

**PLAY PARTNER PREFERENCES IN WILD VERVET MONKEYS**

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## ABSTRACT

Although play appears to be ubiquitous, its evolutionary function(s) are still largely unknown, and many proposed hypotheses remain controversial as they generally lack empirical evidence. I investigated four relevant contemporary hypotheses to make predictions on how primates should optimally choose play partners based on demographic variables. I studied wild vervet monkeys (*Chlorocebus pygerythrus*) in the Samara private game reserve, South Africa, and collected focal sample data relating to play, as well as general scan samples and information on demographic variables. Using these data, I constructed multi-level Bayesian models which allowed me to incorporate many variables that we know structure primate social relationships—such as age, sex, kinship, and rank—simultaneously into the model in order to judge their relative effects. My data most strongly support the dominance hierarchy hypothesis, indicating that the play behaviour in these wild vervets may have benefits related to testing or establishing dominance rank relationships.

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## TABLE OF CONTENTS

<b>LIST OF TABLES .....</b>	<b>VIII</b>
<b>LIST OF FIGURES .....</b>	<b>IX</b>
<b>LIST OF ABBREVIATIONS .....</b>	<b>XI</b>
<b>CHAPTER 1: INTRODUCTION.....</b>	<b>1</b>
1.1    DEFINING PLAY.....	1
1.2    CLASSICAL THEORIES OF PLAY .....	2
1.2.1 <i>Surplus Energy Theory</i> .....	2
1.2.2 <i>Instinct Practice Theory</i> .....	3
1.2.3 <i>Recapitulation Theory</i> .....	4
1.3    CONTEMPORARY HYPOTHESES OF PLAY .....	5
1.3.1 <i>Training for the Unexpected Hypothesis</i> .....	6
1.3.2 <i>Social Skills Hypotheses</i> .....	7
1.3.3 <i>Dominance Hierarchy Hypothesis</i> .....	8
1.3.4 <i>Self-Assessment Hypothesis</i> .....	9
1.4    PLAY IN NON-HUMAN PRIMATES.....	10
1.4.1 <i>Sex Differences</i> .....	10
1.4.2 <i>Play and The Brain</i> .....	11
1.4.3 <i>Group Size Compared to Significant Social Relationships</i> .....	11
1.4.4 <i>Primate Life History and The Surplus Resource Theory</i> .....	13
1.4.5 <i>Play in Adulthood</i> .....	14
1.4.6 <i>Do Primates Support Contemporary Hypotheses?</i> .....	15
1.5    THESIS OUTLINE .....	16
<b>CHAPTER 2: METHODS .....</b>	<b>20</b>
2.1 SAMARA FIELD SITE.....	20
2.1.1 <i>Inner Samara Study Area</i> .....	21
2.1.2 <i>Outer Samara Study Area</i> .....	23
2.2 STUDY SPECIES .....	24
2.3 STUDY POPULATIONS .....	26
2.3.1 <i>Inner Samara Population</i> .....	26
2.3.2 <i>Outer Samara Population</i> .....	27
2.4 METHODS.....	28
2.4.1 <i>Behavioural Data Collection</i> .....	28
2.4.2 <i>Play Bouts and Play Behaviour</i> .....	30
2.4.3 <i>Quantifying Measures</i> .....	33
2.5 STATISTICAL METHODS .....	37
2.5.1 <i>General Model Information</i> .....	37
2.5.2 <i>Specific Parameters for The Four Troop Model</i> .....	39
2.5.3 <i>Specific Parameters for The Juvenile Model</i> .....	40
2.5.4 <i>Specific Parameters for The Kinship Model</i> .....	40

2.5.5 <i>Specific Parameters for The Size Difference Model</i> .....	41
<b>CHAPTER 3: RESULTS</b> .....	<b>42</b>
3.1 FOUR TROOP MODEL RESULTS .....	42
3.2 JUVENILE MODEL RESULTS.....	48
3.3 KINSHIP MODEL RESULTS.....	52
3.4 SIZE DIFFERENCE MODEL RESULTS .....	60
<b>CHAPTER 4: DISCUSSION AND CONCLUSIONS</b> .....	<b>63</b>
4.1 HYPOTHESES SUPPORTED BY THE SAMARA VERVETS .....	63
4.2 HOW DO THESE RESULTS RELATE TO EXISTING LITERATURE? .....	65
4.2.1 <i>The Dominance Hierarchy Hypothesis</i> .....	68
4.2.2 <i>Hypotheses Supported within an Alternate Context</i> .....	71
4.2.3 <i>Comparing Vervets to Capuchins</i> .....	72
4.3 LIMITATIONS .....	74
4.4 FUTURE DIRECTIONS.....	75
<b>REFERENCES</b> .....	<b>78</b>
<b>APPENDICES</b> .....	<b>92</b>
<b>APPENDIX A: TEMPERATURE AND RAINFALL</b> .....	<b>92</b>
<b>APPENDIX B: PAIRWISE PLOTS OF PREDICTOR VARIABLES</b> .....	<b>94</b>
<b>APPENDIX C: POSTERIOR PREDICTIVE CHECKS AND FIXING DISPERSION</b> .....	<b>97</b>

## LIST OF TABLES

<b>Table 2.1</b>	Composition of the Inner Samara Study Troops over the Study Period.....	27
<b>Table 2.2</b>	The annual percentage of scan samples allocated to each behaviour category for adults and juveniles of the Inner Samara Troops.....	27
<b>Table 2.3</b>	Composition of the Outer Samara Study Troop over the Study Period.....	28
<b>Table 2.4</b>	The annual percentage of scan samples allocated to each behaviour category for adults and juveniles of the Outer Samara Troop.....	28
<b>Table 2.5</b>	Descriptions of Behavioural Categories for Scan Sampling.....	29
<b>Table 2.6</b>	Operational Definitions of Play Behaviours.....	30
<b>Table 2.7</b>	Descriptive Statistics for Play Bouts in Both Datasets.....	33
<b>Table 3.1</b>	Posterior Estimates of Play Probabilities for the Four Troop Model.....	42
<b>Table 3.2</b>	Posterior Estimates of Play Probabilities for the Juvenile Model.....	48
<b>Table 3.3</b>	Posterior Estimates of Play Probabilities for the Kinship Model.....	53
<b>Table 3.4</b>	Posterior Estimates of Play Probabilities for the Size Difference Model.....	60

## LIST OF FIGURES

<b>Figure 2.1</b>	Map of South Africa and Study Location.....	20
<b>Figure 2.2</b>	Inner Samara and Outer Samara Study Areas.....	22
<b>Figure 3.1</b>	Posterior Density Plot of the Four Troop Model Using a Poisson Distribution.....	43
<b>Figure 3.2</b>	Rates of Play by (a) Dyad-Sex and (b) Dyad-Age in the Four Troop Model.....	44
<b>Figure 3.3</b>	Rates of Play Compared to Rank Difference Across (a) Dyad-Sex and (b) Dyad-Age in the Four Troop Model.....	45
<b>Figure 3.4</b>	Rates of Play Compared to Groom SRI Across (a) Dyad-Sex and (b) Dyad-Age in the Four Troop Model.....	46
<b>Figure 3.5</b>	Rates of Play Compared to Proximity SRI Across (a) Dyad-Sex and (b) Dyad-Age in the Four Troop Model.....	47
<b>Figure 3.6</b>	Posterior Density Plot of the Juvenile Model Using a Poisson Distribution.....	49
<b>Figure 3.7</b>	Rates of Play in the Juvenile Model According to Dyad-Sex Category.....	50
<b>Figure 3.8</b>	Rates of Play Compared to Rank Difference According to Dyad-Sex Category in the Juvenile Model.....	50
<b>Figure 3.9</b>	Rates of Play Compared to Groom SRI According to Dyad-Sex Category in the Juvenile Model.....	51
<b>Figure 3.10</b>	Rates of Play Compared to Proximity SRI According to Dyad-Sex Category in the Juvenile Model.....	52
<b>Figure 3.11</b>	Posterior Density Plot of the Kinship Model Using a Poisson Distribution.....	54
<b>Figure 3.12</b>	Rates of Play in the Kinship Model According to (a) Dyad-Sex and (b) Dyad-Age Category.....	55
<b>Figure 3.13</b>	Rates of Play Compared to Rank Difference Across (a) Dyad-Sex and (b) Dyad-Age Categories in the Kinship Model.....	56

<b>Figure 3.14</b>	Rates of Play Compared to Groom SRI Across (a) Dyad-Sex and (b) Dyad-Age Categories in the Kinship Model.....	57
<b>Figure 3.15</b>	Rates of Play Compared to Proximity SRI Across (a) Dyad-Sex and (b) Dyad-Age Categories in the Kinship Model.....	58
<b>Figure 3.16</b>	Rates of Play Compared to Kinship Across (a) Dyad-Sex and (b) Dyad-Age Categories in the Kinship Model.....	59
<b>Figure 3.17</b>	Posterior Density Plot of the Size Difference Model Using a Poisson Distribution.....	61

## **LIST OF ABBREVIATIONS**

CI	Credible Interval
ESS	Effective Sample Size Estimates
MGT	Mango Grove Troop
pd	Probability of Direction
PT	Picnic Troop
RBM	River Bend Mob
RST	River Side Troop
SRI	Simple Association Ratio Index
SRT	Surplus Resource Theory

## CHAPTER 1: INTRODUCTION

### 1.1 Defining Play

Although play is phylogenetically widespread, its evolutionary function(s) remain(s) a matter of debate. In addition to being poorly understood, play is also considered to be difficult to define, and the working definition is frequently scrutinised and modified. Burghardt (2005) has identified play as a behaviour that is (1) not immediately, or obviously, fully functional in the context it is expressed; (2) spontaneous and voluntary; (3) different from ‘serious’ behaviour in structure, context, or intensity; (4) the behaviour is performed repeatedly in a similar, but not rigidly stereotyped, form; and (5) performed in the absence of stress. Play can also be costly, as it is energy- and time-consuming, increases conspicuousness to predators, and can increase the likelihood of injury (Lutz et al., 2019). However, if play has no benefit, any costs incurred by an individual should lead to selection against play. Given the ubiquity of play across species (Lewis, 2005; Burghardt, 2005; Graham & Burghardt, 2010), researchers generally agree that there must be some adaptive value to play, and several hypotheses have been put forward to address this (see Section 1.2 below). However, most proposed hypotheses remain disputable as they generally lack empirical evidence (Smith, 1978; Bekoff & Byers, 1998; Power, 2000; Burghardt, 2005), or are not fully supported by available empirical data (Graham & Burghardt, 2010). Furthermore, although the obvious social aspects of play are often considered in these hypotheses, many other variables, such as play partner choice, remain neglected when testing these hypotheses (Lutz et al., 2019). Play is most likely to serve multiple, overlapping adaptive purposes (Bateson, 1981), and the benefits may well change over the course of an individual’s lifetime (Graham &

Burghardt, 2010). This makes it especially important to be explicit with social variables to avoid any ambiguity when generating testable predictions or interpreting the findings of empirical data.

## **1.2 Classical Theories of Play**

Hypotheses relating to play are generally divided into two groups: classical theories, that developed in the nineteenth and early twentieth centuries; and contemporary theories, which were developed after 1920 (Mellou, 1994). Although outdated and flawed, classical theories of play operate as an important steppingstone to contemporary considerations of the function of play. Burghardt (2005) argues that modern theories of play stem from three classical propositions: surplus energy theory, instinct practice theory, and recapitulation theory.

### ***1.2.1 Surplus Energy Theory***

Surplus energy theory is often associated with Friedrich Schiller and Herbert Spencer, who both viewed play as a means of energy regulation (Mellou, 1994). Schiller described play as an “aimless expenditure of exuberant energy”, meaning that play serves no developmental or evolutionary role (Mellou, 1994). When an individual meets all survival and caloric requirements, any excess energy will be exhausted through play.

Spencer attempted to explain the mechanisms behind surplus energy theories and argued that ‘higher’ species of animals (such as mammals) spend more time engaging in play than “lower” species of animals, since lower species spend the majority of their activity budget foraging in order to meet basic energy requirements. Higher species may be more efficient at obtaining food, avoiding predators, and problem solving (Burghardt,

2005). This then generates better nutrition, leading to a surplus of energy that will subsequently require play to dissipate.

Spencer also proposed that play is reflective of an animal's behavioural repertoire. A kitten pouncing on a ball of yarn, for example, will partially gratify its predatory instincts (Burghardt, 2005). The playful behaviour will therefore be, at least partially, related to predatory, social, or sexual instincts. This component of Spencer's theory provided a useful building block for modern theories of play. Although the surplus energy theory suggests a plausible explanation for the proximate causes of juvenile play behaviour, the theory was quickly deemed inadequate. The relationship between metabolic rates, thermoregulation, and physiological demands remains very complex, and there does not seem to be a simple relationship to play frequency or type of play (Burghardt, 2005). We are also seeing that play-like behaviours, once considered absent in the "lower" species that Spencer mentioned, such as birds (Pellis, 1983; Pellis, 1981; Heinrich & Smolker, 1998; Gamble & Cristol, 2002), reptiles, (Lazell & Spitzer, 1977; Dinets, 2015; Burghardt et al., 2002), and fish (Nielsen, 1990; Meder, 1958; Burghardt, 2005), all instances of which actually satisfy the five criteria of Burghardt's (2005) definition of play.

### ***1.2.2 Instinct Practice Theory***

German philosopher, Karl Groos wrote two highly influential books: *The Play of Animals* (Groos, 1998) and *The Play of Man* (Groos, 1901). In the former, Groos explains that the surplus energy theory is insufficient, and proposes his—instinct practice — theory, based on his observations and speculation (Mellou, 1994).

The instinct practice theory (also known as the pre-exercise theory) argues that, through play, juveniles master skills they will need as adults. Groos asserted that animals have a period of youth in order to play, practice through play will perfect an animals' instincts, and that play is necessary to adequately develop mind and body (Burghardt, 2005). Compared to the earlier theories, the instinct practice theory examines play from an ultimate perspective, examining possible values or function(s) of play. It also requires an individual to learn the necessary skills needed as an adult, whereas the surplus energy theory does not require such learning (Mellou, 1994).

One shortcoming with this proposition that needed to be addressed was play in adult animals, since adults should not have to play once their instinctive behaviour has been perfected. However, Groos argued that the proximate pleasures of play are enough to motivate play in adults (Burghardt, 2005).

### ***1.2.3 Recapitulation Theory***

The recapitulation theory is associated with G. Stanley Hall, a major figure in American psychology (Mellou, 1994). Instead of preparing us for the future, Hall argued that play stems from our evolutionary past. This was based on the belief that the development or ontogeny of an individual re-enacts the development or phylogeny of the species (Mellou, 1994). Play in both humans and animals can involve running, hitting, kicking, throwing, avoiding and chasing, which, although still important now, used to be pivotal skills in our evolutionary past. Hall saw play as a means to help children rid themselves of their primitive instincts that are no longer needed in modern day life (Mellou, 1994).

In sum, all these historic theories either viewed play as a means of energy regulation or explained play in terms of instincts. Play was viewed as a purely biologically based occurrence. Their major problem was that they focused on a single ultimate or single proximate explanation, and each theory was considered mutually exclusive (Graham & Burghardt, 2010). However, more recent propositions built on these shortcomings to attempt to approach play from a broader perspective, incorporating matters of development, mechanisms, phylogeny, and adaptive value.

### **1.3 Contemporary Hypotheses of Play**

In current play research, integrating Tinbergen's four ethological aims (Tinbergen, 1963) is considered an important objective. In primates, for example, we have a relatively good understanding of the more proximate developmental, ecological, psychological, and physiological factors that underpin playfulness (See Section 1.4.4, [Burghardt, 2005]). Consequently, many contemporary hypotheses of play are concerned with identifying the functional consequences of play. Importantly, the contemporary hypotheses explored in this thesis, offer enough information about the social aspects of play behaviour that precise and testable predictions can be made about play partner choices. Contemporary hypotheses that lack this information, or are not explicitly concerned with the social aspects of play, such as the "motor training" hypothesis (Bekoff & Byers, 1981), are not explored further. However, this is not to say that hypotheses examined in this thesis are mutually exclusive from those I did not explore, there can be commonalities in aspects of play across multiple hypotheses. However, when considering how animals choose their play partners, and if they do so optimally, the current hypotheses I chose to examine generate diverse predictions.

### ***1.3.1 Training for the Unexpected Hypothesis***

The “training for the unexpected” hypothesis argues that play allows animals to prepare emotionally and physically in order to manage unexpected situations later in life (Špinka et al., 2001). Play behaviour is argued to increase the adaptability of movements used to recover from a loss of control, such as being knocked over, losing one’s balance, or being pinned down. Špinka et al. (2001) also suggests that play can help an animal cope with the emotional aspect of being surprised or temporarily disoriented. The experience of “self-induced” mishaps (i.e., self-handicapping and role-reversal behaviours, see Table 2.6 for operational definitions) during play may help an animal avoid overreactions during a future unexpected situation (Špinka et al., 2001). Dolphins for instance, under safe conditions, seek to create and control novel contexts for themselves and their playmates (Kuczaj & Eskelinen, 2014). The behavioural flexibility and creativity involved in such play may lead to opportunities for individual cognitive development, and preparation for future unexpected affiliative and/or agonistic interactions (Kuczaj & Eskelinen, 2014). Overreaction in the presence of a predator, or in an adverse social interaction with a conspecific, could result in aggression, or decrease an animal’s chance of survival (Špinka et al., 2001).

Thus, Špinka et al. (2001) argue that if play serves as training for the future, animals should choose to play with familiar conspecifics (i.e., social partners with whom they engage in other activities such as grooming and foraging) as this will maximize the benefits while minimizing the risks. Risks can be lessened because animals may be better able to interpret the intentions of a familiar partner, which reduces the risk of cheating and/or injury, which is especially important when being put into vulnerable or “unexpected” situations. Špinka et al. (2001) emphasise that as playing with familiar

conspecifics is so important, familiar partners should be preferred over those who are merely physically matched.

### ***1.3.2 Social Skills Hypotheses***

Several hypotheses (Shimada & Sueur, 2018; Graham & Burghardt, 2010; Smith, 1978) argue that play promotes the development of social skills and the integration of juveniles within a group. Play may potentially aid in reinforcing social status (Bauer & Smuts, 2007), increasing familiarity and social tolerance between individuals (Antonacci et al., 2010), or strengthening relationships (Palagi et al., 2004); and a socially cohesive group may have better chances of survival and reproduction compared to a socially non-cohesive group (Sommerville et al., 2017). Collectively within the play literature, these have been referred to as the “social skills” hypotheses. Social play is generally considered an affiliative interaction between primates, and many authors (Baldwin & Baldwin, 1976; Palagi et al., 2004; Shimada & Sueur, 2014) have suggested that social play strengthens the social bonds important in adult life. However, few studies have systematically determined if social play is a possible factor for the formation and maintenance of social bonds (Shimada & Sueur, 2018). It also seems as though mammals deprived of social play may still develop normal social relationships (Baldwin & Baldwin, 1973). Despite the limited, contradictory evidence, Graham and Burghardt (2010) argue that a lack of social play may lessen an individual’s ability to react appropriately to social stressors and conspecifics, compared to individuals who engaged in regular amounts of social play as juveniles.

In contrast to the ‘training for the unexpected’ hypothesis, the social skills hypotheses argue that animals should prefer to play with unfamiliar conspecifics specifically so as to foster better social integration (Lutz et al., 2019).

### ***1.3.3 Dominance Hierarchy Hypothesis***

The “dominance hierarchy” hypothesis proposes that play serves as a social function, allowing animals to test and establish dominance relationships (Blumstein et al., 2013). This hypothesis posits that play may have both immediate and delayed benefits. Play in juveniles may be a means of determining dominance relationships in the moment and may therefore immediately benefit (or disadvantage) the individual (Pellis & Pellis, 2009). One could theoretically play with every individual in the group to accurately place oneself within the dominance hierarchy, but this is unnecessary if other social information is available. In primates, social information diffuses quite rapidly, allowing for the judgement of dominance relationships indirectly (Seyfarth & Cheney, 2013). The lowest ranking juvenile does not need to play with the highest-ranking juvenile to know where it stands within the hierarchy. Therefore, under the dominance hierarchy hypothesis, we might predict that an animal will play with more closely-ranked individuals than with distantly-ranked individuals, as these closely ranked relationships will need to be tested more frequently for an individual to determine its dominance rank in relation to others. Blumstein et al. (2013) argue that early social play behaviour has functional impacts on future dominance rank and offers correlative evidence in yellow-bellied marmots (*Marmota flaviventris*). Marmots who were dominant in social play bouts as pups, held higher dominance ranks as yearlings, compared to yearlings who held lower dominance ranks during play. We also see support for this hypothesis in wolves (*Canis lupus*), where

play reduced the number of aggressive interactions within a pack, but only when a clear dominance hierarchy existed between group members (Cafazzo et al., 2018). Dominance relationships were reflected accurately throughout play bouts and were rarely reversed. Dyads with a less clear dominance relationship also spent more time playing in a competitive way, compared to dyads where dominance relationships were more certain (Cafazzo et al., 2018).

Contrastingly, in spotted hyenas (*Crocuta crocuta*), dominance relationships are established at a very early age in cubs, and although these hierarchies appear to be inflexible (Drea et al., 1996), they seem to be ignored or absent within the context of a play bout. Additionally, Pellis et al. (1992), by experimentally altering testosterone in neonatal male rats, showed that while this increased juvenile play fighting it did not influence future dominance relationships, and may therefore not have delayed benefits.

#### ***1.3.4 Self-Assessment Hypothesis***

The “self-assessment” hypothesis predicts that animals should play with partners that are equally matched physically, regardless of social familiarity (Thompson, 1998). Thompson (1998) argues that animals play in order to gain immediate feedback on the development of their locomotor and social skills. Play provides an improved assessment of potential risks and costs, which could also be viewed as an alternate interpretation of the training for the unexpected hypothesis, where play influences an animal’s ability to react physically and emotionally to future events (Špinka et al., 2001). However, unlike the training for the unexpected hypothesis where self-handicapping behaviour is expected, under the self-assessment hypothesis, we would expect there to be a “play to win” mentality (Špinka et al., 2001). If self-handicapping behaviours were employed, the

animal would not be gaining an accurate self-assessment. Consequently, animals should engage in competitive play with equally matched partners, as this provides the most valuable feedback (Lutz et al., 2019). Sable antelope (*Hippotragus niger*) calves exhibited strong preferences for partners similarly aged and sexed, and their preferences remained stable over time (Thompson, 1996). These preferences observed in sable calves may indicate that play may be used as a tool for assessing one's own development by continually gaining feedback from developmentally similar peers (Thompson, 1996).

#### **1.4 Play in Non-Human Primates**

Play has been recorded in every observed species of primate (Burghardt, 2005). Developmentally, play begins in infancy and continues throughout the juvenile period, in which play reaches its highest frequency (Pellis & Iwaniuk, 2000). Typically, the incidence of play tapers off once puberty is reached. Play is classified into three, non-mutually exclusive categories: locomotor play, object play, and social play (Petrú et al., 2009; Power, 2000), with social play being the most common (Burghardt, 2005). Play fighting (also known as rough-and-tumble play) is a commonly reported form of social play, and is not only present in primates, but also in a wide range of non-primate species (Pellis & Pellis, 2017).

##### **1.4.1 Sex Differences**

Sex differences in play behaviours are well-documented within the non-human primate play literature (Burghardt, 2005). In social play, males typically engage in rough-and-tumble play more than females, and prefer to play with other males. Hormones can explain many of the sex differences found in non-reproductive behaviours (Beatty, 1984), such as play. However, in order to avoid a purely physiological explanation, we must also

consider other pertinent factors relating to the species in question, such as social structure. In species where males disperse and integrate within new groups, it has been proposed that males engage in play fighting behaviours more than females in order to practice skills needed in combat, as male reproductive success relies heavily on fighting abilities (Burghardt, 2005). There has been some evidence to support this proposal within primates, however the pattern disappears when looking beyond this order (Burghardt, 2005).

#### ***1.4.2 Play and The Brain***

More recently, we have been able to take phylogenetic patterns of play and compare them to brain size in more detail. In primates specifically, there is a positive correlation between social play and the size of brain structures, including the amygdala, cerebellum, and striatum (Lewis, 2003). Controlling for phylogenetic relatedness, Iwaniuk et al. (2001) compared forty-five species across fifteen orders, and found that the prevalence and complexity of play was significantly correlated with brain size, where larger-brained orders had more playful species. However, while the effect was detectable at the family level, the relationship disappeared when comparing at the species level (Iwaniuk et al., 2001).

