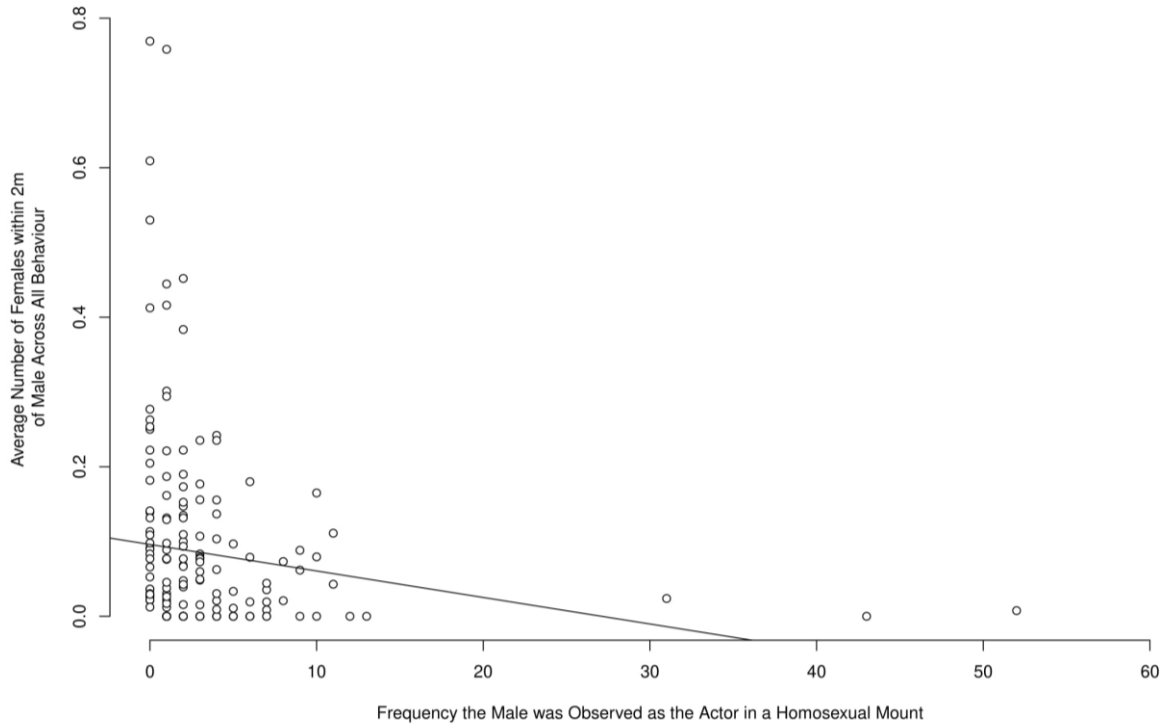

Figure 2. Graph showing the relationship between actor homosexual mount frequency and a male's association with females in its social structure. Figure includes a linear regression analysis. A significant regression equation was found (R^2=0.025, p=0.033). n=179.

Figure 3 shows the relationship between male heterosexual mount frequency and the average number of females in close proximity to males across all behaviour, as a comparison to homosexual mount frequency. Note the male was only ever observed as an actor in this case.