#### ***1.4.3 Group Size Compared to Significant Social Relationships***

There are insufficient data to determine whether other confounding variables, such as group size, could be responsible for modulating social play and brain size simultaneously. Or perhaps group size modulates brain size, which then in turn influences play (Lewis, 2003). However, it is unlikely that the size of social groups, in and of itself, will be sufficient to increase the value of play (Pellis & Iwaniuk, 2000). It is also the case that for

some primates, social play may be limited to the mother (Řeháková, 2018), or to a limited number of peers (Pellis & Iwaniuk, 2000). For primates that do live in large groups and have opportunities for play partner choice, we may expect a larger group size to facilitate more opportunities for play, however, it is more likely the case that the social relationships created between these individuals facilitates play. Mother-offspring dyads, sibling dyads, grooming partners, male alliances, or other smaller subgroup relationships, may be more indicative of the extent of play than simply the number of individuals in the group. For instance, many species of non-human primates exhibit a similar preference to play more with siblings rather than peers (Cheney, 1978; Owens, 1975; Fedigan, 1972; Southwick, 1965; van Lawick-Goodall, 1968). Most non-human primates grow up with older siblings and will typically acquire younger siblings at some point throughout their life (Suomi, 2014). The interactions and relationships between siblings can comprise a major component of sociality, and the functionality of sibling relationships has often been compared to relationships with other peers. Simply put, what benefits are there for a young primate to interact with a sibling, that could not be obtained through other peers similarly aged and sexed to the sibling? The functions, costs, and benefits within any social relationship between two siblings is likely to be unequal (Suomi, 2014; Altmann, 1979), and there are numerous factors that can influence the development of such relationships. For example, it has been shown consistently that the smaller the age difference between siblings, the greater the proportion of time spent together in mutual play activities (Suomi, 2014). The sex of the older sibling is also important. If the older sibling is a female, for example, they are more likely to engage in grooming, and less time in playful interactions with their younger sibling, compared to if the older sibling is a male (Suomi, 2014).

These factors not only increase the difficulty of isolating an adaptive function(s), but also demonstrate that it not simply the number of individuals in the group that may influence play bout frequency and play partner preferences, but it is also the proportion of same-sex and opposite sexed peers, and availability of siblings.

#### ***1.4.4 Primate Life History and The Surplus Resource Theory***

Primates are characterized by having a longer than average mammalian lifespan, a longer juvenile period, and high parental investment in fewer offspring compared to other mammals (Pereira & Fairbanks, 2002; Charnov & Berrigan, 1993). During the extended juvenile period, important skills and behavioural patterns can be developed (Burghardt, 2005). In the Surplus Resource Theory (SRT) model of play, Burghardt (1984) proposes an evolutionary-developmental framework in which certain life history patterns support an increase in playfulness within a species, and primates fit many of the proposed underlying factors. High parental care, for instance, means an infant does not have to immediately forage for resources, find shelter, avoid predation, and fend for itself. This provides a safe time and opportunity for behaviours to be practiced or perfected. High parental care, while it may not directly decrease conspicuous to predators, may also lessen the risks associated with play as there is some level of supervision. Having a longer juvenile period allows for a more complex development of behavioural patterns, such as play. The SRT posits that being a larger mammal in a lineage is also factor that increases playfulness (Burghardt, 1988).

The SRT also provides energetic factors that influence play, including having a nutritious and ample diet (Burghardt, 2005). In primates, folivorous species, whose diet is less energy-rich, play less than frugivorous or omnivorous species (Fagen, 1981;

Burghardt, 2005). According to the SRT, other factors that may support increased playfulness in primates include a need for stimulation, available peers, and periods of low predation risk.

#### ***1.4.5 Play in Adulthood***

Social play is the most likely form of play found in adults, if play should continue into adulthood (Pellis & Iwaniuk, 2000), however adults also may engage in locomotor and object play (Pellis et al., 2019). With object play, juveniles and adults may engage with an object in a similar manner. In Japanese macaques (*Macaca fuscata*), for instance, both adults and juveniles play extensively with objects, especially stones, and both engage in the same basic three-part sequence of pounding stones towards the ground (Pellis et al., 2019). Social play in adulthood most often involves a similar form of the juvenile pattern of ‘play fighting’ (Pellis & Pellis, 1998; Pellis & Iwaniuk, 1999; Pellis & Iwaniuk, 2000). Play fighting in adults most often involves a juvenile partner, and the occurrence of adult-adult play fighting is less common (Pellis & Iwaniuk, 2000). In adult-juvenile play bouts, the play is usually initiated by the juvenile, and rarely by the adult (Fagen, 1981; Pellis & Iwaniuk, 2000). Pellis and Iwaniuk (2000) used comparative methods to determine what factors account for the variance in the phylogenetic distribution of adult-adult play fighting in primates. They examined adult-adult play in primates within a sexual and non-sexual context, and their findings suggest that the original function of play fighting among adults may have involved social assessment and manipulation. In some species, adult play fighting later may have co-opted into a courtship capacity. Their data support the possibility that adult-adult play may have first arisen in primates due to its functional value in non-sexual contexts, and once present,

was co-opted for courtship purposes. This comparative study highlights the importance of considering the functional properties of adult play when examining the much more frequently studied play of juveniles.

#### ***1.4.6 Do Primates Support Contemporary Hypotheses?***

In support of the ‘social skills hypothesis’, Shimada and Sueur (2018) argue that social play between two individuals is more indicative of their future affiliative relationships than social grooming from Japanese macaques. A second study by Shimada and Sueur (2014) suggests that, during social play in the infant and juvenile period, juvenile chimpanzees (*Pan troglodytes*) may form affiliative relationships and learn social techniques to gain more favourable central positions within the social network.

Golden lion tamarins (*Leontopithecus rosalia*) prefer to play with older siblings, and De Oliveira et al., (2003) argue that the younger animal may gain or improve skills related to vigilance by playing with their older siblings. However, when given the opportunity, the tamarins also engaged in inter-specific play with common marmosets (*Callithrix jacchus*), who are similar in body size, but differ in terms of behavioural abilities and experience (De Oliveira et al., 2003). The preference to play with older siblings and enhance social skills lends support to the ‘social skills hypotheses’, while the benefits from innovative inter-specific play support the ‘training for the unexpected’ hypothesis.

Lutz et al. (2019) found that diademed sifaka (*Propithecus diadema*) played more with close social affiliates, but also consistently preferred partners similar in age, sex, rank, and kinship. These data would support both the ‘training for the unexpected hypothesis’ and the ‘self-assessment’ hypothesis. Comparing across species, Lutz et al.

(2019) found that brown capuchins (*Cebus apella*) preferred to play more with animals who were oppositely sexed non-kin, while also preferring similarly ranked partners who were close social partners, thereby lending support for the ‘training for the unexpected’ hypothesis. Hamadryas baboons (*Papio hamadryas*) played with their close affiliative partners, and the strongest play relationships tended to be between closely aged partners and so, like the sifaka, offered support to both the training for the unexpected hypothesis and the self-assessment hypothesis (Lutz et al., 2019). Even though each species had very different play partner preferences, all three species studied by Lutz et al. (2019) offer support for the training for the unexpected hypothesis in some capacity. However, it is important to note that each species also varies with respect to group composition, sexual dimorphism, adult dispersal, and the nature of the dominance hierarchy, and it may be that these are more relevant to explaining observed differences in play partners than membership of a particular taxonomic group.

Behavioural variation during play may be indicative dominance relationships outside of play contexts (Cafazzo et al., 2018), but there seems to be little data available from primates to support the ‘dominance hierarchy’ hypothesis. There is strong evidence that in species where female choice in partners is constrained, that higher ranking males are more likely to be successful in mating efforts (Cowlshaw & Dunbar, 1991), but the nature of how, or if, juvenile play is related to dominance rank is unknown.

## **1.5 Thesis Outline**

The contemporary theories of play (the training for the unexpected, social skills, dominance hierarchy, and self-assessment hypotheses), all offer enough information for precise, testable predictions to be generated based on play partner preferences, and each

offers a different, testable prediction. However, even though play preferences and sex differences in play behaviour are well documented (Caro, 1988; Smith, 1982; Burghardt, 2005), all historic hypotheses, and most contemporary hypotheses of play, neglect these specific social aspects of play behaviour. It is unsurprising then, that most research concerning play does not focus specifically on play partner preferences in relation to contemporary hypotheses.

Lutz et al. (2019) provide a good starting point as they offered support to contemporary hypotheses through studying play partners in three separate species of primates. As mentioned, each species had observed differences in play partner preferences. The differences in social structures may be what is driving the observed differences in play partners, and it is likely the case that, due to the complex relationship between social structure and demographic variables, these hypotheses are not mutually exclusive. Given the marked differences in primate social structures, it is unlikely that a single hypothesis will find support across all primate species. One way to address this possibility, therefore, would be to compare primates with similar social structures, at least in terms of group composition, sexual dimorphism, and adult dispersal.

In this regard, given the species studied by Lutz et al. (2019), the vervet monkey (*Chlorocebus pygerythrus*) is an excellent candidate, as brown capuchins and vervets both have multi-male multi-female groups, are slightly sexually dimorphic, where males are larger than females, and males disperse (Fragaszy et al., 2004; Janson et al., 2012; Izawa, 1980; Pasternak et al., 2013; Renevey et al., 2013).

Consequently, to assess the arguments offered by Lutz et al. (2019), I studied two separate subpopulations of wild, habituated vervet monkeys in the Samara private game reserve, South Africa, EC. I used scan sampling and focal sampling methods to collect

information on demographic variables as well as play behaviours. The aim of this thesis is to investigate which of these contemporary hypotheses best explains partner choice in these subpopulations of wild vervet monkeys in South Africa. Specifically, I test the following predictions:

1. Under the training for the unexpected hypothesis, animals will prefer to play with familiar social partners and should exhibit no preference for physically matched partners.
2. Under the dominance hierarchy hypothesis and if social information is readily accessible, animals should play with more closely ranked conspecifics, as their relationships need to be tested more frequently.
3. Under the social skills hypotheses, animals should show no preference for physically matched partners and avoid playing with familiar social partners. Such a pattern would also provide support for an alternative interpretation of the training for the unexpected hypothesis, as unfamiliar, mismatched partners will provide a better training for dealing with novel and unpredictable situations in the future.
4. Under the self-assessment hypothesis, animals should prefer to play with partners that are similar in either age, sex, or rank, and we would expect no preference for play partners that are familiar social partners outside of play (e.g., grooming).

Using these data, I then construct multilevel Bayesian models, which allow me to consider which individual attributes (age, sex, dominance rank, size) and social networks (grooming partners, proximity networks, relatedness) influence the choice of play partners. I will then be able to determine which, if any, of the above predictions is

supported, and if this is congruent with another species that shares a similar social structure.

In Chapter 2, I describe my general methods, the area where the study was conducted, and differences between the two local field sites and study subpopulations. I also provide an overview of vervet monkey behaviour and social organization. I also explain how relevant variables are quantified and describe my statistical approach. In Chapter 3, I present results from the Samara vervets at the dyadic level, and assess which demographic variables are related to play bout frequency. Finally, in Chapter 4, I discuss the findings from my analyses, and how they relate to my predictions. I also consider the limitations of my thesis, and some potential directions for future research

## CHAPTER 2: METHODS

### 2.1 Samara Field Site

Data considered here were collected from a wild vervet monkey population located within the Samara Private Game Reserve, Eastern Cape Province, South Africa ( $32^{\circ}22'S$ ,  $24^{\circ}52'E$ ). The nearest town to the site is Graaff-Reinet, located approximately 40 km away (see Figure 2.1).

**Figure 2.1**

*Map of South Africa and Study Location*



*Note:* Study location indicated by the yellow star. (Google Earth, 2022)

After 10 years of observation at the first study area, colloquially known as “Inner Samara”, the larger project relocated to another area of the Samara reserve due to the introduction of lions. Consequently, the study area and sub-population of the first 10 years will be referred to as “Inner Samara”, and the “Inner Samara population”, respectively, throughout this thesis. The subsequent, separate study area and sub-population of the last two years will be referred to as “Outer Samara”, and the “Outer Samara population”, respectively. My analyses draw on three years of data from the

initial 10-year period (June 10, 2014, to June 8, 2017), and six months of data from the last two-year period (January 1, 2020 to June 22, 2020). Please see Figure 2.2 for aerial images of the separate study areas.

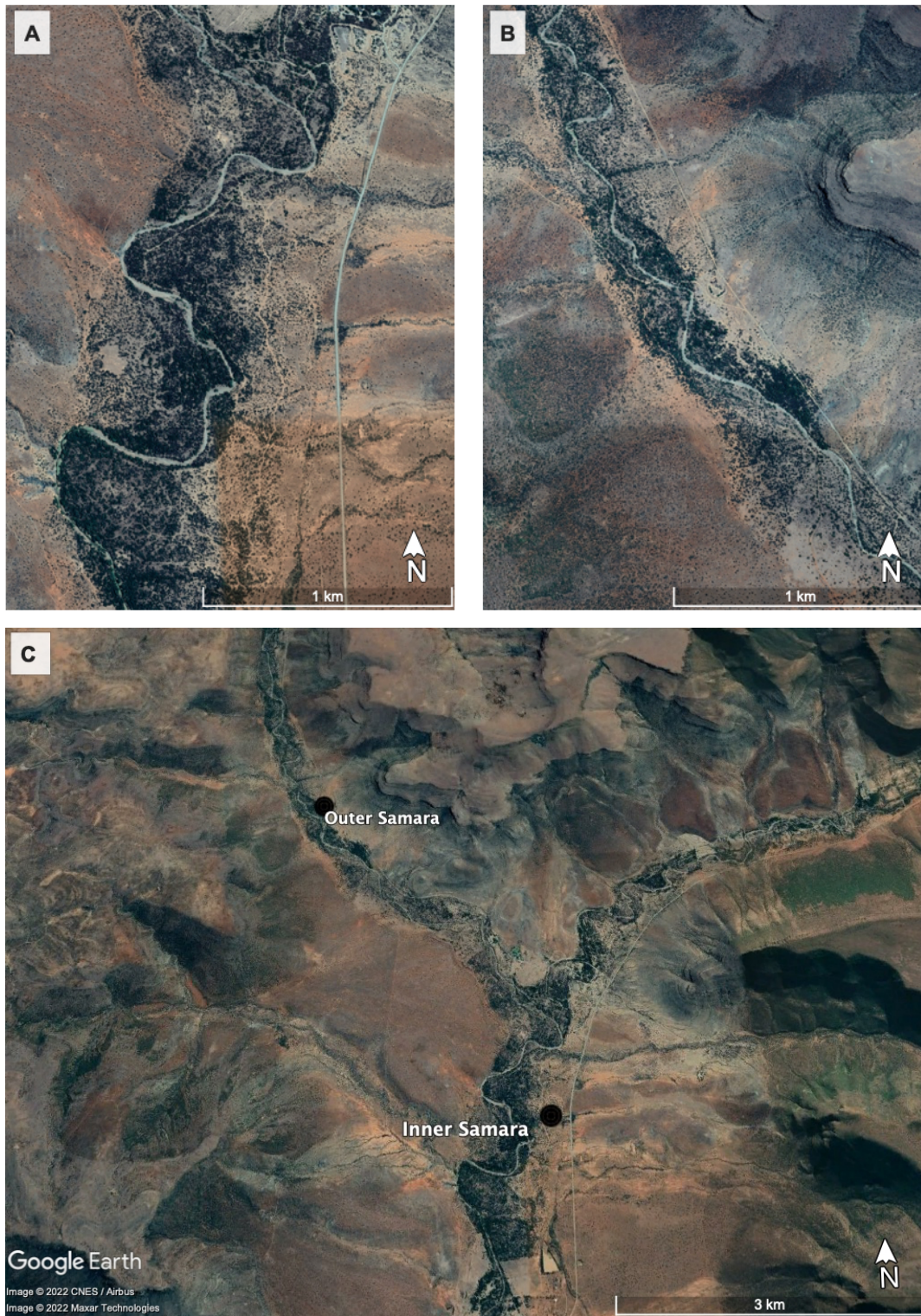
The reserve consists of 27,000 ha of mountains and nama-karoo grasslands (Pasternak et al., 2013). The area receives an average of 330 mm of rain per year, where the wet season ranges from October to March and the dry season from April to September (Pasternak et al., 2013). The area experiences a mean maximum temperature of 27 °C and a mean minimum temperature of 10 °C. The coldest month is July with a mean minimum of 4 °C, while December and January are the hottest months with a mean maximum of 34 °C (Pasternak et al., 2013). The monthly mean maximum and mean minimum temperatures and rainfall throughout the study periods are available in Appendix A.

The field site vegetation can be grouped into two broad categories: open dwarf shrubland on the areas that are drier and slightly higher in elevation, and dense woodland dominated by *Acacia karroo* along the rivers (Pasternak et al., 2013).

### ***2.1.1 Inner Samara Study Area***

The Inner Samara study area is located in the north of the reserve. The Melk (Afrikaans) or Milk (English) River, which flows intermittently and does not dam, transects the study area (Pasternak et al., 2013). The monkeys have no access to artificial water sources and their primary water sources are the river and standing pools in the aftermath of rain (Young et al., 2019a).

**Figure 2.2**  
*Inner Samara and Outer Samara Study Areas*



*Note:* The A) Inner Samara study area, the B) Outer Samara study area, and C) a geographic comparison of the two areas. (Google Earth, 2022)

In addition to the vervet monkeys, the study area hosts stable populations of the following large mammals: buffalo (*Syncerus caffer*), white rhino (*Ceratotherium simum*), zebra (*Equus burchellii*), giraffe (*Giraffa camelopardalis*), kudu (*Tragelaphus strepsiceros*), gemsbok (*Oryx Gazella Gazella*), red hartebeest (*Alcelaphus buselaphus*), duiker (*Sylvicapra grimmia*), springbok (*Antidorcas marsupialis*), eland (*Taurotragus oryx*), chacma baboons (*Papio ursinus*), aardvark (*Orycteropus afer*), warthog (*Phacochoerus africanus*), cape porcupine (*Hystrix africaeaustralis*), scrub hare (*Lepus saxatilis*), and meerkat (*Suricata suricatta*) (Sashaw, 2012).

The study area also includes a variety of predators that elicit alarm calls from the monkeys. Predators include cheetah (*Acinonyx jubatus*), caracal (*Caracal caracal*), black-backed jackal (*Canis mesomelas*), martial eagle (*Polemaetus bellicosus*), Verreaux's eagle (*Aquila verreauxii*), and Cape eagle owl (*Bubo capensis*) (Pasternak et al., 2013). Venomous snakes also elicit an alarm call (Ducheminsky et al., 2014), and have been documented as a source of mortality in Inner Samara (Pasternak et al., 2013). Venomous snake species include the puff adder (*Bitis arietans*), the cape cobra (*Naja nivea*), and the boomslang (*Dispholidus typus*).

### **2.1.2 Outer Samara Study Area**

Located approximately 3.67km away at a 330° heading from Inner Samara is the second study area, Outer Samara. The Melk River also transects Outer Samara. There is a man-made reservoir adjacent to the field site that is filled after rain. While the population of monkeys in Outer Samara also uses the river as the primary water source, they have been observed drinking from the reservoir even though this is outside of their typical home range.

Outer Samara and Inner Samara are separated by a 2.4-metre-high electric fence, and all cheetahs of Samara game reserve are confined to the latter. Therefore, the Outer Samara population of monkeys experience the same predation as the Inner Samara population, except for cheetah. The same non-predators occur within the Outer Samara study area as listed above in Section 2.1.1, with the exception of white rhino, buffalo, and giraffe.

## **2.2 Study Species**

Vervet monkeys are a semi-terrestrial, water-dependant, polytypic clade (*Chlorocebus*) widely spread across woodland-savanna in sub-Saharan Africa and comprising several species (Horrocks, 1986; Haus et al., 2013). The only factors that seem to limit geographic dispersion and population growth are the availability of water, and the presence of large trees for sleeping in at night (Fedigan & Fedigan, 1988). At Samara, vervets typically spend most of each day resting and foraging. Pasternak et al. (2013) provided activity budgets for adult vervets in two habituated Samara troops, and the annual percentage of time allocated to each behaviour was ~32% for foraging, ~25% for moving, ~33% for resting, and ~10% for social behaviour (i.e., grooming or playing).

Vervets live in small, multi-male, multi-female groups (Isbell et al., 1991) that typically range in size from 20-30 individuals. In the Samara game reserve, the dense strip of vegetation along the Melk River, together with the non-viability of dispersion possibilities away from the river, supports a higher population density and uncharacteristically large groups (Pasternak et al., 2013). Therefore, riverine troops in Samara can have as many as 70 monkeys within a troop with a mean of approximately 40 individuals (Pasternak et al., 2013). Troops are vulnerable to the effects of periodic and

severe drought, and group sizes can fluctuate markedly over time. Vervets are territorial and both males and females will respond aggressively to nearby troops within or adjacent to their home territory (Isbell et al., 1990). Nevertheless, territories can overlap extensively and, at Samara, vary from approximately 64 ha to 176 ha (Pasternak et al., 2013).

Females are philopatric and typically remain in their natal group throughout their lives, while males emigrate to neighboring troops when they reach sexual maturity, and then subsequently migrate every 2.5 to 3 years (Isbell et al., 1991; Henzi & Lucas, 1980; Young et al., 2019b). In Samara, the mean duration of residency by non-natal males was 459 days (Young et al., 2019a). Wild male vervets reach sexual maturity at 5-6 years of age, while females become sexually mature around 4-5 years of age (Horrocks, 1986). The adult sex ratio is typically 1.5 females for every one male in each troop (Fedigan & Fedigan, 1988). Vervets usually have linear dominance hierarchies, which are relatively stable in females but which may nevertheless vary across sites in their steepness, suggesting differences in competition for resources (Henzi et al., 2013). Male dominance ranks are more variable over time and point to the importance of physical condition in establishing dominance (Bramblett et al., 1982).

Vervets are sexually dimorphic. At the Samara field site, males weigh an average of 5.9 kg, and females weigh about 3.3 kg (Pasternak et al., 2013). Jarrett et al. (2020) compared two cohorts (2013 and 2014) of Samara juvenile vervets, and their results demonstrated growth parameters varied across the cohorts and also between the sexes within cohorts. At the end of the 800 days (the juvenile period), the average individual of the 2013 Cohort was 0.1 kg heavier than its counterpart from the 2014 Cohort. The 2013 Cohort also achieved a higher growth rate overall, where there was a maximum growth

rate difference of 0.35 g/day, which was reached ~44 days later than the 2014 Cohort (Jarrett et al., 2020). When comparing the sexes within cohorts, there was considerable overlap of maximum growth rate and predicted weight at 800 days between males and females from the 2013 Cohort. The shape of the growth curves were qualitatively similar, however the 2013 males were heavier than the 2013 females, and heavier than both sexes of the 2014 Cohort. Jarrett et al. (2020) also demonstrated differences within the sexes across the two cohorts, where the 2014 females had lower maximum growth rates and reached a lower weight at 800 days. Males from both cohorts had similar maximum growth rates, but the 2014 males were predicted to be lighter at 800 days, meaning they grew more slowly overall and/or were lighter at birth than their 2013 counterparts.

## **2.3 Study Populations**

### ***2.3.1 Inner Samara Population***

The study population of Inner Samara consisted of three troops (PT, RBM, and RST), with a mean total of 129 vervet monkeys across my study period. All troops were fully habituated to human observers, with RBM and RST having been studied since 2008, and PT since 2012. All individuals were uniquely identifiable from natural facial and body markings, ear nicks, and unique tail markings. See Table 2.1 for study population composition throughout the study period.

An activity budget was constructed to reflect the annual allocation of time by the adults and juveniles of all three troops to six activity categories (Table 2.2). The behaviours included in the activity budget fell into one of six mutually exclusive behaviour categories: (i) resting, (ii) foraging, (iii) moving, (iv) socializing, which included allo-grooming and allo-receiving, (v) playing, and (vi) other, which included

aggressive, mating, or other behaviours. See Section 2.4.1 below for operational definitions of behaviour categories.

**Table 2.1**

*Composition of the Inner Samara Study Troops over the Study Period*

<b>Age-Sex</b>	<b>Troop</b>	<b>Count Range</b>	<b>Mean</b>
Adult Females	PT	8-9	8
	RST	8-13	12
	RBM	6-10	9
Juvenile Females	PT	4-9	8
	RST	9-14	12
	RBM	5-16	13
Adult Males	PT	0-5	2
	RST	4-9	6
	RBM	2-6	3
Juvenile Males	PT	4-14	10
	RST	7-12	10
	RBM	7-13	11

**Table 2.2**

*The annual percentage of scan samples allocated to each behaviour category for adults and juveniles of the Inner Samara Troops*

	Resting	Foraging	Moving	Socializing	<b>Playing</b>	Other
<b>Adult</b>	35	28.3	25.1	8.5	0.4	2.9
<b>Juvenile</b>	32.1	28.8	24.7	6.2	6.5	2.1

### **2.3.2 Outer Samara Population**

The study population of Outer Samara consisted of one troop (MGT) of 24 individuals. All individuals were uniquely identifiable from natural facial and body markings, ear nicks, and unique tail markings. The troop had been studied since 2019 and was habituated to human presence. All animals in both subpopulations could therefore be

followed at a distance of between one to five meters. Date of birth was not available for any individual in the Outer Samara population. See Table 2.3 below for study troop composition.

An activity budget was also created for the Outer Samara population to reflect the amount of time allocated by adults and juveniles of MGT to the six behaviour categories over the entire study period. Please see Table 2.4 below.

**Table 2.3**

*Composition of the Outer Samara Study Troop over the Study Period*

<b>Age-Sex</b>	<b>Count Range</b>	<b>Mean</b>
MGT Adult Females	6-7	6
MGT Juvenile Females	7	7
MGT Adult Males	3-6	4
MGT Juvenile Males	4	4

**Table 2.4**

*The annual percentage of scan samples allocated to each behaviour category for adults and juveniles of the Outer Samara Troop*

	Resting	Foraging	Moving	Socializing	<b>Playing</b>	Other
<b>Adult</b>	33.1	30.7	27.9	6	0.1	2.7
<b>Juvenile</b>	30.4	32.7	26.9	5.9	3.5	1.2

## **2.4 Methods**

### **2.4.1 Behavioural Data Collection**

For both study areas, troops were followed for 10 hours a day, five days a week, by at least one observer on each study day. Field assistants were trained for a period of approximately two months, during which time they would be tested on the identification of each individual monkey and were given the opportunity to collect “practice data”. We

could then compare if their practice data aligned with data collected by more experienced field assistants.

Instantaneous scan sampling methods (Altmann, 1974) were conducted on all visible troop members at half-hour intervals using electronic data loggers (Trimble Juno) and proprietary software (Pendragon Forms version 5.1, © Pendragon Software Cooperation, U.S.A.). The scan periods lasted a maximum of 15 minutes. For each scan, the behaviour of each visible monkey was recorded. See Table 2.5 for the complete list of behaviours and descriptions used in our scan-sampling form. For each monkey scanned, we recorded the identity of the nearest adult female, adult male, and juvenile, together with their distances (in metres) from the focal subject. Each animal's location (ground, open, tree, shrub), height above the ground (in metres), use of shade (yes or no), posture (crouch, lie, locomote, sit, stand, or sun bask), distance to yearling (if applicable), and vigilance (environmental, social, not vigilant, human, unknown, other) was noted.

**Table 2.5**

*Descriptions of Behavioural Categories for Scan Sampling*

<b>Behaviour</b>	<b>Description</b>
Resting	Stationary (and positional behaviour: sitting or lying) and not doing any other (not feeding, travelling, or social, i.e., not being groomed) activity.
Moving	When the general activity of the individual is travelling, including short bouts of sitting and looking for the next steps to take or at the next individual in line
Foraging	Ingesting food. Put food into mouth and also chewing food in a feeding bout i.e., if it does not come from cheek pouches.
Auto-groom	When a monkey is grooming their own body
Allo-groomer	When a monkey is grooming another monkey.
Allo-receiver	When a monkey is being groomed by another monkey
Aggression	When the individual being scanned is involved in an aggressive interaction
Allo-mothering	The individual has a baby ventral and is looking after it. This is not their baby. This behaviour usually occurs with juveniles.

Copulating	Individual is mating with another individual at time of scan
Playing	One or more individuals are involved in play bout
Nursing	A female is sitting resting with her infant suckling with the nipple in the mouth.
Swimming	Individual is swimming in river/dam
Other	Monkey is performing an activity which fits none of these categories. Behaviour is described in the comments section

All aggressive interactions that were observed were recorded *ad libitum* in a dominance form on the electronic data logger. This form included the identity of the aggressor, the identity of the victim, and the outcome of the interaction from the perspective of the aggressor (win, lose, draw, unknown). The troop of each individual, conflict allies of the aggressor and victim (if any), surrounding monkeys, and post-conflict distance (in metres) were also recorded. See Young et al. (2017) for detailed methods.

#### **2.4.2 Play Bouts and Play Behaviour**

A play bout was defined as social, locomotor, or object play lasting at least five seconds. This duration was chosen as to be consistent with our scan sampling methods. A play bout might include role-reversals, self-handicapping behaviours, play-face signalling, mouthing/biting, and/or play mounting. See Table 2.6 below for operational definitions. In both data sets, only dyadic play bouts were included. Any play bout that contained more than two individuals was excluded. Play bouts with unknown partners were also excluded from analyses.

**Table 2.6**

*Operational Definitions of Play Behaviours*

<b>Behaviour</b>	<b>Definition</b>
Social Play	A playful interaction between two or more individuals
Object Play	Playful activity with an inanimate or animate object (including own body parts) <sup>1</sup>

Locomotor Play	Locomotor patterns include various movements and postures: running, walking, galloping, jumping, leaping, climbing in an energetic, jerky, and exaggerated way <sup>1</sup> there was no differentiation between solitary or social locomotor play
Rough and Tumble Play	A category of social play. A playful equivalent to agonistic wrestling (the aim is not to harm the play partner); monkeys are holding each other firmly (or only one holds the other) and are attempting to mouth each other and at the same time avoid being mouthed, for example, by pulling the other one's head away; they may be also pushing the other one away by their hindlimbs that helps them to get away from a disadvantageous position; monkeys play wrestle in different positions (standing, lying on a side or back), and these may change continuously; it is usual that monkeys rotate around each other <sup>1</sup>
Mouthing/Biting	A monkey gently bites its play partner or an object, it can be only an attempt to bite, not resulting in a physical contact with mouth/not resulting in injury of the partner <sup>1</sup>
Play-face	Monkey's mouth is wide open for several seconds (much longer than during agonistic behavior), teeth are only slightly exposed, eyes open or closed; no attempts to firmly bite <sup>1</sup>
Role-reversal	Play involves turn-taking where individuals take turns in different roles
Self-handicapping	Individuals put themselves in vulnerable positions or do not wrestle (in rough and tumble play) to their fullest potential. A behavior that puts the animal into unnecessary disadvantageous positions or situations <sup>1</sup>
Play mounting	A monkey positions itself behind the other one as if attempting to copulate; it may perform a few pelvic thrusts; usually it lasts only for a few seconds <sup>1</sup>

<sup>1</sup>. Petrů, Špinka, Charvátová, & Lhota (2009)

All data in this thesis were collected by either by me or field assistants who worked for the larger Samara project. In the Inner Samara dataset, 120,529 scan samples were collected over the three-year period, of which 5145 involved play behaviour. For the Outer Samara dataset, 16,346 scan samples were collected over the six-month period, with 318 scan samples in which play behaviour was recorded. Our data indicate no systematic bias in the number of scan samples collected from different individuals.

In addition to scan sampling methods, I collected continuous-recording focal samples (Altmann, 1974) and *ad libitum* play behaviour for the Outer Samara dataset.

Ten-minute focal samples were collected randomly from all juveniles ( $n = 11$ ) in the troop. A change in behaviour categories was only recorded if the behaviour lasted a minimum of five consecutive seconds. Sampling was biased towards juveniles to maximize the number of play bouts recorded. If an individual was out-of-sight for more than five minutes of the 10-minute focal, the focal was excluded from analyses. If an individual was temporarily unavailable due to group dispersal, another focal subject was used, and the missed focal sample was collected at the next available opportunity. An effort was made to collect relatively equal amounts of focal samples in the morning and afternoon per individual, where morning was defined as sunrise to 1159hr, and afternoon was defined as 1200hr to sunset. Nearest group members of the focal individual were recorded at the beginning and end of the focal observation in order to determine changing proximity and group dynamics throughout the focal sample. A total of 694 (105.8hr. Range: 9.19h-9.79h/individual) focal samples were collected, of which 350 were in the morning and 344 in the afternoon. *Ad libitum records* of play behaviour contributed an additional 436 bouts.

Compared to scan samples, focal sampling and *ad libitum* data collection allowed me to collect information on play bout duration, type of play (social, locomotor, or object), location of play bout (ground, open, tree, shrub), initiator and terminator of bouts, role-reversal, self-handicapping, and the frequency of play-face. Descriptive statistics for play bouts are presented below in Table 2.7.

**Table 2.7***Descriptive Statistics for Play Bouts in Both Datasets*

<b>Age-Sex</b>	<b>Troop</b>	<b>Count Range</b>	<b>Total</b>	<b>Mean</b>	<b>Monthly Average</b>
Adult Females	MGT	0-9	27	4	<b>4.50</b>
	PT	1-18	47	5	<b>1.31</b>
	RST	0-10	52	3	<b>1.44</b>
	RBM	0-6	20	2	<b>0.55</b>
Juvenile Females	MGT	18-82	326	47	<b>54.33</b>
	PT	78-152	1012	112	<b>28.11</b>
	RST	32-183	1446	103	<b>40.11</b>
	RBM	0-141	1158	83	<b>32.16</b>
Adult Males	MGT	0-6	10	2	<b>1.67</b>
	PT	0-30	44	6	<b>1.22</b>
	RST	0-9	40	3	<b>1.11</b>
	RBM	0-35	55	6	<b>1.53</b>
Juvenile Males	MGT	62-162	385	96	<b>64.17</b>
	PT	51-257	2116	163	<b>58.78</b>
	RST	0-395	2382	170	<b>66.17</b>
	RBM	0-242	1827	107	<b>50.75</b>

*Note:* Count range, total, mean, and average monthly number of play bouts for the four study troops across age-sex categories. Count Range, Total, and Mean columns use play bouts from the entire datasets (36 months for PT, RST, and RBM; 6 months for MGT).

### **2.4.3 Quantifying Measures**

#### **2.4.3.1 Age**

For both the Inner Samara and Outer Samara datasets, individuals were grouped into two broad categories, either juveniles or adults based on sexual maturity. Juveniles were defined as those who had not yet reached sexual maturity (from birth to less than ~3.5 years for females, less than ~5 years for males: (Jarrett et al., 2018)). Adults were defined as those who had reached sexual maturity (more than ~3.5 years for females, more than ~5 years for males). Although there were changes in age categories throughout both study periods, there were no play bouts recorded for any individual where play occurred both before and after an individual changed age categories. For example, if I

observed play bouts of a juvenile male, but did not observe any play bouts after he reached adulthood, the individual did not change age categories in my analysis, despite changing age categories over the study period.

#### ***2.4.3.2 Familiar Social Partners***

Familiar social partners, which I defined as social partners outside of play, generally in close proximity, were identified through grooming interactions and proximity measures using the simple association ratio index (SRI). The SRI uses observational data to estimate the probability of observing two individuals together, given that one has been seen (Cairns & Schwager, 1986). The SRI is calculated for each dyadic pair using the formula below developed by Cairns and Schwager (1986):

$$\text{SRI} = \frac{X}{X + Y_{AB} + Y_A + Y_B}$$

Where  $X$  is the number of times a pair of animals were observed in the same group,  $Y_{AB}$  is the number of times both animals were seen in different groups,  $Y_A$  is the number of times  $a$  was observed in the group, but not  $b$ , and  $Y_B$  is the number of times  $b$  was observed un the group, but not  $a$ .

For the Inner Samara dataset, a total of 7542 directed grooming interactions was observed via scan sampling methods. For the Outer Samara dataset, we collected a total of 905 directed grooming interactions. These grooming interactions were then used to create a grooming edgelist, a two-column matrix which tells us which two individuals are connected through an edge. I then used the “netTS” package with the “create.a.network” command, and specified “SRI = TRUE” (Bonnell & Vilette, 2019). This gave me an SRI estimate for each dyadic pair, based on grooming events. I refer to this estimate as the “groom SRI” in my results chapter below.

For proximity measures, I created an edgelist using the focal subject and their nearest neighbor. I used 114693 scan samples from the Inner Samara dataset and 17519 scan samples from the Outer Samara dataset, where the identity of the nearest neighbor was known. I subsequently calculated the SRI score for each dyad using the “netTS” package (Bonnell & Vilette, 2019). The SRI estimate used for the proximity measure is referred to the “proximity SRI” in the results chapter.

#### ***2.4.3.3 Kinship***

Although kinship is not explicitly stated in my predictions based off of the contemporary hypotheses, familiar social partners may very well include individuals who are related, and so I also investigated kinship as a separate variable. In the Inner Samara study area, the identity of mothers, their offspring, and maternal siblings of the monkeys studied within my study period was largely known. I had a total of 950 unique dyads engaging in play bouts, and in 827 of these unique dyads, I knew if the pair consisted of a mother and her offspring (yes/no) and if the dyad consisted of maternal siblings (yes/no). If the relationship of the dyad was unknown in either, or both of these categories, the dyad was excluded from analyses ( $n = 123$ ).

As the Outer Samara study area was relatively new, very little was known about kinship, and it was excluded as a response variable.

#### ***2.4.3.4 Dominance Hierarchies***

To establish dominance hierarchies, I used the aggressive interactions and their outcomes that were collected for each dataset. The Inner Samara and Outer Samara datasets had a total of 32,398 and 1,217 dominance interactions, respectively. Based on the actual temporal sequence of dominance interactions, sequential estimations of

individual dominance strengths could be calculated and expressed as Elo-ratings (Albers & De Vries, 2001). All analyses were conducted in R version 1.4.1717 (R Core Team, 2018). Elo-ratings were estimated using the package “EloRating” (Neumann et al., 2011). Higher Elo scores correspond to more dominant individuals (more winning outcomes), and scores decrease as individuals are more subordinate (more losing outcomes). Individual Elo-ratings can be used to track rank changes and estimate rank order within a group at any specified time. The number of points allotted to an individual after an outcome is determined by the  $k$  value, which was set to the default value of 100 (Neumann et al., 2011).

#### ***2.4.3.5 Physically Matched Partners***

Since growth parameters can vary between cohorts of wild vervet monkeys, and between sexes (Jarrett et al., 2020), the monkeys of Outer Samara were simply grouped into categories based on their estimated physical size at the end of the study period. Two observers (KF and LF) scored the monkeys independently to ensure inter-rater reliability. These size categories were then used as a measure for physically matched partners.

As the study period for the Inner Samara monkeys was over a period of 3 years, these monkeys were not scored based on physical size as there was no single field assistant present over the entire period. As a part of the larger project, monkeys were weighed on a scale, but as this was done non-invasively (see Jarrett et al. [2020] for methods), weight data was not available for each dyad, as some monkeys were never weighed. Therefore, physical size difference between dyads was excluded as a response variable in the Inner Samara data set.

## 2.5 Statistical Methods

All data were imported into R using the “readxl” (Wickham et al., 2019a) package. The social networks were constructed using packages “neTS” (Bonnell & Vilette, 2019), “igraph” (Csardi, 2013), and “dplyr” (Wickham et al., 2019b). The social networks were then plotted using the “ggplot2” package (Wickham, 2016).

### 2.5.1 General Model Information

Four multilevel Bayesian models with Poisson error distributions were generated using the “brms” package (Bürkner, 2017) to test my predictions. I pooled data from both Inner Samara and Outer Samara wherever possible, however some of the predictor variables were not available across both populations. As such, I had to make separate models for any category that was unique to either population (i.e., kinship, and size difference). I ran four chains for 3500 iterations, with convergence of the chains confirmed in each case ( $\hat{R} = 1.00$ ). For all models, bulk effective sample size estimates (Bulk-ESS) and tail effective sample size estimates (Tail-ESS) indicated that the posterior means and medians were reliable. I used the ‘posterior predictive check’ (pp\_check) function to assess the adequacy of model performance (Gabry et al., 2019), and the “testdispersion” function of the “DHARMa” package (Hartig, 2017). Posterior predictive checks for each model are presented in Appendix B. Posterior density distributions and other graphical outputs were generated with the “ggplot2” package (Wickham, 2016), and the “bayestestR” package (Makowski et al., 2019).

Credible intervals (CI) were set to 95% in tables and plots. Upper and lower credible intervals indicate the possible range an effect will fall into, such that we have a 95% probability that the effect will fall somewhere in between the upper and lower CI

values. Our interpretation of any shifts in the posterior estimates, and their directionality, is guided by the extent to which the upper and lower CIs cross zero. As an aid, I also estimated the ‘probability of direction’ (pd) for each effect using the “bayestestR” package (Makowski et al., 2019). The pd estimate ranges from 50% to 100% and uses the posterior distributions to determine the certainty of the direction of an effect (either positive or negative). The conditional and marginal  $R^2$  values were extracted from each model using the “bayes\_R2” function from the “brms” package (Bürkner, 2017). The conditional  $R^2$  value represents the variance of both the random and fixed effects, where the marginal  $R^2$  value represents the variance of the fixed effects (predictors) in the model (Gelman et al., 2019).

A Poisson distribution was chosen for these models given that my dependent response variable (play weight between a dyad) was count data. As I was interested in variables relating to who plays (rather than who does not), I did not have any zeroes in my response variable (i.e., dyads that never played). However, a Poisson model expects there to be zeroes in the dataset, and so I first transformed the dataset by subtracting all weights by a value of one (i.e., play weights of one count were transformed to weights of zero counts, counts of two were transformed to a count of one, etc.).

I set weakly informative priors centered on zero (i.e., normal (0,1)) for each model. All predictor variables were centred and scaled. For my categorical predictor variables of age and sex, I used juvenile-juvenile dyads and mixed-sex dyads as my references. In each model I controlled for number of scan samples for each monkey across the study period (as they varied from individual to individual) by setting an offset variable using the total number of scan samples of the combined dyad over the study

period. Model main effects are presented in summary statistics for posterior estimates, standard errors (SE), upper and lower 95% CIs, bulk and tail effective sample size estimates, and probability of direction estimates.

After each model had run, I also produced pairwise plots for predictor variables to ensure they were not correlated with one another (See Appendix B) using the “pairs” function of the “graphics” package (R Core Team, 2018). The predictor variables of kinship, grooming SRI, and proximity SRI were not correlated with one another, and this is discussed further in Section 4.4.

### ***2.5.2 Specific Parameters for The Four Troop Model***

In my first model, I used play bout data from all four troops across both datasets. I planned to include all dyad-age and dyad-sex categories, however as there were so few adult-adult dyads, I excluded this category from analysis. Data were analyzed using a multilevel Bayesian model with Poisson error distributions. The focal identity, partner identity, focal troop, partner troop, and study area (either Inner Samara or Outer Samara) were entered as crossed random effects. Predictor variables included: age, sex, rank difference, groom SRI, and proximity SRI.

My initial analysis of residuals for this model (using the “pp\_check” function of the “brms” package: Figure C.1; [Bürkner, 2017]; using the “testdispersion” function of the “DHARMA” package: Figure C.2; [Hartig, 2017]) revealed overdispersion in the data, meaning my data had more variance than the Poisson model expected. As suggested by Hilbe (2017), I adjusted for the overdispersion by using a negative-binomial model, which corrected the overdispersion (Figure C.3 and C.4) and revealed the same relative estimates

as the initial overdispersed Poisson model (Figure C.5). As such, results are presented from the Poisson model as posterior interval estimates in Table 3.1.

### ***2.5.3 Specific Parameters for The Juvenile Model***

I wanted to be sure the effects of the first model were not dramatically influenced by the low proportion of adult-juvenile dyads included in the model, and so I ran the first model again, but with the adult-juvenile dyads excluded. I analyzed the juvenile-juvenile play bouts using a multilevel Bayesian model, specifying a Poisson error distribution. The focal identity, partner identity, focal troop, partner troop, and study area were entered as crossed random effects. Predictor variables included: sex, rank difference, groom SRI, and proximity SRI.

Like the previous model, the initial analysis of residuals for this model revealed overdispersion in the data (See Figure C.6 and C.7 in the appendix). I ran the model again using a negative binomial error structure, which adjusted for the overdispersion (C.8 and C.9) and resulted in similar estimates to the Poisson model (Figure C.10). Results are presented from the Poisson model as posterior interval estimates in Table 3.2.

### ***2.5.4 Specific Parameters for The Kinship Model***

To explore the effects of kinship, I included only dyads where relatedness was known from the Inner Samara population, and again used a multilevel Bayesian model, with a Poisson error distribution. The focal identity, partner identity, focal troop, and partner troop, were entered as crossed random effects. Predictor variables included: sex, rank difference, groom SRI, proximity SRI, and kinship. Again, posterior prediction checks revealed overdispersion (Figure C.11 and C.12), which I corrected by switching the model type to a negative binomial (Figure C.13 and C.14). Estimates from both

models were comparable (Figure C.15) and I present posterior interval estimates from the Poisson model in Table 3.3.

#### ***2.5.5 Specific Parameters for The Size Difference Model***

Physical size difference is the last variable related to my predictions to be explored, and so I also constructed a fourth multilevel Bayesian model with a Poisson error distribution, to explore the effects of physical size difference between dyads in the Outer Samara population in relation to play bouts. As I only had size difference information available in the MGT troop, the data frame was smaller than the previous three models ( $n = 71$  unique dyads). The focal identity and partner identity were entered as crossed random effects. Predictor variables included: sex, age, rank difference, groom SRI, proximity SRI, and size difference. Using the “pp\_check” function (Gabry et al., 2019), I assessed model performance to be adequate (C.16), however the “testdispersion” function of the “DHARMA” package (Hartig, 2017) revealed underdispersion in the Poisson model (C.17). I attempted to correct the underdispersion by switching the model type to a hurdle Poisson, a negative binomial, and a hurdle negative binomial, all of which did not correct the underdispersion (See Figure C.18). However, given that the model converged, bulk-ESS, tail-ESS indicated that the posterior means and medians were reliable, and the “pp\_check” indicated adequate model performance we still present the results from the size difference model with a Poisson error distribution (Table 3.4).

## CHAPTER 3: RESULTS

With the combined datasets from both study periods, I found female-female dyads had the lowest proportion of play bouts recorded (18.7%), followed by mixed sex dyads (37.8%), with male-male dyads accounting for the largest proportion of play bouts (43.5%). When looking at play bouts by age category, juvenile-juvenile dyads accounted for the highest proportion of play bouts (94.6%), whereas adult-juvenile and adult-adult dyads only accounted for a very small proportion (5.3% and 0.02%, respectively).

### 3.1 Four Troop Model Results

The Four Troop Model main effects are presented in summary statistics for posterior estimates, standard errors (SE), upper and lower 95% CIs, bulk and tail effective sample size estimates, and probability of direction estimates in Table 3.1 and Figure 3.1 below.

**Table 3.1**

*Posterior Estimates of Play Probabilities for the Four Troop Model*

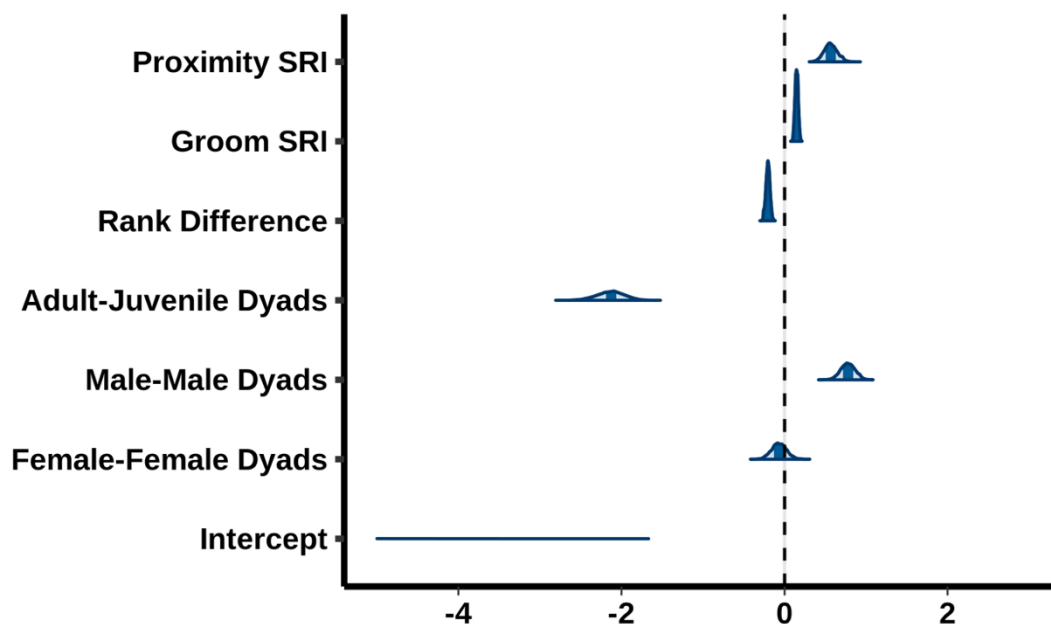
Effect	Parameter	Estimate	S.E.	l-95%	u-95%	Bulk	Tail	PD
				CI	CI	ESS	ESS	
<b>Population-Level Effects</b>	Intercept (Juvenile-Juvenile dyads)	-7.38	1.11	-9.73	-5.01	2985	3128	100%
	Female-Female Dyads	-0.07	0.09	-0.25	0.12	1424	3094	77.07%
	Male-Male Dyads	0.78	0.09	0.60	0.95	1017	755	100%
	Adult-Juvenile Dyads	-2.13	0.17	-2.48	-1.81	3191	4870	100%
	Elo Rank Difference	-0.20	0.03	-0.26	-0.15	1601	275	100%
	Groom SRI	0.15	0.02	0.11	0.19	7638	5678	100%
	Proximity SRI	0.57	0.08	0.41	0.73	1931	586	100%

	sd(Focal ID)	0.43	0.05	0.34	0.54	1427	2837	--
<b>Group-Level Effects</b>	sd(Focal Troop)	0.47	0.49	0.02	1.84	1596	1885	--
	sd(Partner ID)	0.61	0.06	0.50	0.73	1527	3410	--
	sd(Partner Troop)	0.50	0.51	0.03	1.94	1252	2009	--
	sd(Study Area)	1.59	1.72	0.06	5.81	834	231	--

*Note:* Sex is relative to mixed-sex dyads. Age is relative to juvenile-juvenile dyads. S.E.: Standard Error of the estimate, CI: credible interval, Bulk ESS: bulk effective sample size estimate, Tail ESS: tail effective sample size estimate, PD: probability of direction. N = 1024.  $R^2$  marginal = 0.247,  $R^2$  conditional = 0.537.