Figure 3

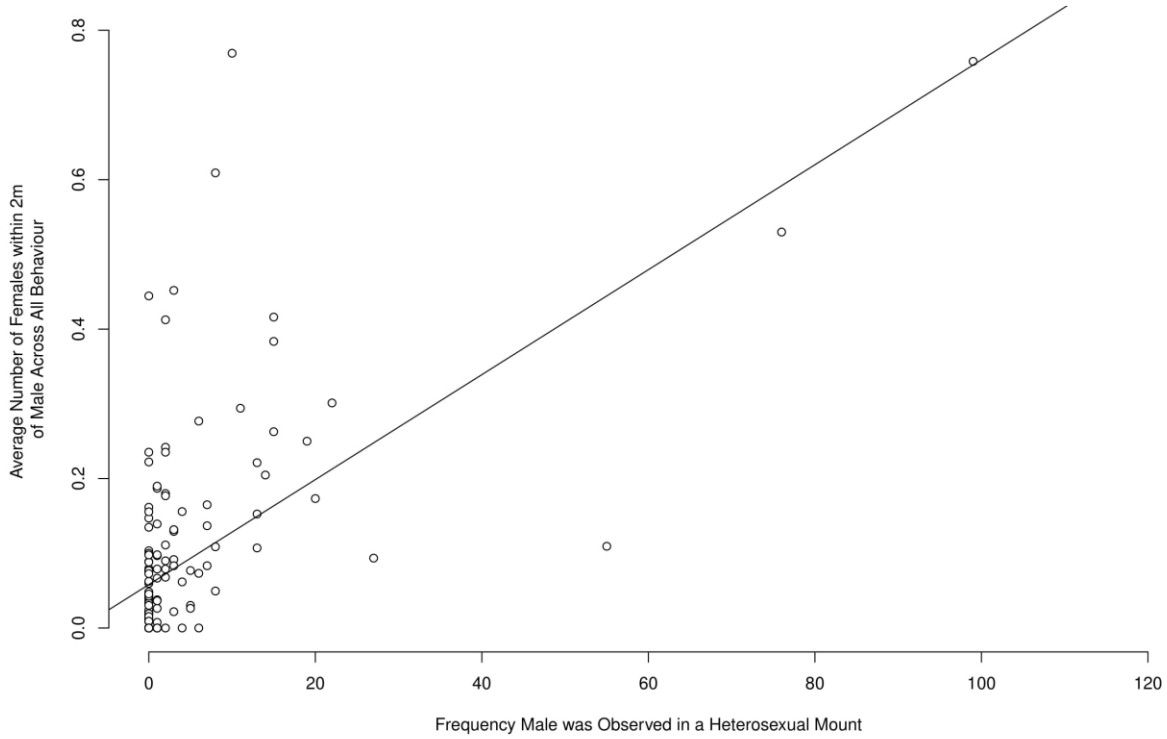

Figure 3. Graph showing the relationship between heterosexual mount frequency and a male's association with females in its social structure. Figure includes a linear regression analysis. A significant regression equation was found (R^2=0.348, p<0.001). n=166.

Figure 4 shows the relationship between the average number of females in close proximity to males across all behaviour and male homosexual mounting as a proportion of all mounts the male was observed in. This was characterised as the male's homosexual activity ratio. Note that the data used was only when the male was an actor.