**Figure 3.1**

*Posterior Density Plot of the Four Troop Model Using a Poisson Distribution*



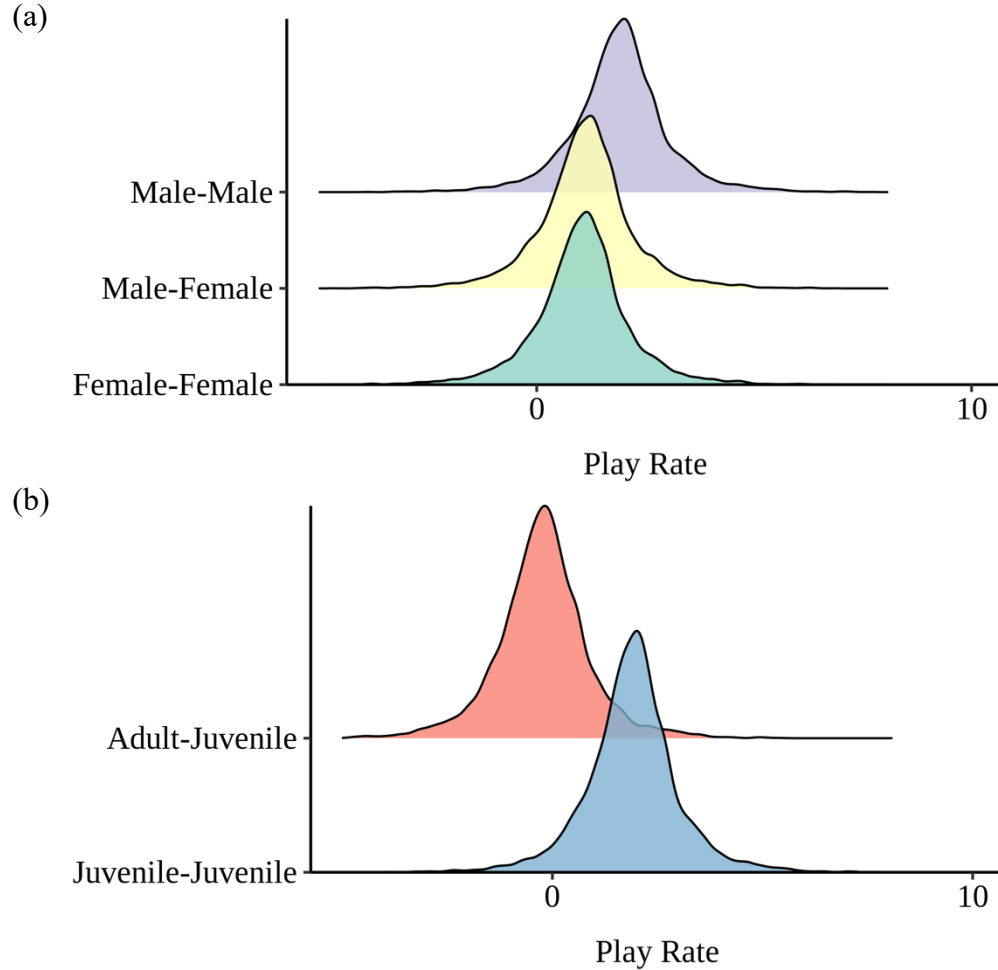
*Note:* Posterior estimates of play partner probabilities. Density plots indicate the range of rates predicted by the model, where the distance from 0 indicates the strength of the effect, and the width of the curve indicating the uncertainty of the estimate. Sex is relative to mixed-sex dyads. Age is relative to juvenile-juvenile dyads

**Age and Sex.** Compared to mixed-sex dyads, I found that male-male dyads played more frequently (Figure 3.2a). The effect direction for female-female dyads in comparison to mixed-sex dyads was unclear ( $pd = 77.07\%$ ). However, as seen in the

density plot Figure 3.2 below, male-female-and female-female dyads have similar play bout ranges. Compared to juvenile-juvenile dyads, I found play frequency to be negatively correlated with adult-juvenile dyads. Specifically, adult-juvenile dyads were less likely to engage in play bouts (Figure 3.2b).

**Figure 3.2**

*Rates of Play by (a) Dyad-Sex and (b) Dyad-Age in the Four Troop Model*



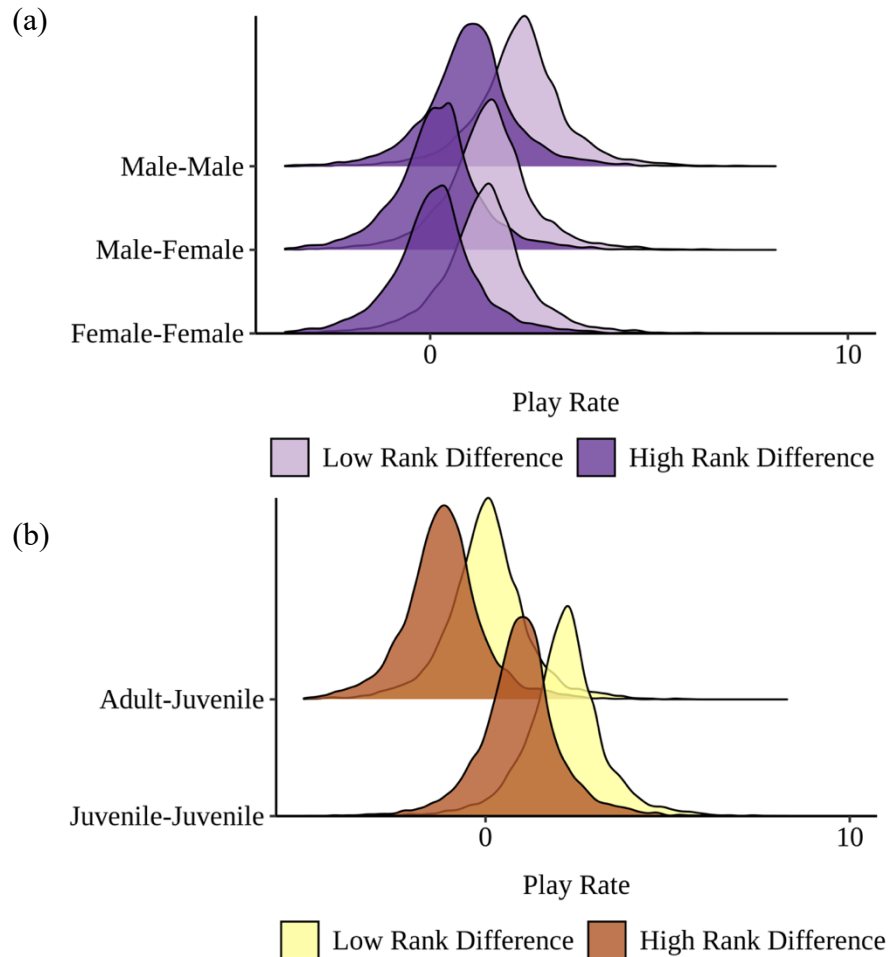
*Note:* Density plots present the range of play rates predicted by the model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 3.1).

**Rank Difference.** I found that rank difference had an effect on play bout frequency, where the smaller the difference in dominance rank between a dyad, the higher the play rate. In all dyad-sex and dyad-age categories, dyads who had a lower rank

difference engaged in more play bouts compared to dyads where there was a larger difference in rank (Figure 3.3).

**Figure 3.3**

*Rates of Play Compared to Rank Difference Across (a) Dyad-Sex and (b) Dyad-Age in the Four Troop Model*

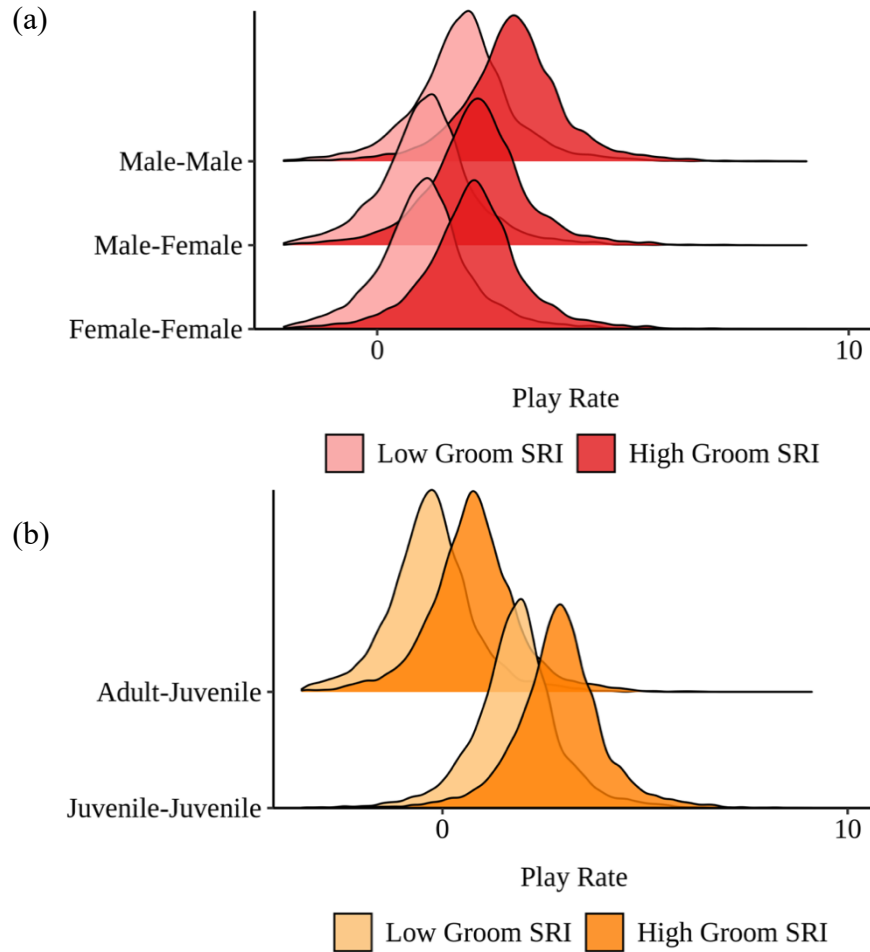


*Note:* Density plots present the range of play rates predicted by the four troop model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 3.1).

**Groom SRI.** I found a positive correlation between play bouts and groom SRI, where those who had higher groom SRI scores (indicating more grooming events between the dyad) had higher rates of play. As shown in the density plots below (Figure 3.4), the positive relationship between groom SRI and play rate was consistent in all dyad age and sex categories.

**Figure 3.4**

*Rates of Play Compared to Groom SRI Across (a) Dyad-Sex and (b) Dyad-Age in the Four Troop Model*

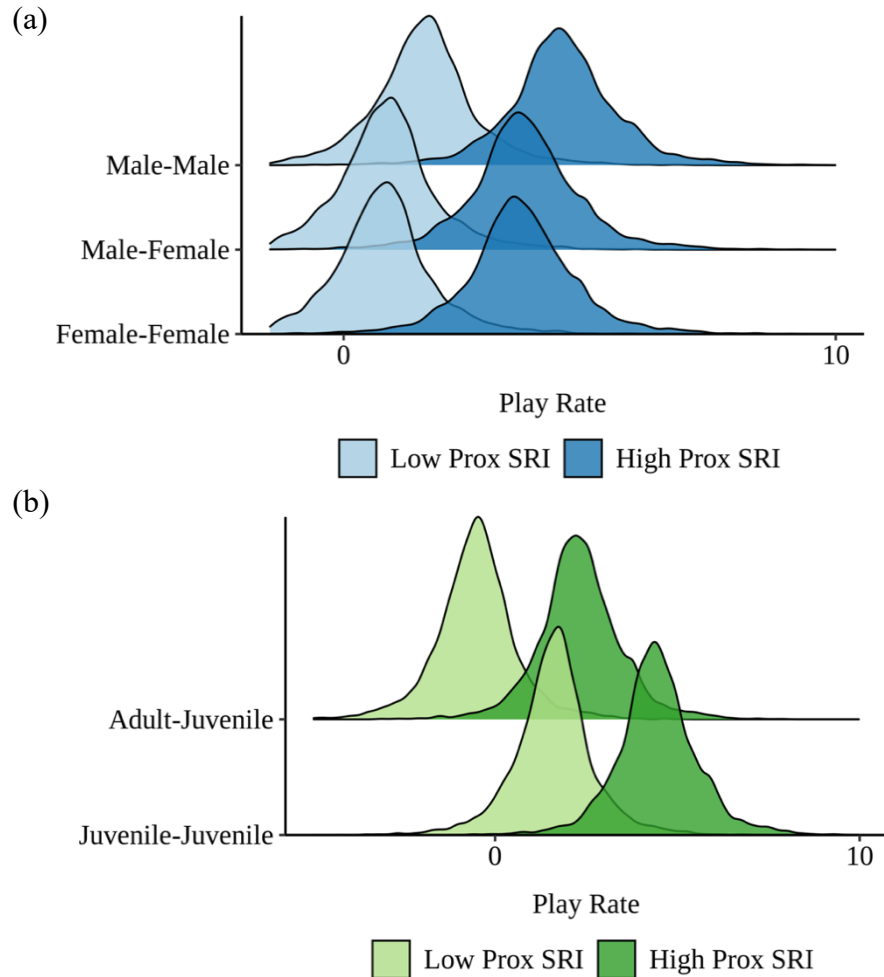


*Note:* Density plots present the range of play rates predicted by the four troop model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 3.1).

**Proximity SRI.** I also found a positive correlation between proximity SRI and play rates. Meaning dyads generally in close proximity had higher rates of play. This was consistent across all age and sex dyad categories (See Figure 3.5)

**Figure 3.5**

*Rates of Play Compared to Proximity SRI Across (a) Dyad-Sex and (b) Dyad-Age in the Four Troop Model*



*Note:* Density plots present the range of play rates predicted by the four troop model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 3.1).

My model revealed variation with respect to group-level effects (Table 3.1). There was variation across individual focal identities, and across individual partner identities. There was no group-level variation between the two study areas, between the focal troop or partner troop. The conditional  $R^2$  for my model was 0.537, and the marginal  $R^2$  was 0.247. A comparison of marginal and conditional  $R^2$  values suggests that the random effects account for ~29% of the variance within this model.

### 3.2 Juvenile Model Results

The Juvenile Model main effects are presented in summary statistics for posterior estimates, standard errors (SE), upper and lower 95% CIs, bulk and tail effective sample size estimates, and probability of direction estimates in Table 3.2 and Figure 3.6 below.

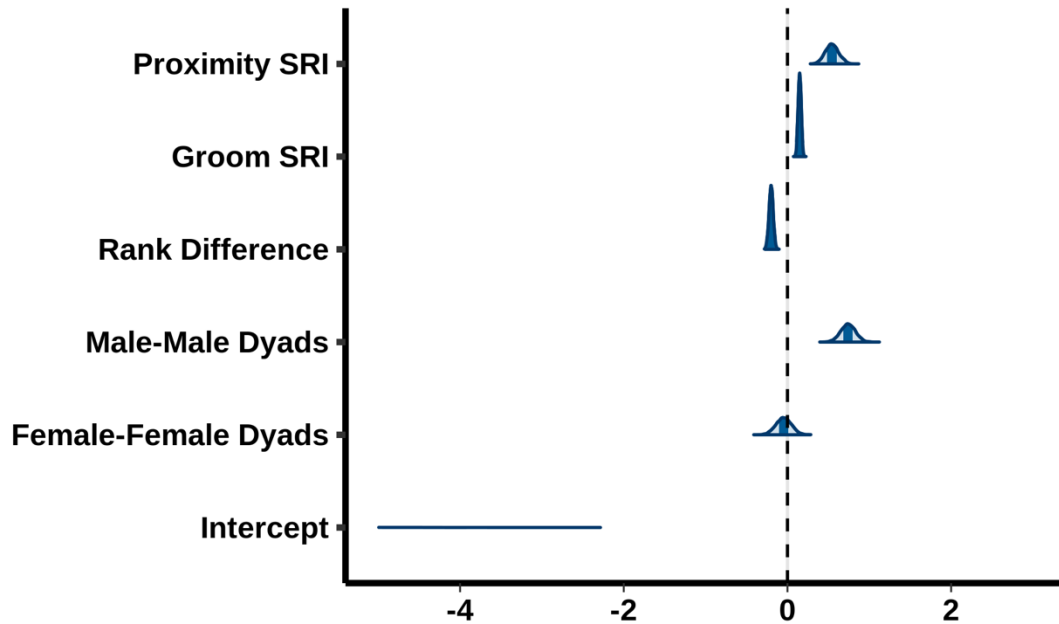
**Table 3.2**  
*Posterior Estimates of Play Probabilities for the Juvenile Model*

Effect	Parameter	Estimate	S.E.	l-95% CI	u-95% CI	Bulk ESS	Tail ESS	PD
<b>Population-Level Effects</b>	Intercept (Male-Female Dyads)	-7.39	1.06	-9.53	-5.02	3015	2971	100 %
	Female-Female Dyads	-0.05	0.10	-0.23	0.14	1111	2518	68.89%
	Male-Male Dyads	0.74	0.09	0.56	0.92	965	2149	100%
	Elo Rank Difference	-0.20	0.03	-0.25	-0.15	5141	4459	100%
	Groom SRI	0.15	0.02	0.11	0.19	6135	5263	100%
	Proximity SRI	0.54	0.08	0.39	0.71	4647	4934	100%
<b>Group-Level Effects</b>	sd(Focal ID)	0.46	0.05	0.36	0.57	1464	2524	--
	sd(Focal Troop)	0.50	0.52	0.02	1.93	1288	1409	--
	sd(Partner ID)	0.56	0.06	0.45	0.68	1292	2542	--
	sd(Partner Troop)	0.46	0.53	0.02	1.89	1392	1863	--
	sd(Study Area)	1.42	1.18	0.07	4.51	3287	2814	--

*Note:* Sex is relative to mixed-sex dyads. S.E.: Standard Error of the estimate, CI: credible interval, Bulk ESS: bulk effective sample size estimate, Tail ESS: tail effective sample size estimate, PD: probability of direction. N = 820.  $R^2$  marginal = 0.209,  $R^2$  conditional = 0.494.

**Figure 3.6**

*Posterior Density Plot of the Juvenile Model Using a Poisson Distribution*

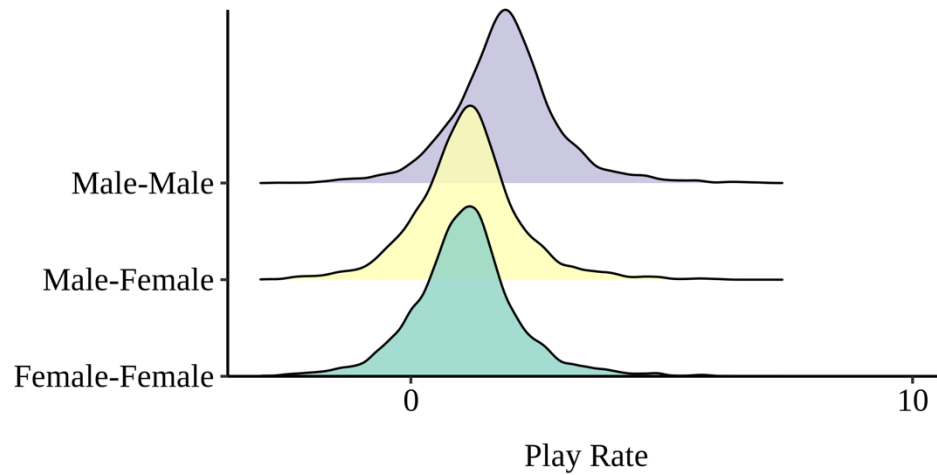


*Note:* Posterior estimates of play partner probabilities. Density plots indicate the range of rates predicted by the model, where the distance from 0 indicates the strength of the effect, and the width of the curve indicating the uncertainty of the estimate. Sex is relative to mixed-sex dyads.

**Sex.** In my juvenile model focussing on play bouts between only juveniles, the effects of sex on play are comparable to our previous model. Male-male dyads had higher rates of play in comparison to mixed-sex dyads, and the direction of effect of the female-female dyads remained uncertain (pd = 68.89%). Rates of play in the juvenile model are plotted below (Figure 3.7) in density plots.

**Figure 3.7**

*Rates of Play in the Juvenile Model According to Dyad-Sex Category*

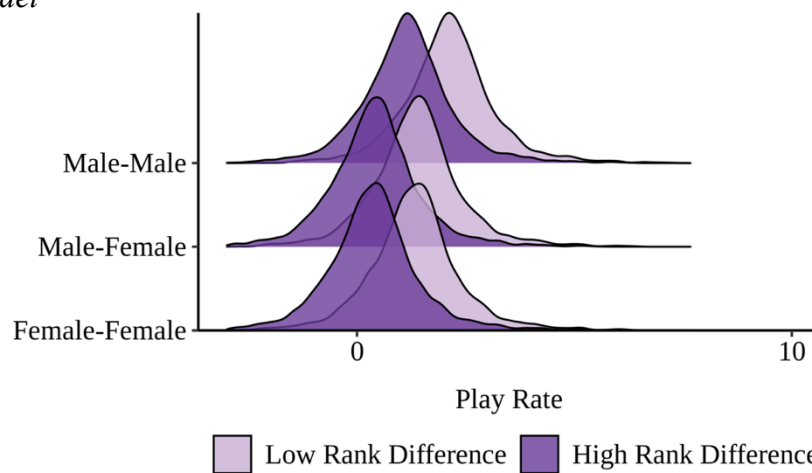


*Note:* Density plots present the range of play rates predicted by the juvenile model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 3.2).

**Rank Difference.** Rank difference also had a negative correlation with play bouts in our juvenile model, where the smaller the difference in rank, the more play bouts the dyad would engage in. This effect was consistent across dyad-sex categories as shown below in the density plot Figure 3.8.

**Figure 3.8**

*Rates of Play Compared to Rank Difference According to Dyad-Sex Category in the Juvenile Model*

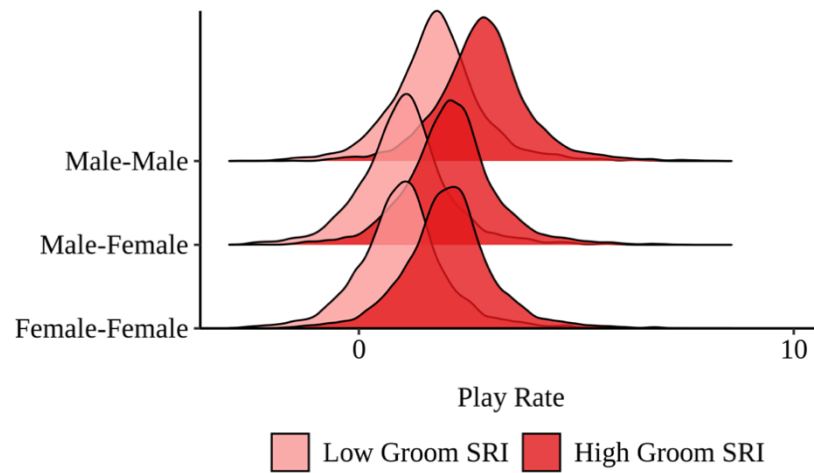


*Note:* Density plots present the range of play rates predicted by the juvenile model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 3.2).

**Groom SRI.** The juvenile model also found that more play bouts occurred in dyads that had a higher groom SRI score. Meaning dyads who more frequently groomed had higher rates of play than dyads that groomed less. See Figure 3.9.

**Figure 3.9**

*Rates of Play Compared to Groom SRI According to Dyad-Sex Category in the Juvenile Model*

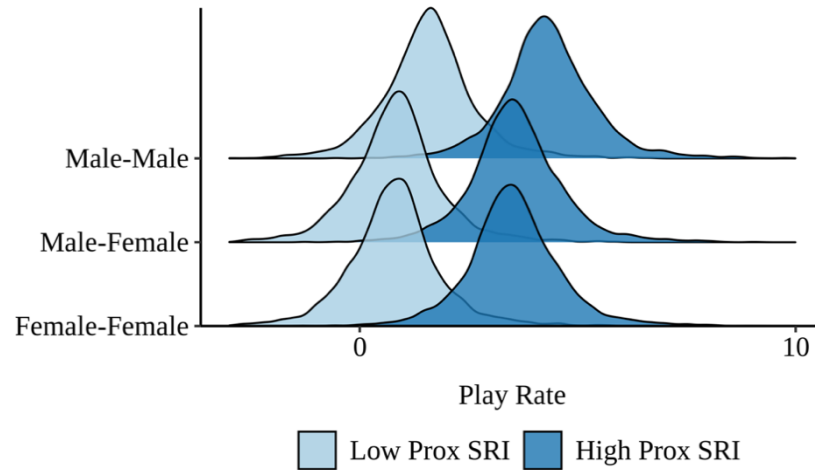


*Note:* Density plots present the range of play rates predicted by the juvenile model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 3.2).

**Proximity SRI.** Like groom SRI, proximity SRI also had a positive correlation with play bouts in the juvenile model. Where dyads who spent more time in close proximity to each other had higher rates of play compared to dyads that do not. This effect was similar across each dyad-sex category (See Figure 3.10).

**Figure 3.10**

*Rates of Play Compared to Proximity SRI According to Dyad-Sex Category in the Juvenile Model*



*Note:* Density plots present the range of play rates predicted by the juvenile model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 3.2).

My juvenile model revealed variation with respect to group-level effects (Table 3.2). There was variation across individual focal identities, across individual partner identities, and between the two study areas. There was no group-level variation between the focal troops or partner troops. The conditional  $R^2$  for this model was 0.494, and the marginal  $R^2$  was 0.209. A comparison of marginal and conditional  $R^2$  values suggests that the random effects account for ~29% of the variance within the model.

### 3.3 Kinship Model Results

The Kinship Model included 883 unique dyads where kinship was known, from the Inner Samara population. Model main effects are presented in summary statistics for posterior estimates, standard errors (SE), upper and lower 95% CIs, bulk and tail effective sample size estimates, and probability of direction estimates in Table 3.3 and Figure 3.11 below.

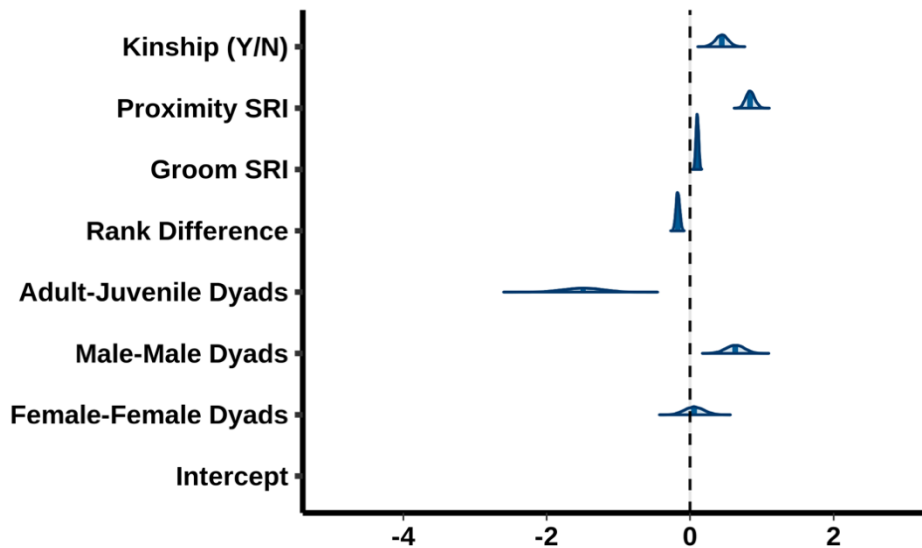
**Table 3.3**  
*Posterior Estimates of Play Probabilities for the Kinship Model*

Effect	Parameter	Estimate	S.E.	l-95%	u-95%	Bulk	Tail	PD
				CI	CI	ESS	ESS	
<b>Population-Level</b>	Intercept (Mixed-Sex Dyads)	-7.32	0.62	-8.67	-5.99	1521	1817	100%
	Female-Female Dyads	0.06	0.14	-0.21	0.33	541	1191	66.50%
	Male-Male Dyads	0.63	0.13	0.38	0.89	534	1148	100%
	Adult-Juvenile Dyads	-1.52	0.27	-2.05	-1.02	2043	4025	100%
	Elo Rank Difference	-0.17	0.03	-0.23	-0.12	4969	5365	100%
	Groom SRI	0.10	0.02	0.07	0.14	5302	5340	100%
	Proximity SRI	0.85	0.06	0.74	0.97	2185	3043	100%
	Kinship (Y/N)	0.45	0.09	0.28	0.62	5160	5021	100%
	sd(Focal ID)	0.65	0.08	0.51	0.83	935	2158	--
<b>Group-Level</b>	sd(Focal Troop)	0.81	0.67	0.15	2.69	1441	2002	--
<b>Effects</b>	sd(Partner ID)	0.87	0.09	0.69	1.07	985	1866	--
	sd(Partner Troop)	0.38	0.49	0.01	1.77	1351	2783	--

*Note:* Sex is relative to mixed-sex dyads. Age is relative to juvenile-juvenile dyads. S.E.: Standard Error of the estimate, CI: credible interval, Bulk ESS: bulk effective sample size estimate, Tail ESS: tail effective sample size estimate, PD: probability of direction. N = 833.  $R^2$  marginal = 0.389,  $R^2$  conditional = 0.548.

**Figure 3.11**

*Posterior Density Plot of the Kinship Model Using a Poisson Distribution*

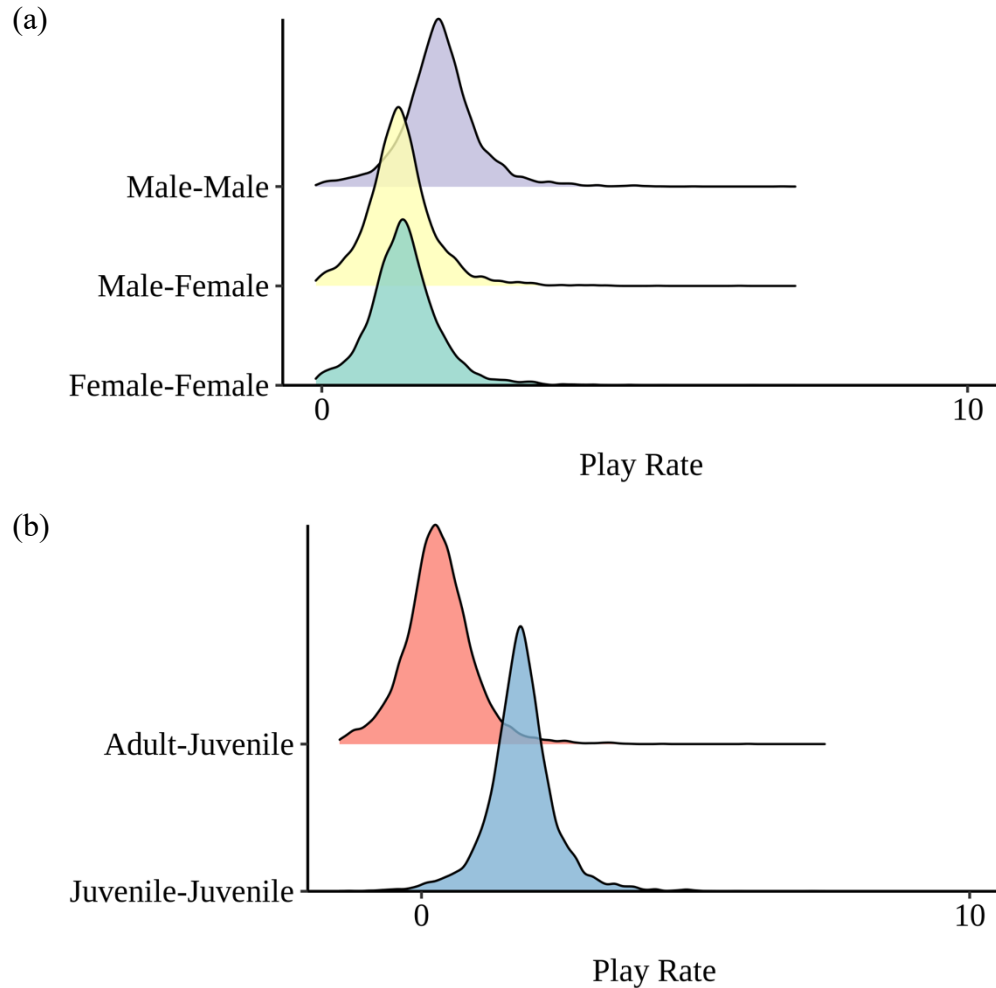


*Note:* Posterior estimates of play partner probabilities. Density plots indicate the range of rates predicted by the model, where the distance from 0 indicates the strength of the effect, and the width of the curve indicating the uncertainty of the estimate. Sex is relative to mixed-sex dyads. Age is relative to juvenile-juvenile dyads

**Age and Sex.** As with my previous models, I found that in comparison to mixed-sex dyads, male-male dyads played more frequently. This model was also uncertain about the direction of effect of the female-female dyads ( $pd = 66.50\%$ ). Adult-juvenile dyads were less likely to play in comparison to juvenile-juvenile dyads. Density plots are presented below.

**Figure 3.12**

*Rates of Play in the Kinship Model According to (a) Dyad-Sex and (b) Dyad-Age Category*

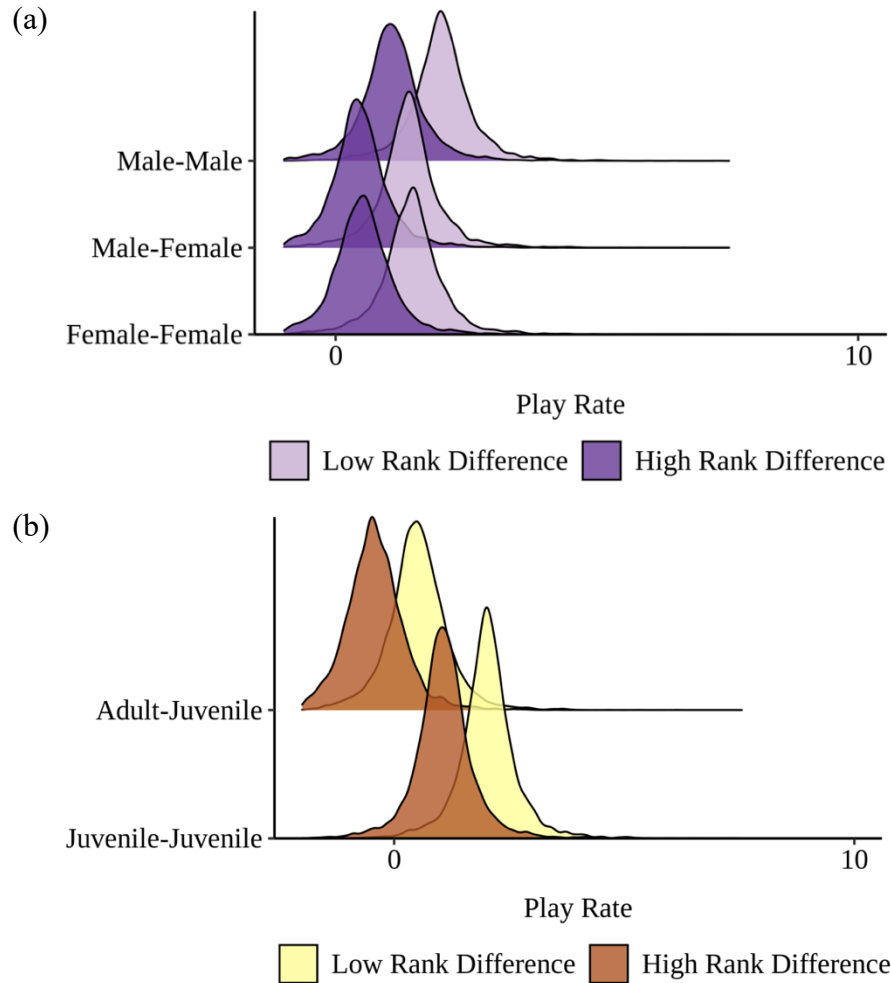


*Note:* Density plots present the range of play rates predicted by the kinship model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 3.3).

**Rank Difference.** Similar to the previous models, I found a negative correlation between dominance rank difference and play bout frequency. Dyads with smaller differences in dominance ranks were more likely to have more play bouts. This effect was consistent across dyad-sex and dyad-age categories as shown in Figure 3.13.

**Figure 3.13**

*Rates of Play Compared to Rank Difference Across (a) Dyad-Sex and (b) Dyad-Age Categories in the Kinship Model*

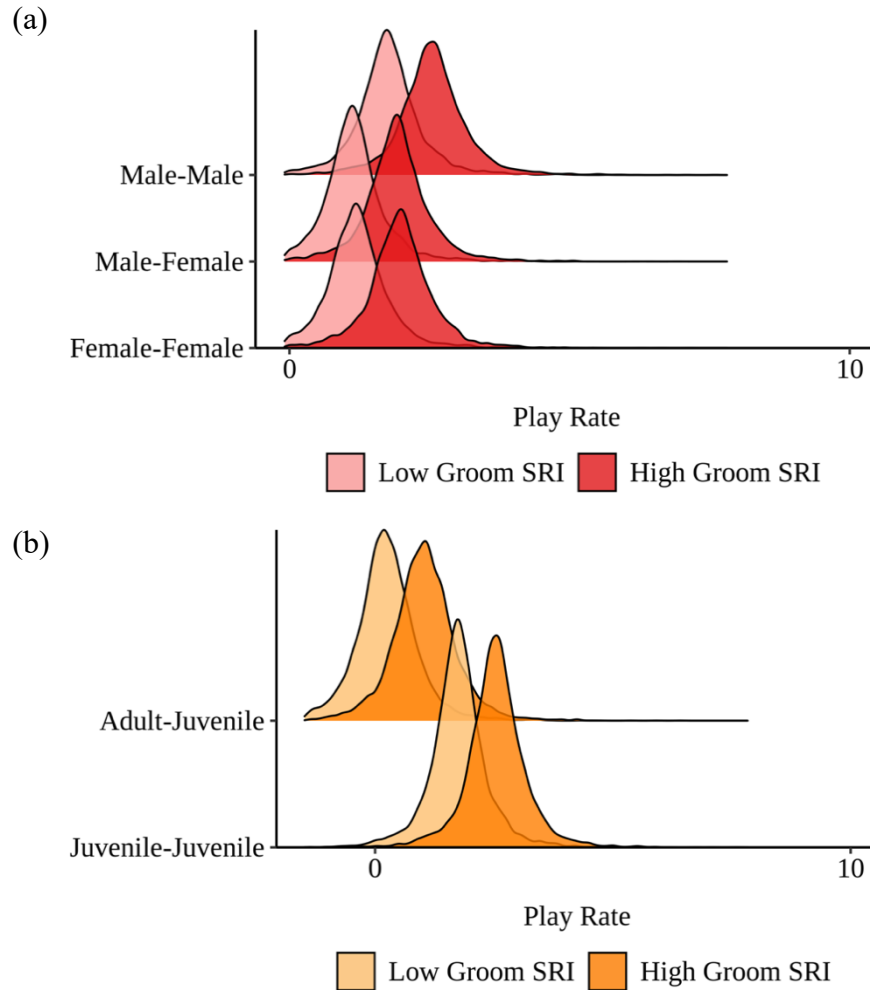


*Note:* Density plots present the range of play rates predicted by the kinship model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 3.3).

**Groom SRI.** I found that Groom SRI rates between dyads were positively correlated with play rates in the kinship model. A dyad with higher grooming SRI scores (more grooming events between the dyad) also had more play bouts. Density plots with dyad-age and dyad-sex categories are shown below.

**Figure 3.14**

*Rates of Play Compared to Groom SRI Across (a) Dyad-Sex and (b) Dyad-Age Categories in the Kinship Model*

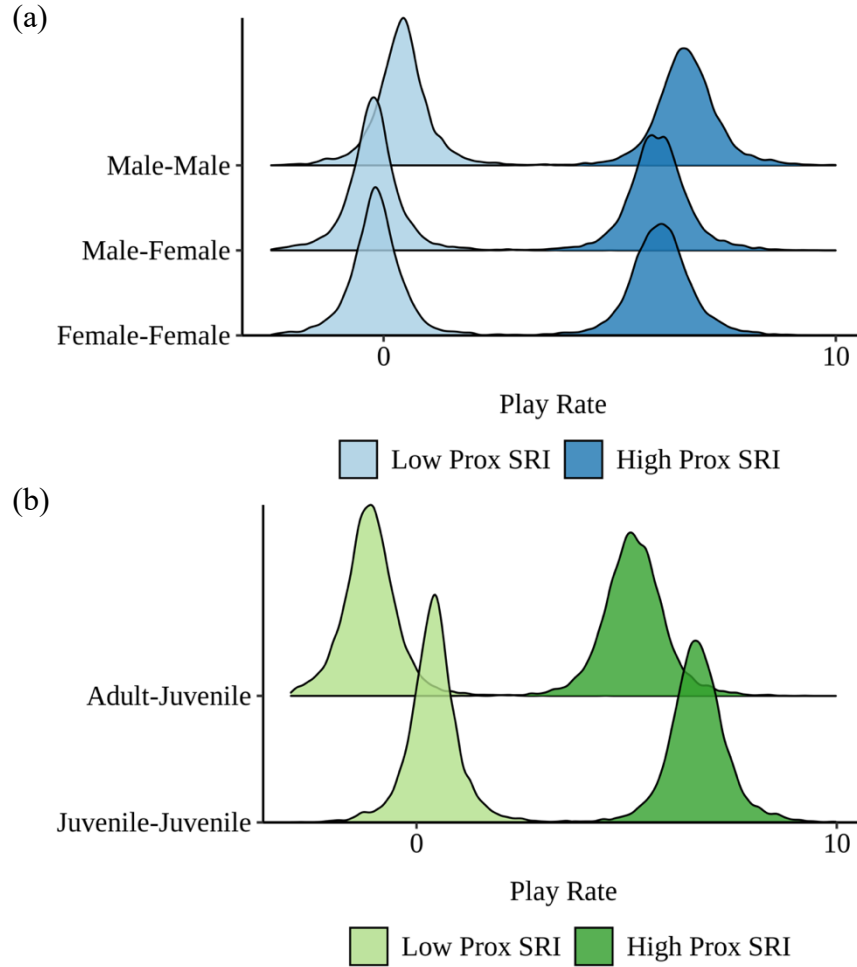


*Note:* Density plots present the range of play rates predicted by the kinship model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 3.3).

**Proximity SRI.** Like my previous models, the kinship model also found that with higher proximity rates between a dyad, the higher the rate of play. The previous density plots of the kinship model have been similar to the four troop model and juvenile model, however I saw with the proximity SRI density plots (Figure 3.15), the differences between a high and low proximity SRI score were more pronounced.

**Figure 3.15**

*Rates of Play Compared to Proximity SRI Across (a) Dyad-Sex and (b) Dyad-Age Categories in the Kinship Model*

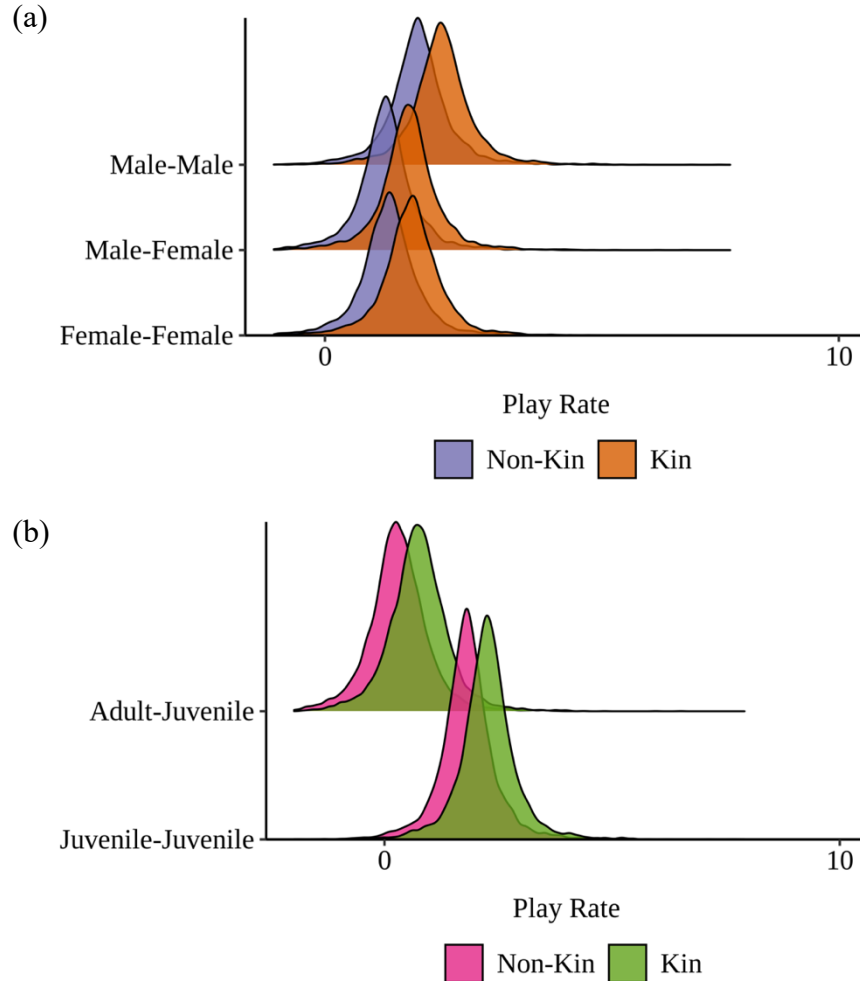


*Note:* Density plots present the range of play rates predicted by the kinship model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 3.3).

**Kinship.** I found evidence that related dyads (which included maternal siblings and mother-offspring dyads) had higher rates of play bouts compared to non-related dyads in the kinship model.

**Figure 3.16**

*Rates of Play Compared to Kinship Across (a) Dyad-Sex and (b) Dyad-Age Categories in the Kinship Model*



*Note:* Density plots present the range of play rates predicted by the kinship model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 3.3).

The kinship model revealed variation with respect to group-level effects (Table 3.3). There was variation across individual focal identities, across individual partner identities, and between focal troops. There was no group-level variation between the partner troops. The conditional  $R^2$  for our model was 0.548, and the marginal  $R^2$  was 0.389. A comparison of marginal and conditional  $R^2$  values suggests that the random effects account for ~16% of the variance within this model.

### 3.4 Size Difference Model Results

The Size Difference Model included 71 dyads where physical size information was available from the MGT troop. Model main effects are presented in summary statistics for posterior estimates, standard errors (SE), upper and lower 95% CIs, bulk and tail effective sample size estimates, and probability of direction estimates in Table 3.4 and Figure 3.17 below.

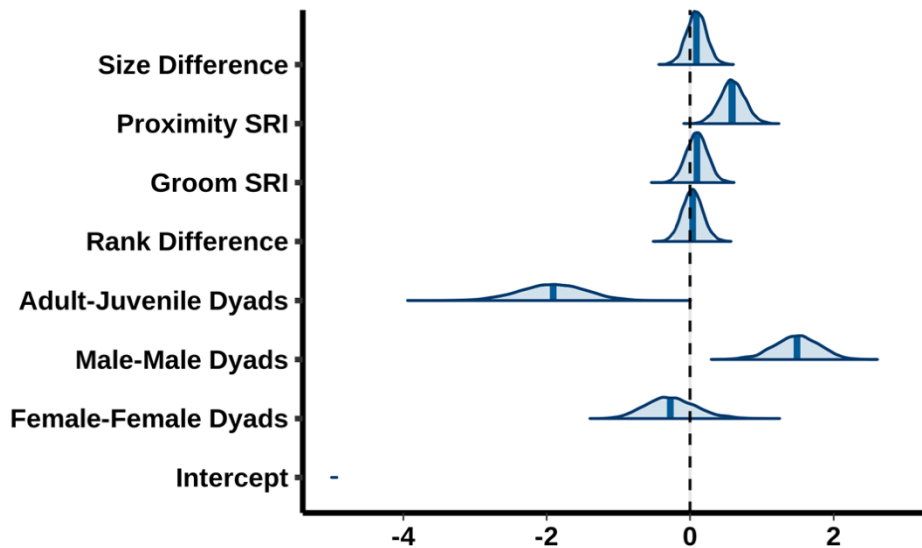
**Table 3.4**  
*Posterior Estimates of Play Probabilities for the Size Difference Model*

Effect	Parameter	Estimate	S.E.	l-95%	u-95%	Bulk	Tail	PD
				CI	CI	ESS	ESS	
<b>Population-Level Effects</b>	Intercept (Mixed-Sex Dyads)	-6.45	0.34	-7.16	-5.83	3094	4334	100%
	Female-Female Dyads	-0.26	0.35	-0.90	0.50	2891	4452	77.56%
	Male-Male Dyads	1.48	0.32	0.82	2.08	3752	4839	100%
	Adult-Juvenile Dyads	-1.92	0.46	-2.84	-1.04	5623	4988	99.99%
	Elo Rank Difference	0.04	0.14	-0.24	0.33	6651	5497	59.57%
	Groom SRI	0.10	0.15	-0.19	0.39	8058	5791	74.69%
	Proximity SRI	0.59	0.17	0.25	0.93	5437	5144	99.90%
	Size Difference	0.09	0.14	-0.19	0.36	5491	4998	74.70%
<b>Group-Level</b>	sd(Focal ID)	0.45	0.24	0.07	0.99	1759	2105	--
<b>Effects</b>	sd(Partner ID)	0.77	0.23	0.44	1.30	2847	3963	--

*Note:* Sex is relative to mixed-sex dyads. Age is relative to juvenile-juvenile dyads. S.E.: Standard Error of the estimate, CI: credible interval, Bulk ESS: bulk effective sample size estimate, Tail ESS: tail effective sample size estimate, PD: probability of direction. N = 71.  $R^2$  marginal = 0.519,  $R^2$  conditional = 0.885.