Figure 4

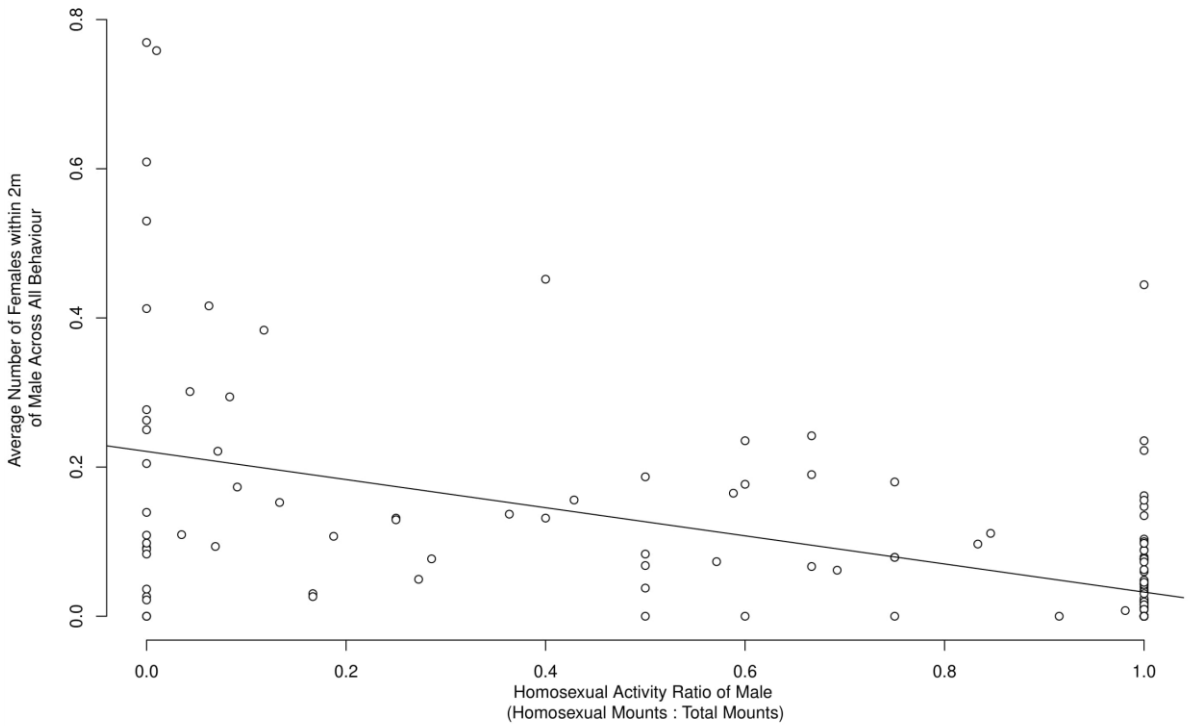

Figure 4. Graph showing the relationship between homosexual activity and a male's association with females in its social structure. Figure includes a linear regression analysis. A significant regression equation was found (R^2=0.280, p<0.001). n=166.

DISCUSSION

These results show that social structure does influence homosexual male behaviour in rhesus' macaques. However, the results also indicate that it is much more complex than an influence of social structure alone. Many theories for homosexual activity exist, and the results collected can help assess these differing explanations. The focus in this case is mostly on how male affiliation or male access to reproductive opportunity can influence homosexual activity, but social structure underpins the basis for several other key theories discussed as well (Poiani, 2010). As seen across the five behavioural states, social structure is not a static component of a society, but a much more dynamic factor that is constantly affecting behaviour in different ways (Hinde, 1976). Despite this, there are consistent patterns, especially between sexes, that show stable differences in the overall social structure. This was observed in the obtained results, as the average number of males in close proximity to males was

significantly lower than the average number of females in close proximity to males across the whole study period. The known social structure of macaques is a multi-male multi-female grouped system (Dunbar, 1988). This would suggest males spend equal time in close proximity to females and males. The adult male : female sex ratio in this investigation was 1 : 1.04, which is consistent with an average sex ratio on Cayo Santiago of 1 : 1. This ratio is due to provisioning and lack of predators on the island (Berard et al., 1993). This suggests there should be no difference in proximity between sexes unless the social structure is more than a simple mixed-sex group. The results reject the null hypothesis and therefore do support a more complex social structure, where males are in closer proximity with females more often than with other males.

This form of social structure has been recorded more often than a simple multi-sex population in Cayo Santiago rhesus' macaques (Rawlins & Kessler, 1986). Females do not disperse and usually remain in their natal troop (Albers & Widdig, 2013). Furthermore, males will not be observed in close proximity with other males that often, as males disperse from their natal troop and integrate into another troop (Rawlins & Kessler, 1986). This means males spend more time alone or within a group that has a consistent number of females. The number of males within a troop will fluctuate more as there is constant migration (Kaufmann, 1967). It is also known that the acceptance of a male rhesus' macaque into a new troop is a tough but tolerated process, as the new male will experience a hostile response from the troop, usually through violence (Rawlins & Kessler, 1986). A social structure of this nature can give rise to stronger social affiliation between males, in order to increase the chance of survival in newly joined troops, and a variation of reproductive opportunity across all males (Poiani, 2010). The results of our investigation provide evidence that these factors could be part of the explanation for the presence of homosexual activity within the population. Evidence is also given against some alternative existing explanations.

The results of this macaque social structure give evidence against the theories that homosexual activity is influenced by a sex ratio bias, or by sexual segregation. The theory of sex ratio bias states

that homosexual activity will occur due to the unavailability of other-sex sexual partners (Frigerio, Weiss & Kotrschal, 2001). The theory of sexual segregation declares that same-sex sexual activity will occur due to ecological and social factors preventing the two sexes from mating (Ruse, 1981). This population of rhesus' macaques was found to have an equal adult sex ratio and is observed to integrate frequently with the opposite sex. As seen in this study and previous investigations, male homosexual activity in this rhesus' macaque population is very frequent (Carpenter, 1942). Therefore, the results do not provide evidence that these two theories are the case for the homosexual activity observed in rhesus' macaques. However, sexual segregation may be difficult to observe as there is no physical segregation, yet there could be social segregation affecting behaviour (Ruse, 1981).