**Figure 3.17**

*Posterior Density Plot of the Size Difference Model Using a Poisson Distribution*



*Note:* Posterior estimates of play partner probabilities. Density plots indicate the range of rates predicted by the model, where the distance from 0 indicates the strength of the effect, and the width of the curve indicating the uncertainty of the estimate. Sex is relative to mixed-sex dyads. Age is relative to juvenile-juvenile dyads

The size difference model had difficulties predicting the direction of effect for many of my predictor variables. I was unable to determine whether size difference, groom SRI, rank difference, or female-female dyads in relation to mixed sex dyads, had any influence on play bout frequency. I did find a positive correlation between proximity SRI and play frequency, male-male dyads (in comparison to mixed-sex dyads), and play frequency, and a negative correlation between adult-juvenile dyads (in comparison to juvenile-juvenile dyads) and play frequency. The predictor variables that the model was confident with all had the same direction of effect compared to previous models. However, there was much more uncertainty in this model as shown by the wider ranges of posterior estimates in Figure 3.17.

The size difference model revealed variation with respect to group-level effects (Table 3.4), where there was variation across individual focal identities, and partner identities. The conditional  $R^2$  for my model was 0.885, and the marginal  $R^2$  was 0.519, and a comparison of the two suggests that the random effects account for ~37% of the variance within this model.

## CHAPTER 4: DISCUSSION AND CONCLUSIONS

The goal of this thesis was to determine which, if any, of the contemporary hypotheses of play – the training for the unexpected, dominance hierarchy, social skills, and self-assessment hypotheses – were supported by the vervet monkeys in the Samara Game Reserve. Here, I will summarize my overall findings, discuss how they relate to the existing literature, reflect on the limitations of my study, and outline future research directions.

### 4.1 Hypotheses Supported by the Samara Vervets

I found that adult-juvenile dyads played much less frequently than juvenile-juvenile dyads. In comparison to mixed-sex dyads, male-male dyads were more likely to have higher frequencies of play bouts. These age and sex effects were consistent across all four models. Both proximity SRI and grooming SRI had a positive relationship with play bouts – dyads who were more often spatially associated, and who groomed together often, played the most. As the kinship model indicated, kin preferred to play with kin rather than non-kin. In terms of dominance rank, I found that animals with similar dominance rankings were more likely to have higher rates of play than those with differing dominance rankings. Finally, I found no effect of body size difference on play bouts. I found full support for one of my predictions, and at least partial support for two out of four of my predictions.

*Under the training for the unexpected hypothesis, animals will prefer to play with familiar social partners and should exhibit no preference for physically matched partners.*

I found that the Samara vervets showed a preference to play with familiar social partners (partners engaged in activities outside of play, and partners in close spatial proximity) and satisfy both components of my definition, as I found increased play bouts both between individuals who groomed more frequently, and between individuals who were often in close spatial proximity to one another. I did not find that animals preferred to play with physically matched partners (low size difference score between the dyad), nor with physically mismatched partners (high size difference score between the dyad). As such, my findings only partially support the training for the unexpected hypotheses, as these data only met the first criterion—that the animals will prefer to play with familiar social partners.

***Under the dominance hierarchy hypothesis and if social information is readily accessible, animals should play with more closely ranked conspecifics, as their relationships need to be tested more frequently.***

Since vervets are a highly gregarious species and are likely to be in close proximity to other members of their group (2-3 m on average, Nord [2021]), I assumed that social information was readily accessible to our study groups. I found support in that the Samara vervets preferentially played with more closely-ranked conspecifics, where more play bouts occurred between dyads in which there was a smaller rank difference. This lends support to the dominance hierarchy hypothesis.

***Under the social skills hypotheses, animals should show no preference for physically matched partners and avoid playing with familiar social partners. Such a pattern would also provide support for an alternative interpretation of the training for the unexpected hypothesis, as unfamiliar, mismatched partners will provide a better training for dealing with novel and unpredictable situations in the future.***

I found no relationship between play and physically matched, or physically unmatched, partners. With respect to familiar social partners, the opposite was true – I found clear evidence that animals preferred to play with familiar social partners. Thus, I found no support for the social skills hypothesis.

***Under the self-assessment hypothesis, animals should prefer to play with partners that are similar in either age, sex, or rank, and we would expect no preference for play partners that are familiar social partners outside of play (e.g., grooming).***

I found that the Samara monkeys preferred partners of the same age, sex, and rank. However, contrary to the second component of this prediction, I did find a strong preference for play partners that are familiar social partners. Thus, like the training for the unexpected hypothesis, I found only partial support for the self-assessment hypothesis.

#### **4.2 How Do These Results Relate to Existing Literature?**

When it comes to age and play, Pellis et al. (2010) has proposed that examining play in adulthood may be beneficial in order to tease apart immediate and delayed functions of play, since play at a later stage in life (i.e., adulthood) is likely to have a more immediate benefit. However, adult-adult play was rare in Samara vervets, only constituting 0.02% of recorded play bouts. This is unsurprising as adult-adult play is quite rare in the cercopithecidae family (Pellis & Iwaniuk, 2000). However, given that the cercopithecidae family of primates is studied at a higher frequency than other primate families (Di Fiore & Rendall, 1994), the overarching view that play is a mainly a juvenile-specific behaviour may not be consistent across all primates (Pellis & Iwaniuk, 2000). Additionally, in species where adult-adult play is infrequent, adults may use play-fighting in their social interactions with juveniles, which may influence their relationship

with other adults in the troop who are affiliated to that juvenile (Pellis & Iwaniuk, 2000). Play between adults and juveniles was only observed in a small proportion of my data, but it would be interesting to see if play bouts were occurring with juveniles who had a higher-ranking mother. Female vervets are generally unconstrained when it comes to male partner choice, and affiliation (albeit indirectly) may be beneficial, especially during the mating season.

As for sex and play, sex differences are common (especially in social play and play fighting), and these differences have been reviewed extensively (Power, 2000). Generally, males initiate play more frequently than females (Graham & Burghardt, 2010), and prefer to play with other males (Burghardt, 2005). Sex differences in play behaviour have been documented in many primate species (Brown, 1988; Raleigh et al., 1979; Brown & Dixson, 2000; Lonsdorf et al., 2014; Paukner & Suomi, 2008), and these sex differences continue to occupy a prominent role in play research. The Samara population was consistent with much of the literature relating to sex differences, as male-male dyads played at a higher frequency than mixed sex dyads, and the lowest rates of play recorded were between female-female dyads. However, play-related sex differences appear to be variable in some species, and may be influenced by the availability of same-sexed and opposite-sexed peers. For instance, male rhesus macaques (*Macaca mulatta*) raised in mixed-sex peer groups displayed higher frequencies of play than male infants reared in social groups with only male peers (Goldfoot, 1978). Fluctuations in male-female ratios in birth cohorts may therefore influence play frequencies from year to year in my study population.

My findings related to dominance rank corroborate other evidence that mammals initiate and play more with individuals that they can potentially dominate during play

(Biben, 1986; Owens, 1975). Experiencing subordinate or disadvantaged positions during play may be of value as it allows for the individual to practice defensive strategies that could be used in an aggressive interaction (Ward et al., 2008). However, play is unlikely to occur if an individual consistently maintains a dominant position, according to the 50-50 rule (Pellis & Pellis, 1998), which states that in order for play to occur, both participants must “win” an equal proportion of play encounters (Aldis, 1975; Pellis, 2002; Altmann, 1962). In order for play to remain playful (as opposed to escalating into aggression) and reciprocal, some degree of cooperation is necessary (Pellis & Pellis, 2017; Iki & Kutsukake, 2022). A preference to have a play partner who differs in rank, but not greatly, would support both competition, and cooperation within a play bout.

Familiar social partners are often described for primates (Puga-Gonzalez et al., 2009), but not necessarily in relation to play behaviour. For instance, in male vervet coalition formation, males are more likely to form coalitions with males with whom they are often associated, and with those who they are more likely to groom with (Freeman et al., 2016). However, as Freeman et al. (2016) suggested, it may be the case that there is a simple proximity effect that may be amplified by grooming (Noë & Sluijter, 1990; Puga-Gonzalez et al., 2009; Hemelrijk & Puga-Gonzalez, 2012). Males who associate more frequently are simply more likely to be close by when an aggressive interaction arises, and may be more likely to participate, particularly if they have been grooming partners (Freeman et al., 2016). Similarly, one might predict that juveniles are being opportunistic and are just playing with another juvenile in close proximity, and this may be amplified by whether or not the pair has groomed in the past. However, as our pairwise plots indicated (Appendix B), there was no correlation between grooming rates and spatial

proximity, indicating each of these predictor variables was influencing play bouts independently of one another.

As previously mentioned (see Section 1.4.3), many species of non-human primates exhibit preference to play more with siblings than peers (Cheney, 1978; Owens, 1975; Fedigan, 1972). However, kin-preferred play may also result from a simple proximity effect. Large primate social groups often consist of a smaller set of female subgroups, which in some cases are matrilineally based (Kudo & Dunbar, 2001). Depending on the composition of these subgroups (i.e., if we assume juveniles are in the same clique as their mother), the effect of kinship found on play frequency may be due to proximity. Again, we produced pairwise plots comparing kinship to both spatial proximity and grooming SRI, and found that these three predictor variables were uncorrelated. Vervets also have a short, distinct, birthing season, and there will likely be a narrower distribution of age differences in potential play partners, in comparison to a species that gives birth randomly throughout the year (e.g., baboons). Although I found distinct effects of age in relation to play frequency, the cohort effect (the effects of the year of birth) may be worth investigating further to see if there is variation in play frequency within and between cohorts. A future analysis may benefit by accounting for subgroup composition, sex ratio, and the cohort effect, in addition to the effects measured in this analysis.

#### ***4.2.1 The Dominance Hierarchy Hypothesis***

Overall, my results largely supported the dominance hierarchy hypothesis. The Samara vervets, and their play partner preferences, indicated that a potential benefit to playing may be related to testing or establishing dominance rank relationships.

Determining the extent to which play behaviour has benefits relating to dominance rank is complicated given the complex relationship between male and female vervet dominance hierarchies (Young et al., 2017), and we may expect there to be sex-specific benefits related to play. Previous data, mostly with captive vervets, has shown a strong matrilineal influence on the relative rank of all individuals in the group (Bramblett et al., 1982; Horrocks & Hunte, 1983; Fairbanks, 1980). For example, Bramblett et al. (1982), in a study on captive animals, found that females generally track the positions of their mothers more consistently than their male counterparts, and the females of high-ranking matriline are typically higher ranked than their male siblings. Bramblett et al. (1982) also found that females in low-ranking matriline are likely to rank lower than their male siblings, and that juveniles enter the hierarchy low in relative rank, but climb to positions appropriate to their matriline at approximately four years of age. Given these findings, it may be the case that play behaviour serves an immediate benefit to juveniles in establishing and testing dominance ranks in the period before the effects of the matriline are clear. However, these findings related to matrilineal rank acquisition have come from either captive populations of vervets (i.e., Bramblett et al., 1982; Fairbanks, 1980), or vervet troops with small population sizes (i.e., Horrocks & Hunte, 1983), both of which do not characterize my study animals.

Within the Samara population, dominance ranks are shallower compared to other vervet populations, and rank and grooming effects typically expected by a matrilineal hierarchy are absent (Henzi et al., 2013). Samara vervets showed no preference to groom up the dominance hierarchy, showing no evidence that females attempt to maintain coalitions or grooming relationships with high-ranking females (Henzi et al., 2013). This might indicate that the Samara vervets do not sustain matrilineal kin association (Henzi et

al., 2013), or that the process of adult rank acquisition has changed (Horrocks & Hunte, 1983). Nonetheless, it appears that my study population does not follow typical matrilineal rank acquisition historically documented in vervets, and as such, play may be useful in establishing and testing dominance ranks, as a juvenile cannot guarantee it will fall into rank under its mother. Given this, I would expect females to be affected disproportionately if these vervets do indeed use play to navigate its rank trajectory (since females in other populations track their mothers rank more consistently than males) and may expect females to play more in the Samara population compared to a separate vervet population that follows typical matrilineal rank acquisition.

It seems unlikely that specific juvenile playmates later become allies as adults (Sharpe, 2005b; Graham & Burghardt, 2010), especially in male vervet monkeys, where adult males frequently emigrate to new groups (Henzi & Lucas, 1980; Young et al., 2019a). Play is likely to serve some immediate benefits to juveniles, and if play has the ability to increase the short-term survival of juveniles it may also have measurable evolutionary consequences (Fagen & Fagen, 2004). Thus, during periods where juvenile mortality rates are high, we would expect a higher probability of immediate benefits compared to delayed benefits (Burghardt, 1984).

The Samara vervet population is likely to experience such periods of high mortality given the volatile nature of the semi-arid Karoo region in which our field site is located (Dean & Milton, 1999), and its susceptibility to the increasing risks of climate change (Hoffman et al., 2009). Previous research on the Samara vervets has demonstrated that a reduction in available food and standing water is linked to an increase in mortality rates (Young et al., 2019a). Harsher environmental conditions which are expected to increase due to climate change, may not only increase rates of mortality, but may also

affect other behaviours of this study population (Varsanyi, 2021). As such, play behaviour may change as environmental conditions become harsher, specifically in periods where juvenile mortality rates are high, which may also alter components or frequencies of play behaviour in order to accommodate a shift to favoring immediate benefits rather than delayed benefits.

#### ***4.2.2 Hypotheses Supported within an Alternate Context***

During play, animals may engage in acrobatic maneuvers, such as leaps or rotations that are absent in other contexts (Pellis et al., 2014). Such maneuvers may be used in attacking or defending oneself from a partner during a play fighting context, where there is some competition over gaining an advantage, or gaining access to a species-typical body target. Pellis et al. (2014) tested four non-mutually exclusive hypotheses related to acrobatic maneuvers during play using data from a captive troop of vervet monkeys, as well as the wild vervets of Inner Samara. It was predicted that such acrobatic strategies engaged during play may promote physical training, be a means of training for the unexpected, function as a play signal, or may be used as a tactic to evade or facilitate playful attack and defense. Both the captive and wild troops showed similar patterns, where the body target competed for during fighting is the shoulder area, and defensive bites were mostly directed at the head, especially the side of the face (Pellis et al., 2014). The vast majority of acrobatic maneuvers recorded, indicated such tactics of attack and defense were employed. The combat hypothesis was best supported as most acrobatic maneuvers functioned to gain access to, or block access to the body part targeted during play. However, the non-combat maneuvers also seemed to support two of the other proposed hypotheses, since the movements employed were indicative of a self-

handicapping behaviour, and seemed to elicit play from a potential partner in some instances. This may indicate a communicatory function. Additionally, self-handicapping behaviours are often associated with the training for the unexpected hypothesis as these tactics may often lead to a loss of control, and train the animal to react appropriately cognitively and emotionally in an unexpected situation (Pellis et al., 2014). Again, it is worth noting that both the wild and captive troops exhibited the same targets and patterns of acrobatic maneuvers, making the conclusions of the study applicable to vervet monkeys in general, and indicates acrobatic maneuvers may be a component of play that are consistent across different contexts.

Although the study by Pellis et al. (2014) and this thesis both explore play behaviours within the same population (Inner Samara), the different components of play investigated (acrobatic maneuvers vs. play partner preferences) lead us to several different hypotheses supported by a single population. This supports the notion that play may serve multiple, overlapping adaptive functions (Bateson, 1981; Graham & Burghardt, 2010).

#### ***4.2.3 Comparing Vervets to Capuchins***

Lutz et al. (2019) compared three primate species across three lineages (i.e., capuchins, hamadryas baboons, and diademed sifaka), and found each species had differing play partner preferences. The capuchins specifically are of interest here, as even though they are a different lineage compared to vervets, they have very similar social structures. The capuchins in the study by Lutz et al. (2019) preferred to play with oppositely sexed non-kin, and preferred similarly ranked partners who are close social partners. The Samara vervets also had a preference for similarly ranked partners and close

social partners, but contrary to the capuchins, I found that vervets preferred similarly sexed and related individuals as partners.

These differences observed in play partner preferences between capuchins and the Samara vervets may be due to a variety of reasons. First, the contemporary hypotheses I explored here may not universally describe play in all species (Sharpe, 2005a). The group sizes between the vervets and capuchins were also very different. Activity budgets between wild and captive populations can also differ (Kummer, 1965; Khan, 2013), and in this case, the capuchins in Lutz et al. (2019) were captive while the vervets in my study were wild and faced ecological pressures such as drought. However, while certain aspects of social structure have been shown to differ noticeably between wild and captive populations (Balasubramaniam et al., 2018), it is still uncertain whether these variations in social structure translate into differences in play partner preferences (Lutz et al., 2019). Play is also likely to be multi-functional (Graham & Burghardt, 2010), and there seem to be species-specific and context-specific benefits to play. For instance, play may be a conflict management strategy, and play seems to serve an immediate function in preventing tension between individuals (Palagi et al., 2006). In captive chimpanzees, Palagi et al. (2004) found that significantly more play occurred between unrelated and immature subjects in the pre-feeding window compared to the control condition. Although play does not promote co-feeding necessarily, play may be used to prevent high-excitement contexts (pre-feeding) from escalating into aggression (immediate benefit) within the context of a captive population (Palagi et al., 2004).

Another complexity we face is that even with the increasing experimental and comparative evidence for play, play behaviour does not appear to fall neatly into phylogenetic categories (Graham & Burghardt, 2010). There is good indication of

whether play is present or absent across taxonomic groups and the general traits associated with its occurrence (Graham & Burghardt, 2010); however, trying to relate specific aspects of play (such as play partner preferences) to variable social structures within and between taxa has proven difficult.

### **4.3 Limitations**

There are some limitations in the study presented. First, the entirety of the Outer Samara study period, and some of the Inner Samara period occurred within drought years. Drought years are characterized by low levels of rainfall, reduced food, and the absence of standing water (Young et al., 2019a). Play is a behaviour that can taper off dramatically if there are more pressing issues to immediate survival, such as food and water shortages (Burghardt, 2005). Peak mortality rates within my study population occur when food availability is low and standing water is absent (Young et al., 2019a), and so I would expect there to be further repercussions on activity budgets. Young et al. (2019a) has demonstrated that monkeys within the Samara population alter their behaviour within a drought period by resting more, at the expense of feeding, moving, and social behaviour. Play was not analyzed independently (it was lumped into the category of social behaviour), but Young et al. (2019a)'s findings are likely applicable to this study, and we might expect the frequency of play expressed in this study period to be less compared to non-drought periods.

No infants (individuals less than one year old) were available to study during the Outer Samara study period, most likely due to the drought and lack of resources. Infants were omitted from the Inner Samara data as well, as the identity of the infant was not available in many cases. In a small sample ( $n=4$ ) of vervet infants, Govindarajulu et al.

(1993) found that infants may also exhibit preferences for play partners, where infants played more with those in their own year-class compared to older individuals. The infants increased the number of play partners as they aged, but other members of the same birth year remained preferred partners (Govindarajulu et al., 1993). As discussed, it is unlikely that the number of play partners in itself will influence play partner preferences, however it would have been ideal to have all demographic groups available to observe.

Several of the hypotheses tested required a comparison of physically matched partners. With the non-invasive weighing process, we were unable to collect the weights of all monkeys, and weights were not collected systematically (e.g. some monkeys used the scale much more frequently than others). In the Outer Samara dataset we had grouped each individual into a category based on size, however this dataset was much smaller than the Inner Samara dataset. We found that age did have an influence on number of play bouts in all of our models, and although we may assume juvenile-juvenile dyads are closer in size than adult-juvenile dyads, we did not make any inferences on physical size in relation to play bouts based on age. Having weight data would have been a more accurate measure of size comparisons. If we had enough weight datapoints, it would have also allowed us to compare physical growth over time in relation to play frequency.

#### **4.4 Future Directions**

The results presented here generate several testable predications that may be used to guide future research on wild vervet monkey populations. This investigation of play partner preferences in wild vervets indicated that there may be some benefit related to dominance rank. However, the specific mechanism of how play may benefit dominance rank, whether that be through testing or maintaining dominance relationships, is

unknown. It may be useful firstly, to determine how juveniles in my study population come to rank, as they do not sustain matrilineal kin associations (Henzi et al., 2013). Secondly, it may be beneficial to compare the play partner preferences of my population to a separate wild population of vervets that follows rank acquisition patterns typical of matrilineal vervet societies.

Additionally, as mentioned, the vervet troops of the Samara field site are likely to be affected by harsher environmental conditions due to climate change, which will likely increase stress levels and mortality rates (Young et al., 2019a). This will likely have further repercussions on a myriad of behaviours in wild vervets, including play behaviour. Specifically, we may see play frequency decrease even further, or disappear entirely, given that play appears to be a low-priority behaviour in many species (Thornton & Waterman-Pearson, 2002; Barrett et al., 1992). It would be useful to document not only how the frequency of play is affected, but also the types of play expressed, the partner preferences, and the specific components of play (e.g., self-handicapping behaviours, role-reversals, play-face, etc.) that are influenced over the course of a drought. As the play literature generally agrees that play must serve some immediate or delayed function, gauging how other behaviours are affected (if at all) when play decreases or is absent entirely, may be useful in determining plausible functions in wild vervets.

Multilayer network techniques (Finn et al., 2019) are becoming increasingly desirable, as they allow us to quantify how different interaction levels may influence one another. Bonnell et al. (2020) have developed a dynamic multilayer approach that allows for the comparison of interaction layers over time. Such an analysis would be useful in play research, as it would allow us to quantitatively compare how different layers (e.g.,

grooming interactions, dominance interactions, play bouts, kinship, proximity, etc.) relate to one another over time and across varying levels of ecological stress.