Other studies of nonhuman primates provide results that do show sexual segregation as a factor in homosexual activity. In female Japanese macaques, some homosexual behaviour was explained by the lack of physical access to a male (Gouzoules & Goy, 1983). Several species of squirrel monkeys also exhibit homosexual behaviour (Talmage-Riggs and Anschel, 1973), and there is evidence of social sexual segregation (Coe & Rosenblum, 1974). Therefore, the segregation of sexes cannot be written off entirely as a theory of homosexual behaviour. The effects of social segregation in rhesus' macaques may be more complex; the rhesus' macaque population structure could involve social segregation of individual males within troops or complete exclusion of males from troops (Hassett, Rupp & Wallen, 2010), as opposed to discrete physical segregation between the two sexes. Alternative theories of homosexual activity can help examine these relationships between males and macaque troops.

Other explanations of homosexual activity can be questioned by the results collected in Figure 1. Parker and Pearson (1976) state that individuals may engage in homosexual activity to increase the likelihood of motivating a heterosexual partner to mate. In the case of male rhesus' macaque homosexual behaviour, this theory would suggest that male homosexual mounting events would occur in close proximity to females, so females can observe the mount in order to become motivated to copulate by the behaviour. However, the results in Figure 1 show that homosexual mounting events

happened with a significantly lower number of females in close proximity than heterosexual mounting. This gives evidence against the theory of heterosexual motivation, meaning male rhesus' macaque homosexual mounting does not exist for heterosexual partner arousal and may indicate that there are other underlying explanations for homosexual mounting to occur within an area consisting of fewer females. However, the increase in the frequency of male sexual mounts when females are in numbers of 15 or more (see Figure 1) suggests that sexual activity could still be slightly influenced by the attempt to motivate the opposite sex. The spike in frequency at 15+ is larger for heterosexual mounts, so the arousal of heterosexual partners may be achieved by the male's demonstration of participation in other heterosexual copulations (Hauser, 1993), rather than its involvement in homosexual mounting.

Figure 1 uses the measure of female proximity to mount events, which does not include information about the social structure over longer periods of time. The proximity of males to females across long periods of time, instead of at one specific moment, is a more appropriate measure proxy of social structure in rhesus' macaques that can be used to analyse other theories of homosexual activity (Whitehead, 1997).

Social affiliation is another theory for the existence of homosexual behaviour (Fairbanks, McGuire & Kerber, 1977). Strong social affiliation can be seen in inter-sex pairings as a product of mate-guarding (Dubuc et al, 2012), but also in intra-sex pairings as a product of grooming (Maestripieri & Hoffman, 2012). The results of this study imply strong bonds between individuals could also be reinforced through homosexual activity. We can assess bonds between males by comparing variations in male interactions of different age groups, as age can be a variable in determining affiliation in free ranging rhesus' macaques (Loy, 1971). In rhesus' macaques, subadult males are observed to be much more independent from kin, as they have more frequent interactions with other males in the process of moving away from their natal troop (Maestripieri & Hoffman, 2012). In combination with this, adult male macaques are observed more frequently around females, as they compete for access to

reproductive opportunities (Bercovitch, 1997). Younger male rhesus' macaques are also observed to have social interactions with a higher number of the population, whereas older adult males allocate their time to fewer, more specific individuals (Liao et al., 2018). From the results, these fewer individuals that older adult males associate with are suggested to be females, as they were observed in close proximity to a greater number of females than other males. The form of social structure observed in this investigation can link to patterns in homosexual activity. The results show that subadult male macaques were seen on average to be more involved in same-sex mounts than adult males were. This could be due to social bonding of subadult males, as they begin to affiliate with males from outside of their natal troop. Social affiliation between males is a factor that influences the frequency of homosexual activity (Silk, 1994), and the more frequent occurrence of homosexual activity in subadult male macaques could be a behaviour influenced by the bonding of new partnerships. However, the theory of social affiliation states that males will continue to reinforce a bond using homosexual activity throughout adulthood as well (Wrangham, 1993). This means homosexual behaviour in this rhesus' macaque population should remain at a high frequency in the adult male category as well, yet from the results obtained, it is shown to be less frequent. This gives reason to believe that subadult males are engaging in homosexual activity as a product of alliance formation, rather than for affiliation alone. Subadult males may engage in high levels of homosexual behaviour to form new bonds of cooperation (Vasey, 1995), and homosexual activity could then occur less frequently in older males as bonds have already been established prior to adulthood. The behaviour may still continue to persist however, for occasional reinforcement of the social partnership (Fairbanks, McGuire & Kerber, 1977). Thus, the results suggest male homosexual behaviour in rhesus' macaques ensues due to the forming of novel alliances and the constant affiliation of these new-found bonds. The age of the males seems to play an important role in determining when these alliances are formed within the social structure. Same-sex alliances in nonhuman primates are known to have reproductive advantages (Kirkpatrick et al., 2000), and homosexual activity may be a behaviour used to strengthen these same-sex bonds (Smuts & Watanabe, 1990).

The theory of social affiliation alone should be applied with caution, however. In this investigation, social affiliation is measured by the proxy of proximity. This assumes that males will be socially bonded if they are at a close distance to each other, but in many instances, this may not be the case. It is not unknown for rhesus' macaques to be close to each other by chance, in scenarios such as foraging alone but within the same area (Hill, 1999). Therefore, in terms of assessing the bond of individuals, using proximity as a measure does have its weaknesses. Nevertheless, homosexual activity seems to be influenced by the bonding of subadult males and adult males. The investigation assumes that proximity relationships reflect affiliation between individuals, and affiliative bonds have been noted to be the most likely factor of close proximity in other studies of rhesus' macaques (De Waal & Luttrell, 1988). Hence, the measure of proximity can be classed as a valid measure of socials bonds in this species of monkey.

Social affiliation is also seen in other nonhuman primates as a factor of homosexual activity. Captive female chimpanzees are observed to rub genitalia as a way of reinforcing social bonds (Anestis, 2004). Affiliative mounting is also observed in wild orangutans (Fox, 2001). Therefore, the theory of social affiliation can exist in different social structures. As long as affiliative bonding still exists as a part of the structure, the overall social system can take many forms and homosexual activity will still persist. However, in male rhesus' macaques, results suggest that homosexual activity occurs at a higher frequency than in orangutans, as orangutan homosexual mounting is rarely observed (Poole, 1987). Thus, the overall social structure could impact the rate at which these affiliative bonds are formed and reinforced by homosexual activity.

One of the main social structure theories that can be reviewed with the results collected is that individuals will engage in homosexual activity more frequently if they have limited access to reproductive opportunities (Wolfe, 1986). The priority of access model was first analysed in a number of primate species, observing adult female monkey grooming patterns (Seyfarth, 1977). It was found that higher-ranking females received more grooming than other ranked females, and that grooming

would occur between females of adjacent rank (Seyfarth, 1977). The social structure of the macaque population could mean that males of a lower rank within the population may not have the same access to females that high-ranking males may have (Dubuc et al., 2011). This could increase the frequency of lower-ranked male rhesus' macaque homosexual activity, which has been previously noted in female Japanese macaques (Wolfe, 1986). The linear regression of homosexual mount involvement frequency against female access in this study was non-significant. This means that individuals observed in more homosexual mounts were not considered to be in close proximity to fewer females. However, in Figure 2, a significant correlation was found between social structure and homosexual actor mount frequency. When compared to the nonsignificant regression of homosexual mount involvement, it could be suggested that the social structure has a greater influence on a male's behavioural choice to mount, as opposed to the male being mounted. This could be explained by assuming the act of mounting homosexually is due to sexual frustration as a product of a limited access to reproductive opportunity (Dagg, 1984).

For the linear regression of heterosexual mount frequency in Figure 3, the results showed a significant regression equation. The more a male was observed in heterosexual activity, the more females it would be in close proximity to. Figure 4 shows how overall sexual activity changes with male social structure. This shows significant results, as males that were observed less frequently in close proximity to females were much more likely to engage in homosexual activity than heterosexual activity. This can be explained by a male reproductive skew, correlated with the priority of access model (Dubuc et al., 2011). The access to heterosexual activity can be influenced strongly by the social structure (Manson, 1992), whereas in these results, homosexual activity seems to be influenced by heterosexual activity access as a product of social structure. This means the social structure is impacting male homosexual activity through individual accessibility to females and reproductive chances. This may be dependent on rank, as high-ranking male rhesus' macaques have been seen to have higher reproductive success (Berard, 1999; Smith, 1981).

The form of a ranked social structure is likely to exist in Cayo Santiago rhesus' macaques because of the presence of alpha and beta males in the population (Nurnberg et al., 1994). Furthermore, it is known that alpha males have greater reproductive success relative to their group (Berard et al., 1993), so limited reproductive success could influence lower-ranked males to engage in homosexual mounting events. With the results collected, assumptions have been made in terms of rank, but it is clear that some males do not have the same access to reproductive opportunities as other males. There is a possibility that this is not due to rank, though based on previous studies, it appears to be a likely factor (Dixson, 2015). The results clearly show that a male's position in the social structure is shaping its involvement in homosexual behaviour. From the results, no matter where the position within the social structure, all males seem to participate in some form of sexual behaviour, whether it is homosexual or heterosexual. If a male has less access to heterosexual opportunities, it is may use homosexual behaviour more frequently as a substitute mechanism (Leca, Gunst & Vasey, 2014).