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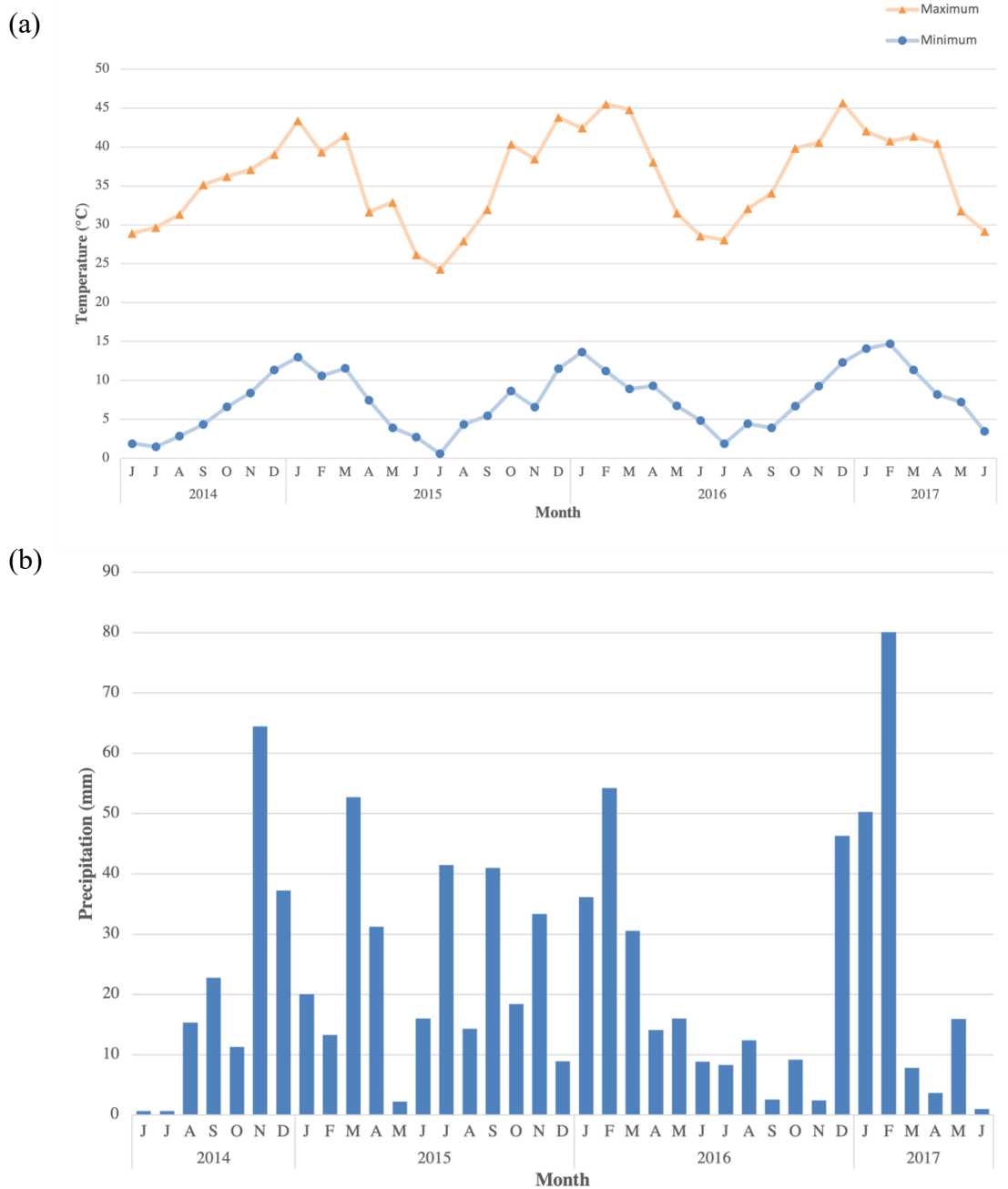
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## APPENDICES

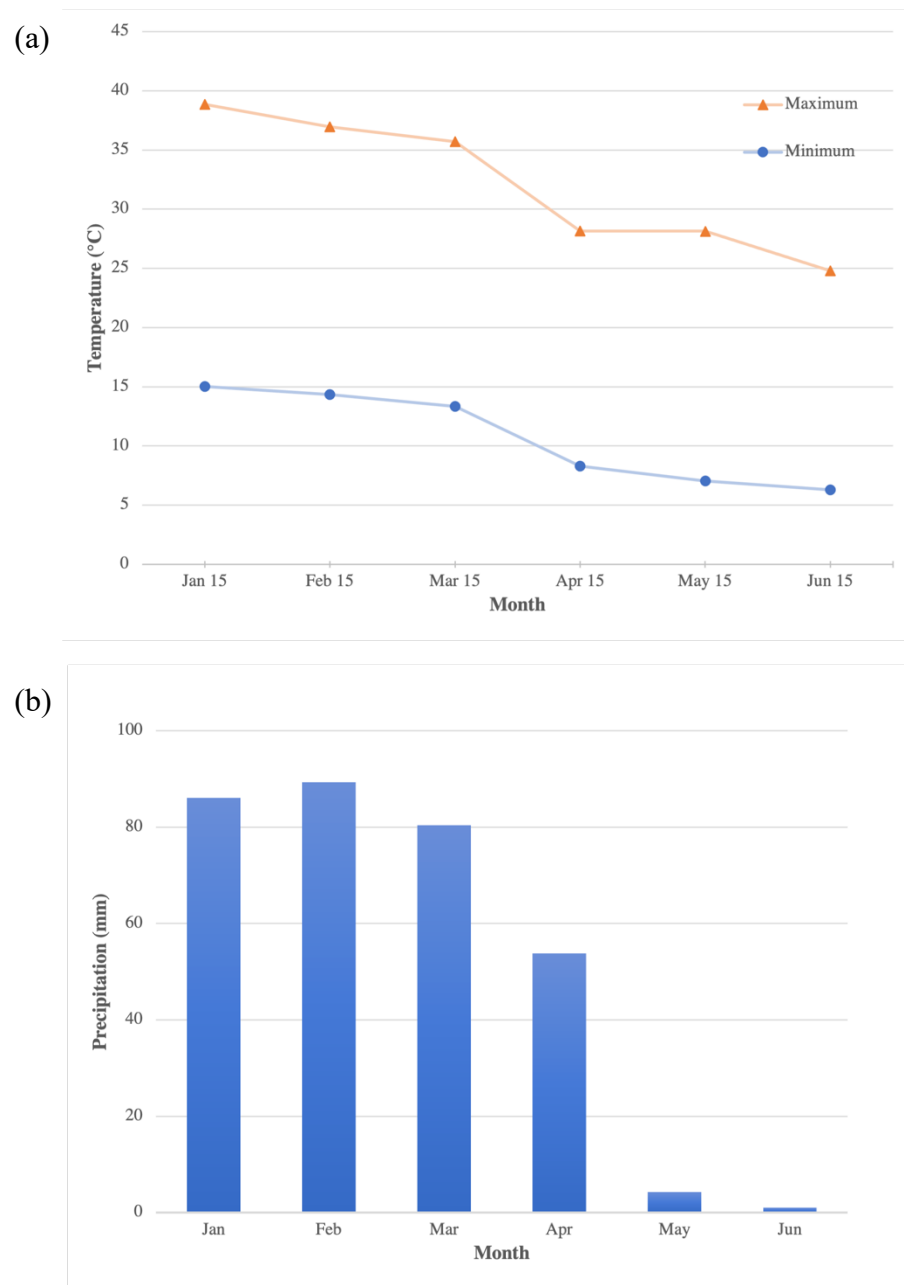
### Appendix A: Temperature and Rainfall

**Figure A.1** *Temperature and Rainfall Across the Inner Samara Data Collection Period*



*Note:* (a) Monthly mean maximum and minimum temperatures for the study period and (b) Monthly rainfall for the study period of the Inner Samara population (June 2014 - June 2017).

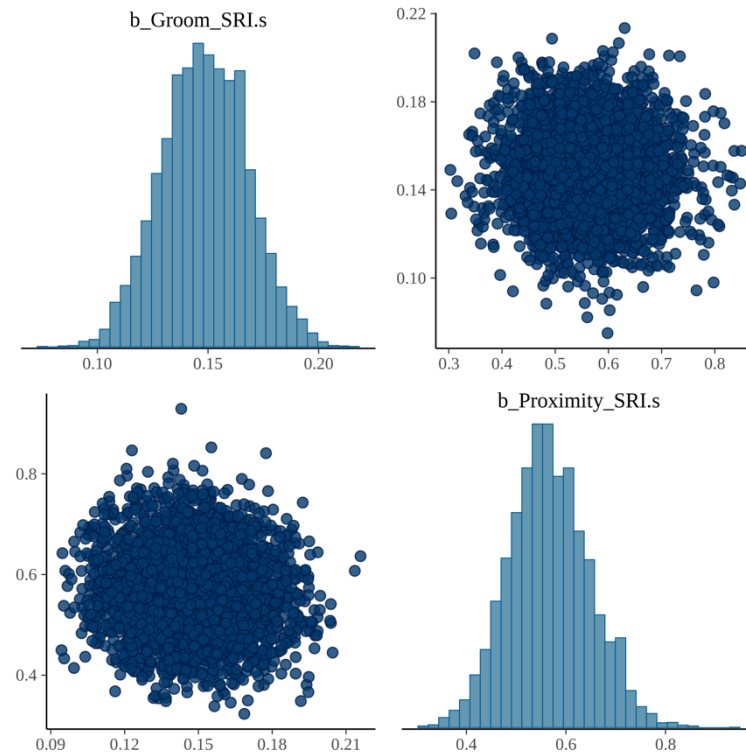
**Figure A.2** *Temperature and Rainfall Across the Outer Samara Data Collection Period*



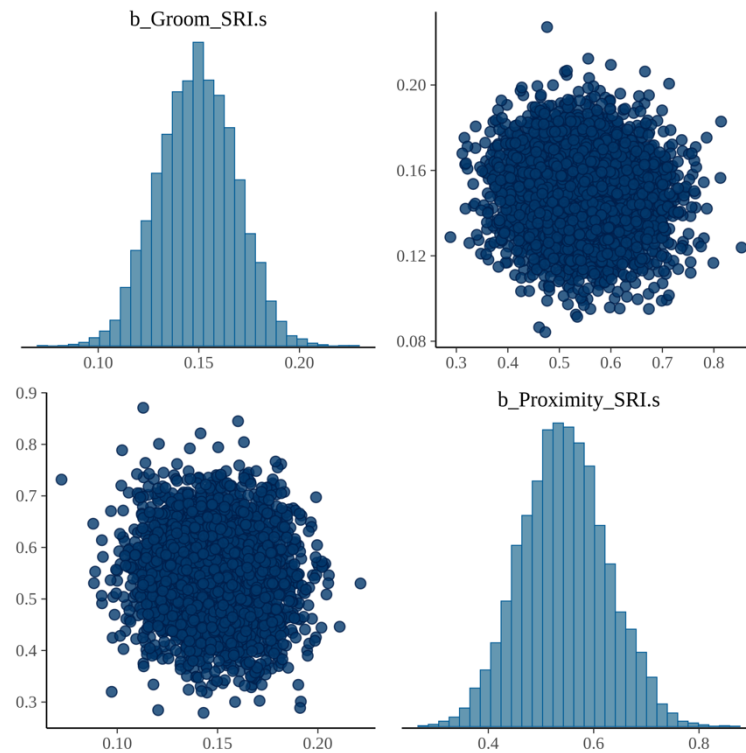
*Note:* A) Monthly mean maximum and minimum temperatures for the study period and B) Monthly rainfall for the study period of the Outer Samara population (January 2020 – June 2020).

## Appendix B: Pairwise Plots of Predictor Variables

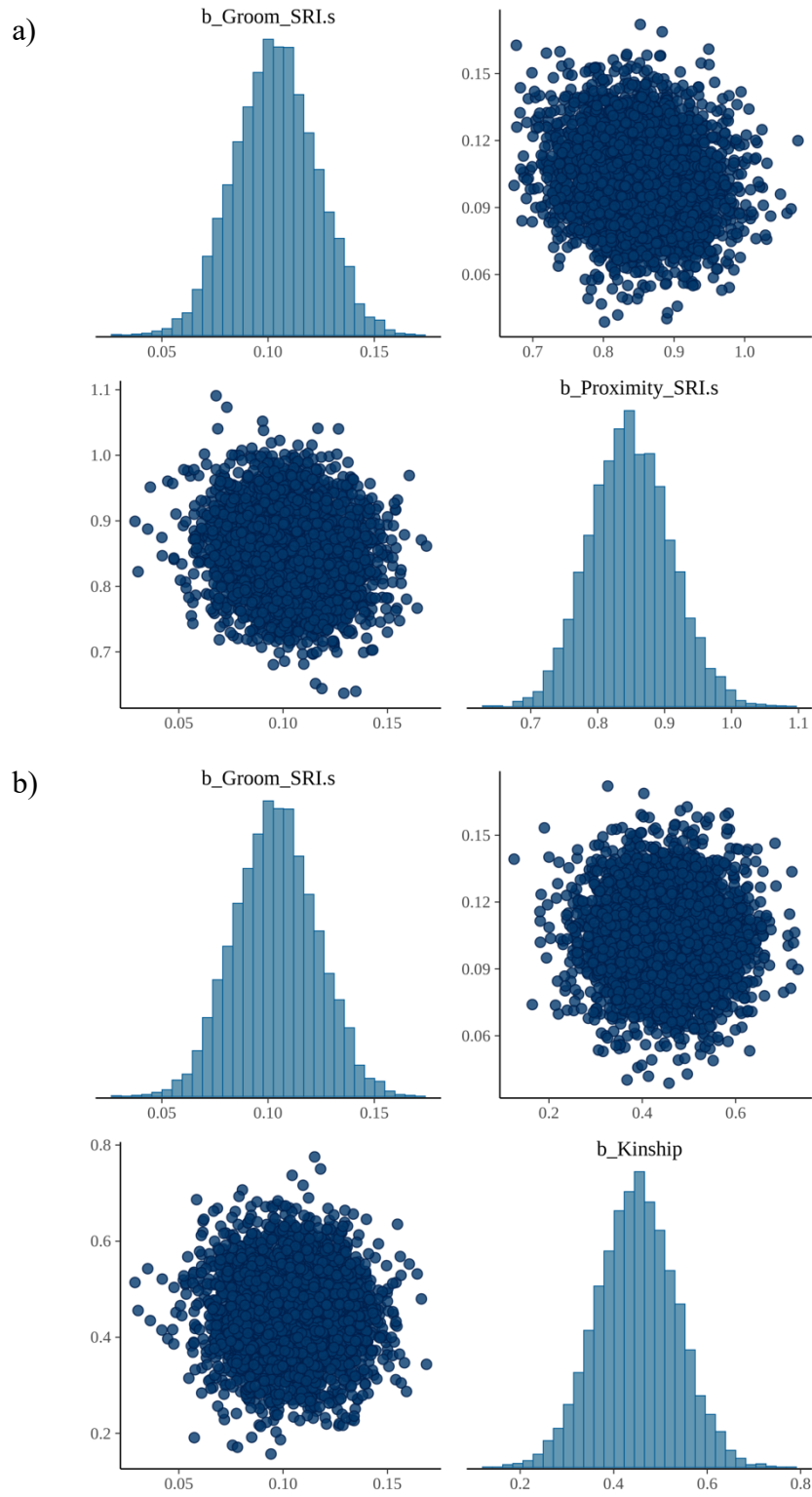
**Figure B.1** *Pairwise Plots Comparing Groom SRI with Proximity SRI in the Four Troop Model*

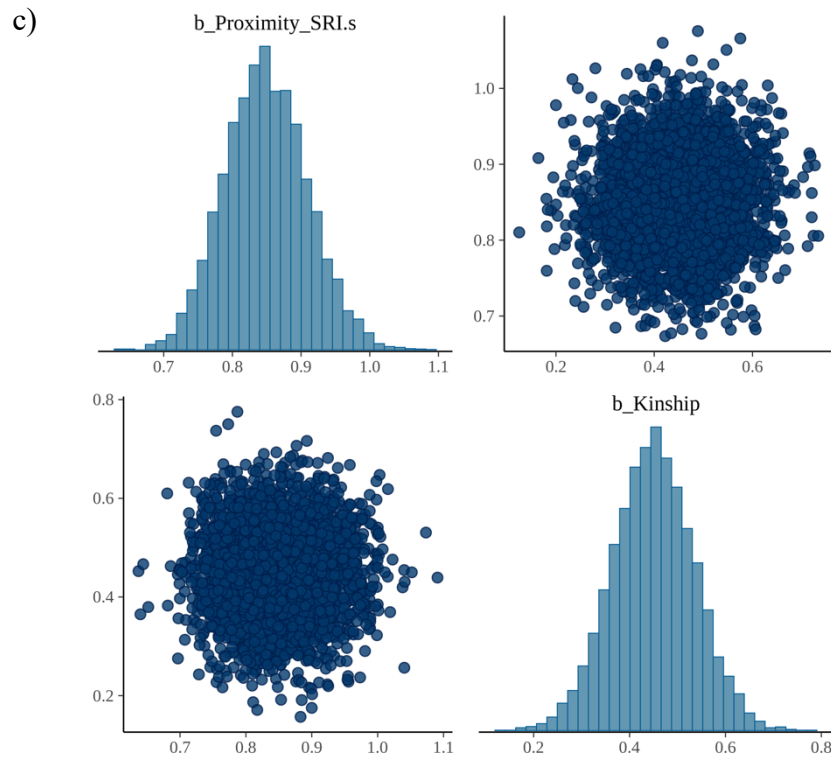


**Figure B.2** *Pairwise Plots Comparing Groom SRI and Proximity SRI in the Juvenile Model*

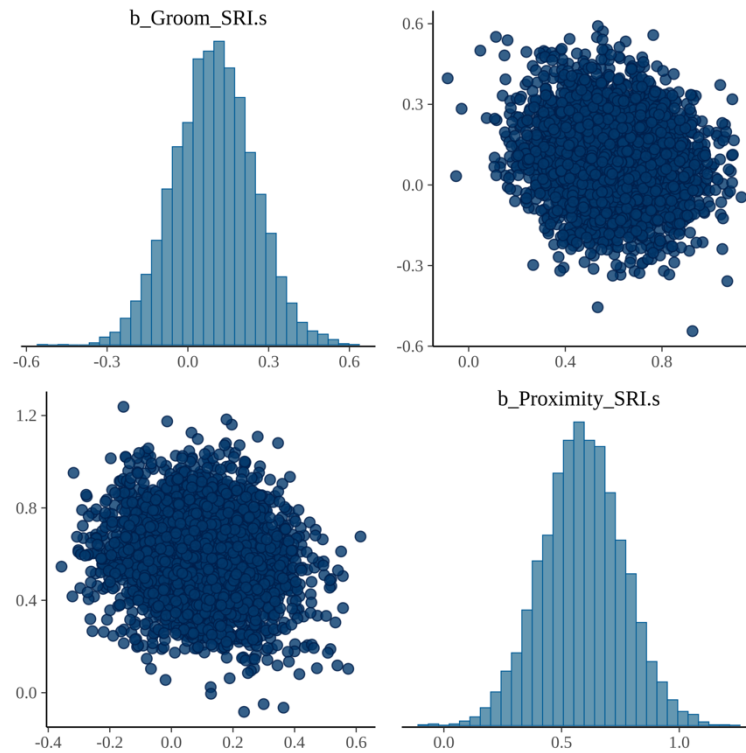


**Figure B.3** *Pairwise Plots Comparing a) Groom SRI and Proximity SRI, b) Groom SRI and Kinship, and c) Proximity SRI and Kinship in the Kinship Model*



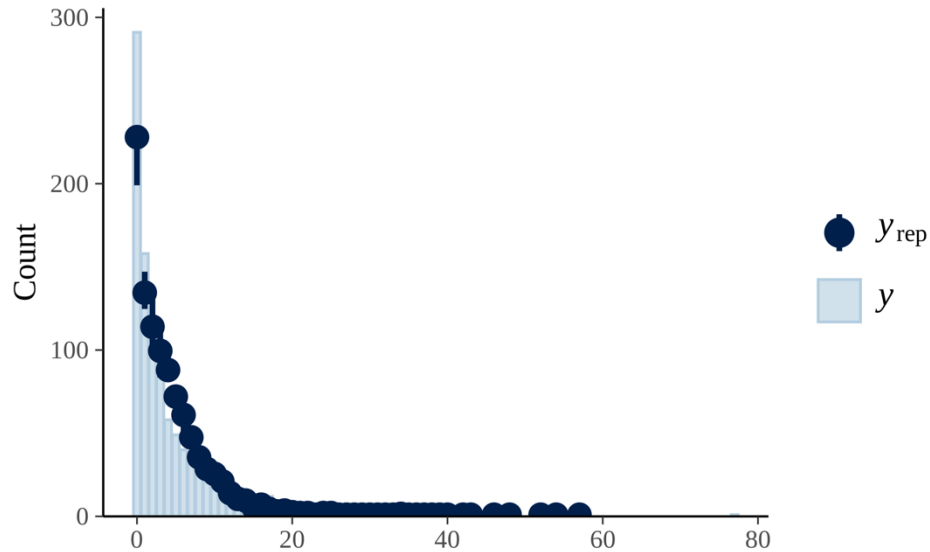


**Figure B.4** *Pairwise Plots Comparing Groom SRI and Proximity SRI in the Size Difference Model*



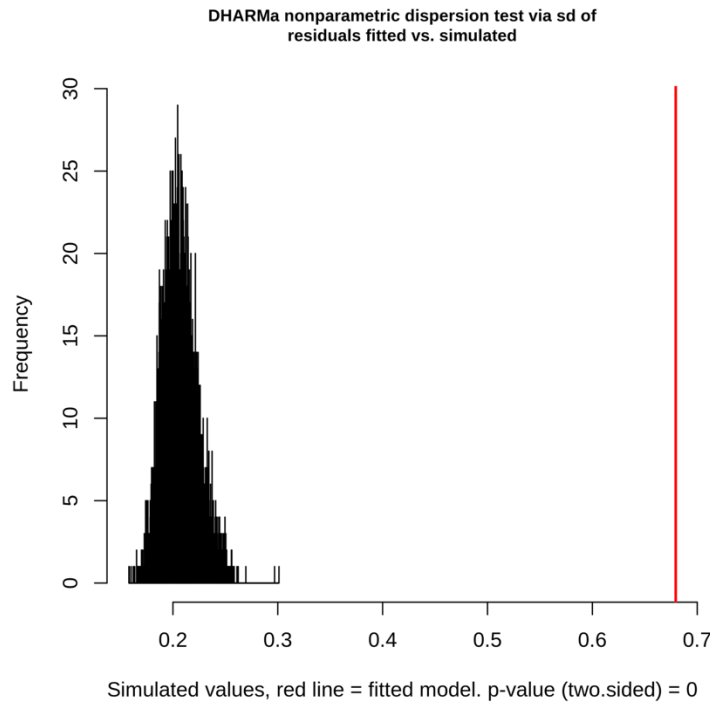
## Appendix C: Posterior Predictive Checks and Fixing Dispersion

**Figure C.1 Comparing the Observed Outcome Variable (Play Weights) to Datasets Simulated from the Posterior Predictive Distribution of the Four Troop Model Using a Poisson Distribution**

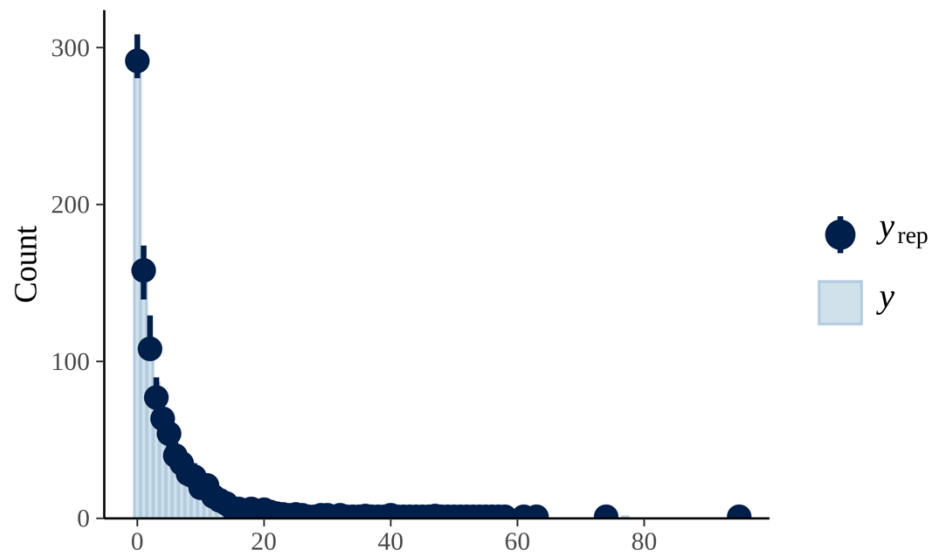


*Note:*  $Y$  represents the actual representations from the model, where the  $Y_{REP}$  represents the possible model representations.