The ranking of males within the social structure seems to play an important part in homosexual behaviour. Considering this, the hypothesis of homosexual activity occurring as a display of dominance by the mounter has been rejected in previous studies (Akers & Conaway, 1979). However, it has been found that the two rhesus' macaque males involved in a homosexual mount have a significantly smaller rank distance between them than estimated by the null hypothesis (Clive, 2017). If males of a lower rank have less access to females, they are more likely to engage in homosexual activity with a male in a similar position in its social structure, rather than mounting a male of significantly less rank. This begins to form a larger, more complex theory of why male homosexual activity in rhesus' macaques occurs. It can be suggested that male rhesus' macaque homosexual behaviour takes place because the lower-ranked males in the social structure are engaging in same-sex mounting. This could be a result of their rank restricting their reproductive opportunity (Wolfe, 1986).

There is support in other nonhuman primates for the idea that limited access of males to females could be a factor of homosexual activity. Virunga mountain gorillas in an all-male group engage in

frequent homosexual interactions (Yamagiwa, 1987). The complete lack of access to females has been noted as a key aspect of homosexual activity in this group (Edwards & Todd, 1991). There are distinct differences between the social structure of an all-male group of gorillas and of a mixed-sex group observed in rhesus' macaques. However, even though male macaques are present in the same population as females, the access of lower-ranked males to reproductive opportunities may be so restricted that it resembles the same lack of access observed in Virunga mountain gorillas. In captive Japanese macaques, spatial proximity as a proxy measure of social structure was also seen to link closely with hierarchal relationships (Corradino, 1990). This gives reason to believe the proximity measures collected in our results could also link with rank, but further research in this area would be necessary. A more detailed analysis of the rhesus' macaque social structure, with the inclusion of a dominance hierarchy, would be required to conclusively determine rank's effect on homosexual activity.

There are limits to the method of proximity as the sole proxy measure of social structure. The building of a social structure based on only one type of data does not always suffice to explain the entire system (Jacobs & Petit, 2011). Social network analysis (SNA) is a more improved method on proximity data counts, as a multi-layered model can be produced to study group-scale behaviour using spatial proximity data as well as specific behaviour between individuals, such as grooming patterns (Sueur et al., 2011). With the sole use of proximity in our study, the social structure of rhesus' macaques is assumed to be simplistic. The presence of a simple structure in primates is unlikely to be the case (Itani, 1985), but a study with a simpler approach can be just as beneficial as a complex approach such as SNA. This is because spatial proximity is a reliable proxy of primate social motivation on broader studies over long periods of time (Ballesta et al., 2014). It can provide the foundation for future studies that can then adopt a more complex and specific SNA method (Wey et al., 2008).

There are also many other theories of homosexual activity in existence that are not associated with the social structure of a primate population, many of which are related to the genetics of individuals

(Poiani, 2010). This investigation only evaluates the effect of the population on behaviour, and not individual factors. No clear conclusions can be made about why homosexual activity occurs in rhesus' macaques, but it can be suggested from this study that characteristics of the rhesus' macaque social structure can affect the frequency of occurrence of homosexual activity. It has been found that the ontogeny of an organism can also influence sexuality (Roper, 1996), so further research into different theories would be valuable in gaining a larger analysis of the multitude of factors that can play a role in homosexual activity.

The results indicate how the social structure can influence homosexual activity in several different ways. Although females are not directly involved in male same-sex mounting, competition for access to females has an indirect relationship with the frequency of occurrence of the behaviour. It would usually be assumed that homosexual activity is independent of the opposite sex (Sommer & Vasey, 2006), but the results suggest that the relationship between males and females is a crucial element. However, this part of the social structure is not the only influence on homosexual activity. Limited reproductive opportunities mixed with strong male social affiliation and alliance formation seems to be the concoction of factors in this rhesus' macaque population that are weighted the heaviest in underpinning the social structure effect on male homosexual activity.