**Figure C.2 Overdispersion in the Four Troop Model When Using a Poisson Distribution as Revealed Using the Dharma Nonparametric Dispersion Test**

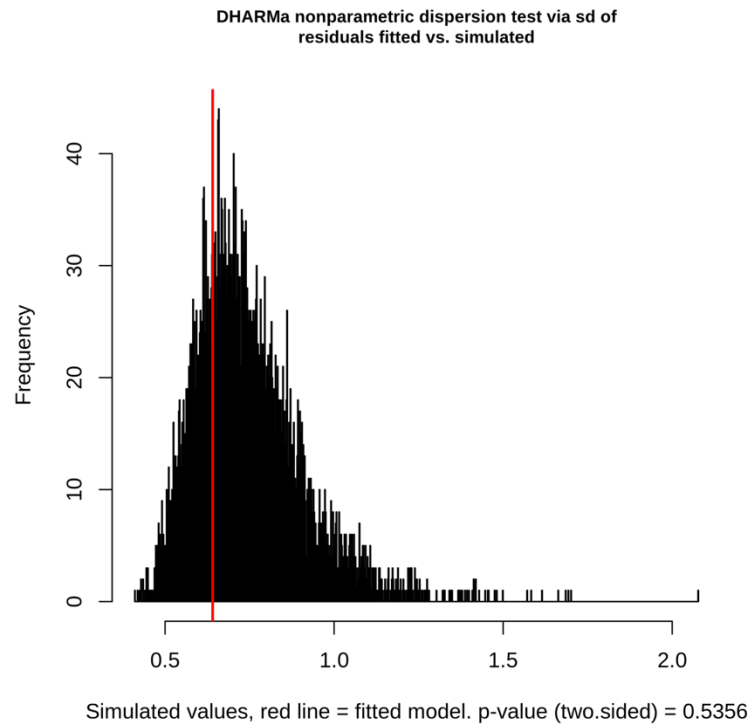


**Figure C.3 Comparing the Observed Outcome Variable (Play Weights) to Datasets Simulated from the Posterior Predictive Distribution of the Four Troop Model Using a Negative Binomial Distribution**

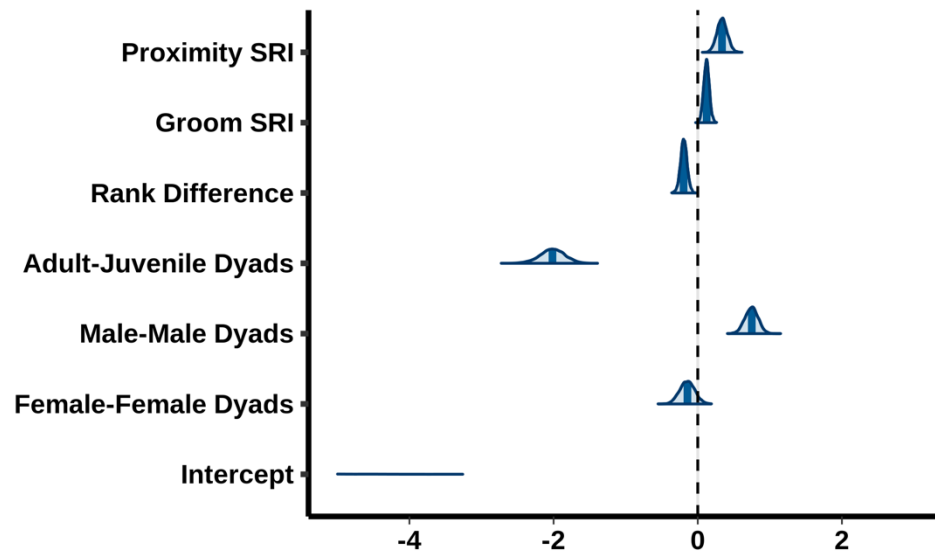


*Note:*  $Y$  represents the actual representations from the model, where the  $Y_{REP}$  represents the possible model representations.

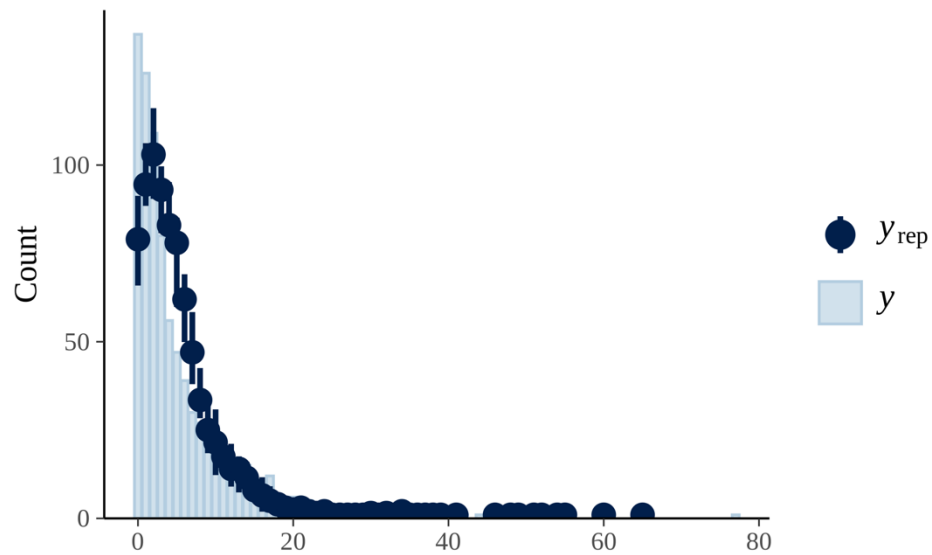
**Figure C.4 No Overdispersion in the Four Troop Model When Using a Negative Binomial Distribution as Revealed Using the Dharma Nonparametric Dispersion Test**



**Figure C.5 Posterior Density Plot of the Four Troop Model Using a Negative Binomial Distribution**

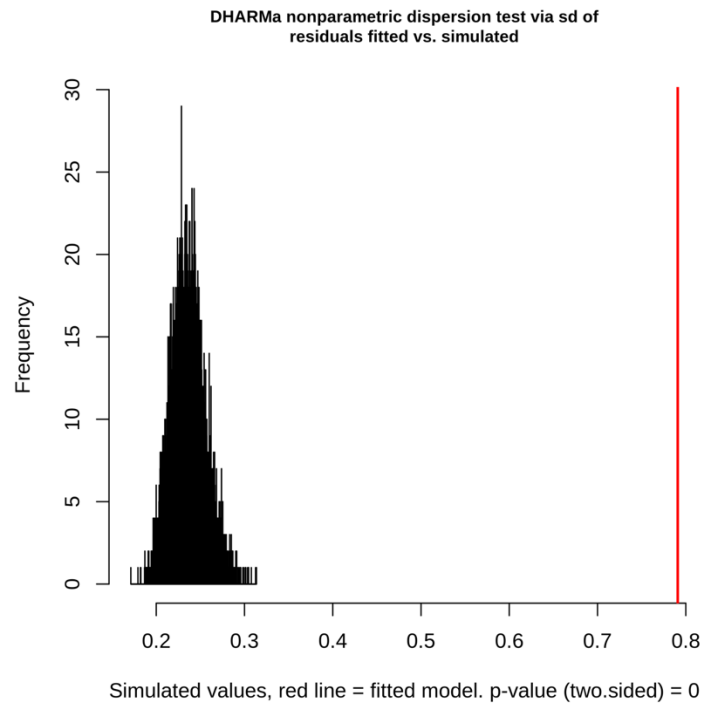


**Figure C.6 Comparing the Observed Outcome Variable (Play Weights) to Datasets Simulated from the Posterior Predictive Distribution of the Juvenile Model Using a Poisson Distribution**

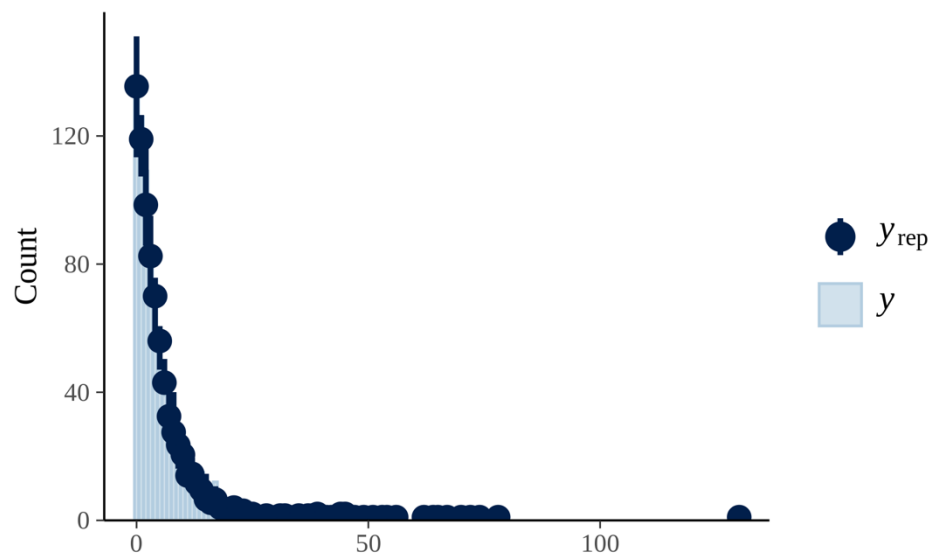


*Note:*  $Y$  represents the actual representations from the model, where the  $Y_{\text{REP}}$  represents the possible model representations.

**Figure C.7 Overdispersion in the Juvenile Model When Using a Poisson Distribution as Revealed Using the DHARMA Nonparametric Dispersion Test**

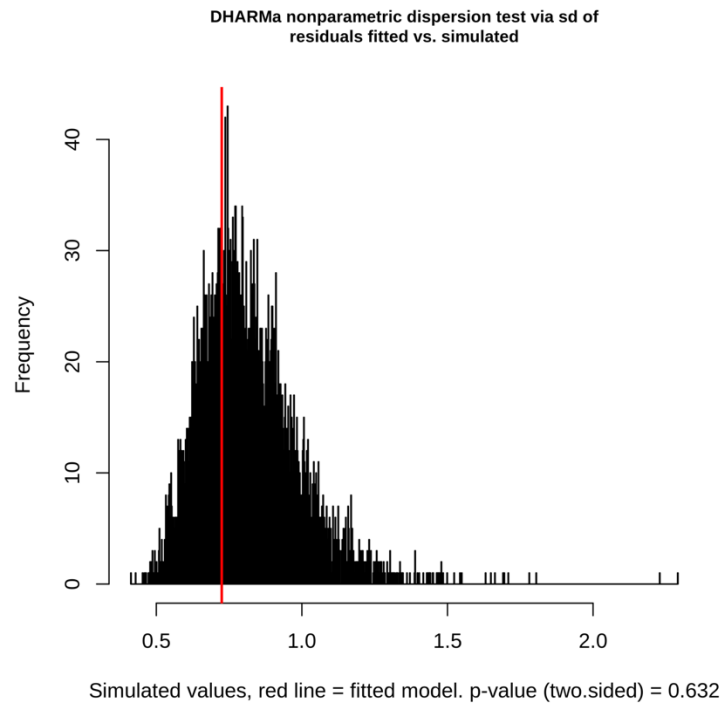


**Figure C.8 Comparing the Observed Outcome Variable (Play Weights) to Datasets Simulated from the Posterior Predictive Distribution of the Juvenile Model Using a Negative Binomial Distribution**

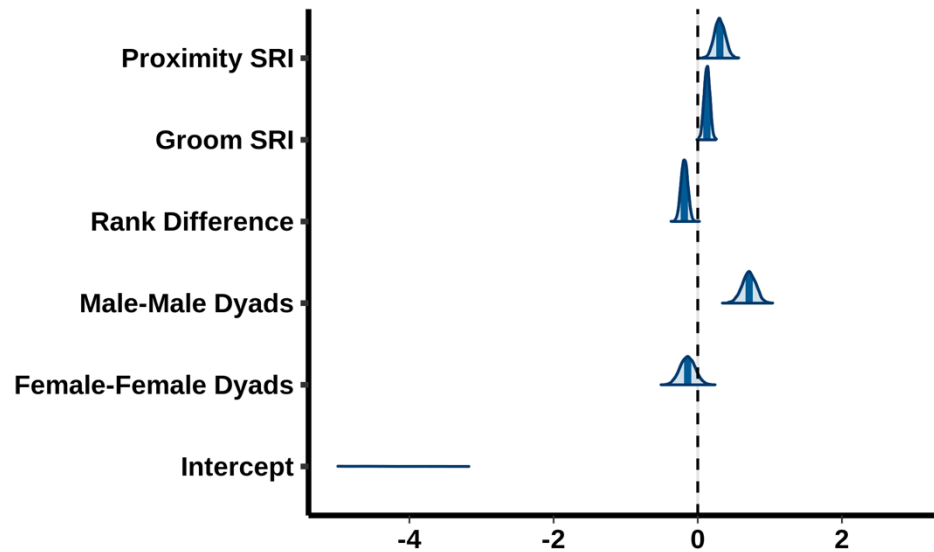


*Note:*  $Y$  represents the actual representations from the model, where the  $Y_{REP}$  represents the possible model representations.

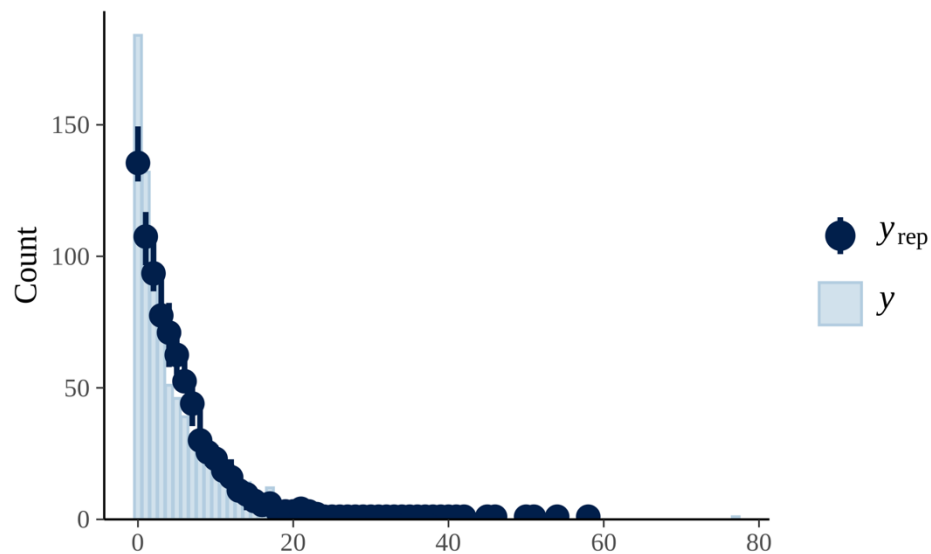
**Figure C.9** *No Overdispersion in the Juvenile Model When Using a Negative Binomial Distribution as Revealed Using the DHARMA Nonparametric Dispersion Test*



**Figure C.10** *Posterior Density Plot of the Juvenile Model Using a Negative Binomial Distribution*

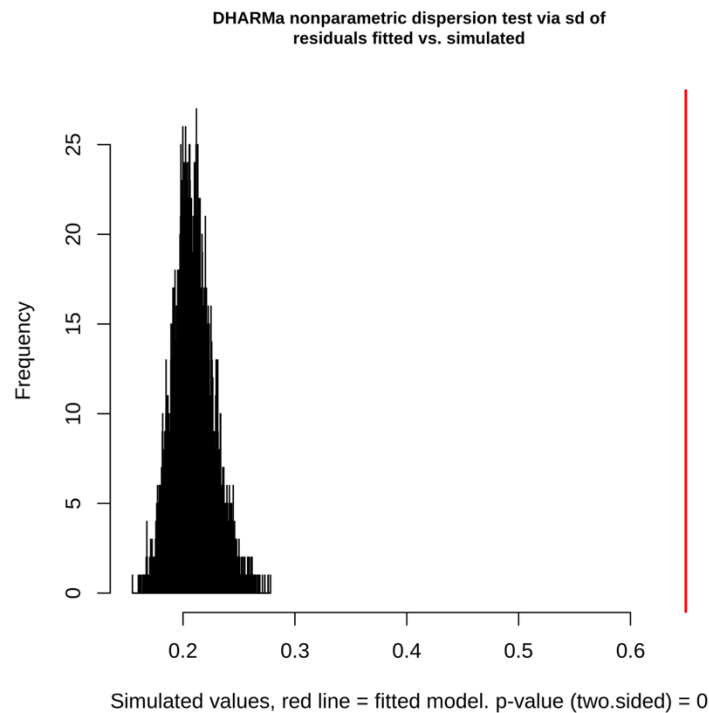


**Figure C.11 Comparing the Observed Outcome Variable (Play Weights) to Datasets Simulated from the Posterior Predictive Distribution of the Kinship Model Using a Poisson Distribution**

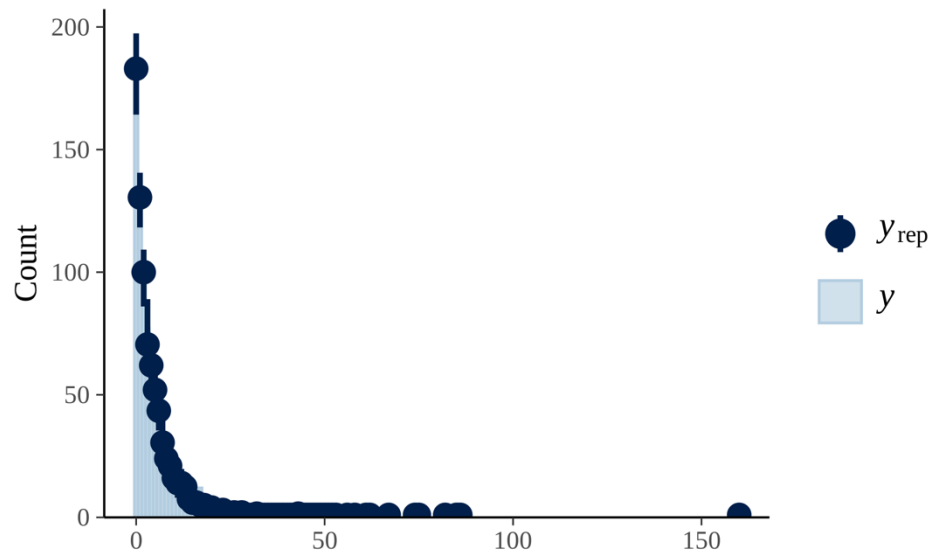


*Note:*  $Y$  represents the actual representations from the model, where the  $Y_{REP}$  represents the possible model representations.

**Figure C.12 Overdispersion in the Kinship Model When Using a Poisson Distribution as Revealed Using the Dharma Nonparametric Dispersion Test**

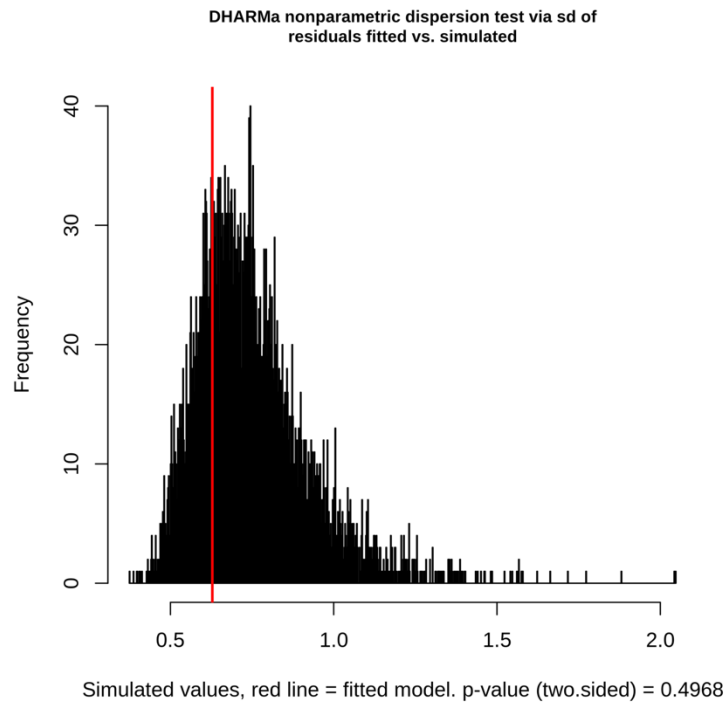


**Figure C.13 Comparing the Observed Outcome Variable (Play Weights) to Datasets Simulated from the Posterior Predictive Distribution of the Kinship Model Using a Negative Binomial Distribution**

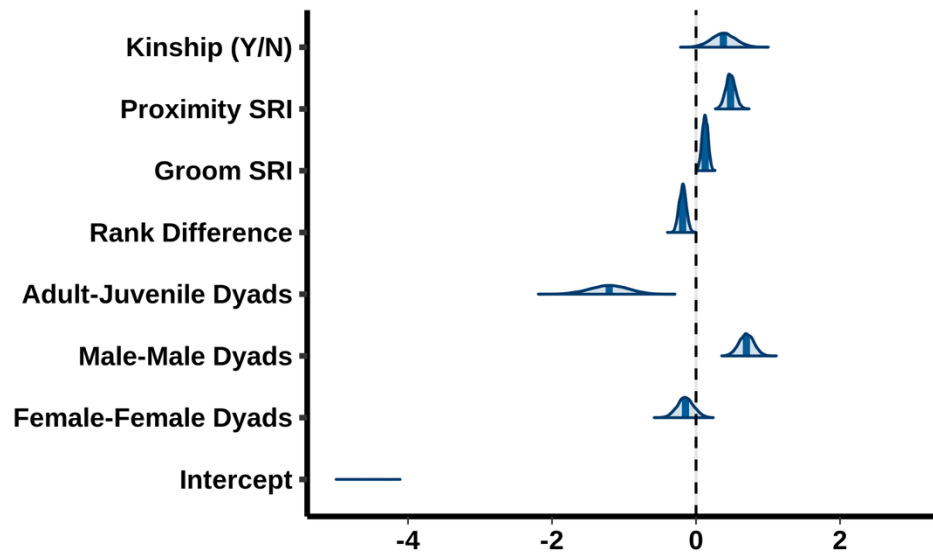


*Note:* Y represents the actual representations from the model, where the  $Y_{\text{REP}}$  represents the possible model representations.

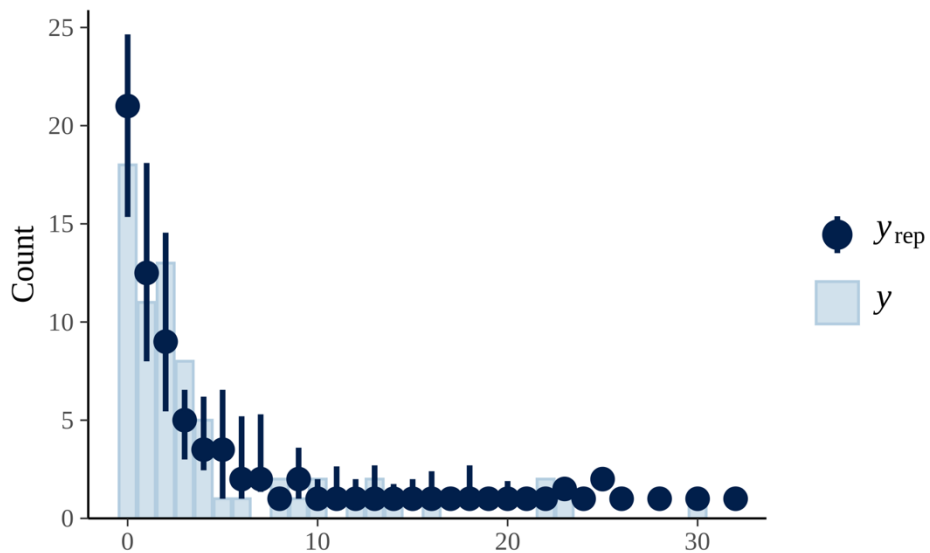
**Figure C.14 No Overdispersion in the Kinship Model When Using a Negative Binomial Distribution as Revealed Using the Dharma Nonparametric Dispersion Test**



**Figure C.15** *Posterior Density Plot of the Kinship Model Using a Negative Binomial Distribution*

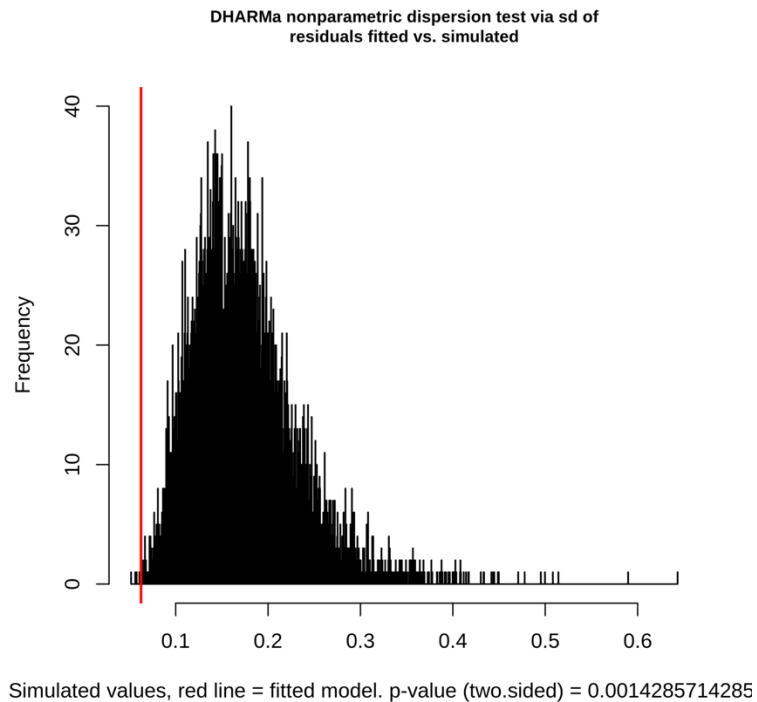


**Figure C.16** *Comparing the Observed Outcome Variable (Play Weights) to Datasets Simulated from the Posterior Predictive Distribution of the Size Difference Model Using a Poisson Distribution*



*Note:*  $y$  represents the actual representations from the model, where the  $y_{rep}$  represents the possible model representations.

**Figure C.17 Underdispersion in the Size Difference Model When Using a Poisson Distribution as Revealed Using the Dharma Nonparametric Dispersion Test**



**Figure C.18 Underdispersion in the Size Difference Model When Using a (a) Hurdle Poisson, (b) Negative Binomial, and (c) Hurdle Negative Binomial as Revealed Using the Dharma Nonparametric Dispersion Test**