Patterns of how social structure affects homosexual behaviour are still more complex, however. Significant results have been found to give confidence to several theories of homosexual activity, but only in one species of primate. The results are to be taken with caution when extrapolated to other species, as the social structure of rhesus' macaques is dissimilar to many nonhuman primate species (Rawlins & Kessler, 1986). The population structure of the Cayo Santiago rhesus' monkeys also changes seasonally (Brent et al., 2013), so the results collected in our study period could vary greatly to results obtained from a dataset over another example period of September to December. Although the three months of this study is a sufficient period of time to gain statistically significant social

structure patterns, seasonal variations are not considered. Therefore, the comparison of the results to other species must be performed cautiously.

Understanding social evolution requires the inclusion of homosexual activity as a component of sexual selection (Vasey, 1995). With a detailed comprehension of homosexual activity in primates, we can begin to understand the justifications for such an abundant existence of an apparent paradoxical behaviour through many lineages (Poiani, 2010). The results of this study show that the social structure of a primate population is an important element to investigate further, to help develop the knowledge of homosexual behaviour. This captivating behaviour is poorly understood in primates, despite the first reports of primate homosexuality being published over 75 years ago (Vasey, 1995). The more that can be uncovered about primate homosexual activity, the closer the scientific community becomes to a developed understanding of its evolution (Sommer & Vasey, 2006). Discovering these significant social structure patterns in rhesus' macaques should inspire research into other species and may even contribute to securing greater insight into the evolution of human homosexual behaviour (Muscarella, 2000).

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APPENDICES

Figure S1

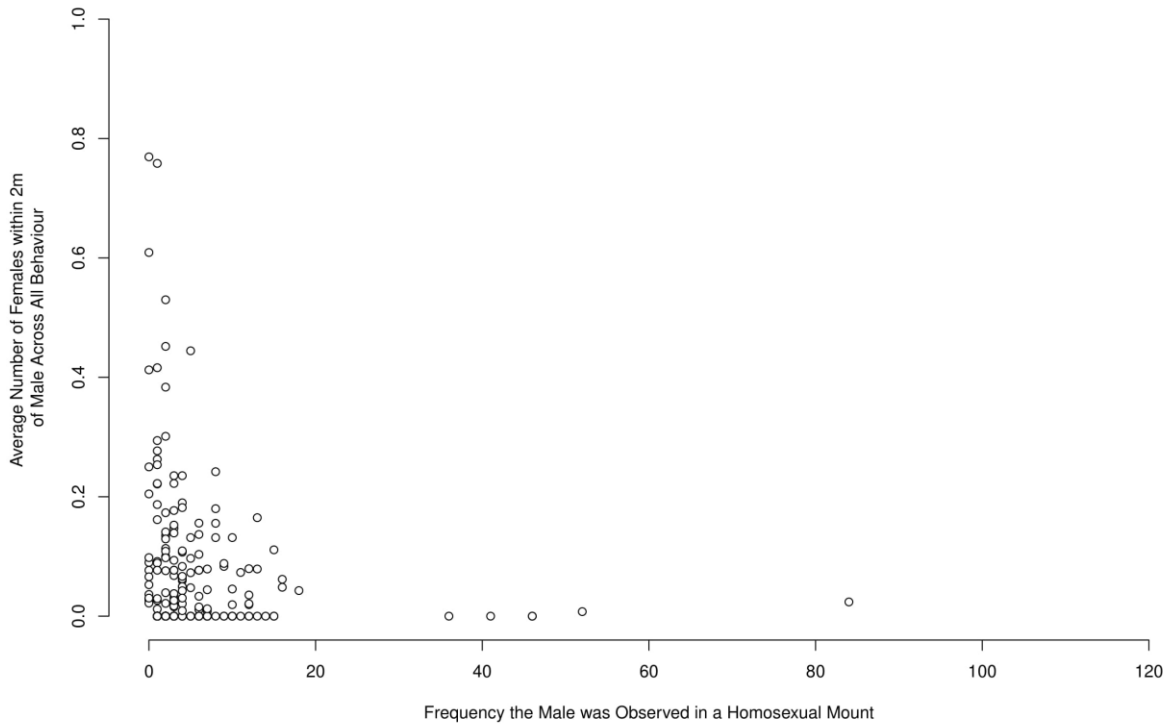

Figure S1. Graph showing the relationship between male homosexual mount involvement frequency and a male's association with females in its social structure. n=218.