A Cross-Species and Cross-Cultural Comparative Analysis of Sex and Gender Differences in Rough and Tumble Play

CATHERINE LAURA MARLEY

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A Cross-Species and Cross-Cultural Comparative Analysis of Sex and Gender Differences in Rough and Tumble Play

Catherine Laura Marley

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Department of Anthropology

Durham University

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Abstract

Rough and tumble play (RTP) is a form of physically active social play common across diverse social mammals, including humans, which likely provides vital opportunities for the development of physical and social skills. Where adult behaviours are differentiated by sex or gender, RTP is expected to take correspondingly different forms in juveniles. However, we do not yet have a good understanding of how and why sex/gender differences in RTP vary across non-human species and human societies. The first aim of this thesis was to investigate cross-species variation in sex differences in RTP in non-human mammals through the lens of behavioural ecology and life history theory. A systematic review revealed that male biases in RTP are not as consistent as predicted and many studies report a lack of, or inconsistent, sex differences. Contrary to expectations, phylogenetic comparative analyses found no evidence that measures of male-male competition in adults predict male biases in juvenile RTP across species. The second aim of the thesis was to investigate variation in gender differences in RTP in human subsistence societies using cross-cultural data through the lens of cultural evolution. I found that RTP is more common in boys, although in most societies both girls and boys engage in some form of RTP. Gender differences in RTP were not predicted by marriage system or other potentially relevant variables, and were not strongly affected by shared cultural history or spatial proximity. Taken together these results suggest that RTP is a complex, highly variable behaviour which may change rapidly in response to social and environmental factors. I consider potential interactions between biological, cultural, and contextual factors which may explain these findings, call for future work which considers biocultural approaches to sex and gender differences in RTP, and suggest methodologies for improving future research.

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List of Abbreviations

RTP – rough and tumble play

SCCS – Standard Cross Cultural Sample

MCMC – Markov chain Monte Carlo

OCM – Outline of Cultural Material

CI – credible interval

D-PLACE – Database of Places, Language, Culture, and Environment

Declaration

I declare that no material contained in this thesis has previously been submitted for a degree in this or any other institution, and that the thesis is not based on joint research.

Statement of Copyright

Chapter 3 is based on the publication 'A systematic review of sex differences in rough and tumble play across non-human mammals' (Marley, Pollard, Barton and Street, 2022), which was published in Behavioural Ecology and Sociobiology, and has been reformatted to match university guidelines.

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Chapter 1: Introduction

Rough and tumble play (RTP), a form of physically active social play, is a widespread behaviour across mammals (Heintz et al., 2017). The widespread nature of RTP across mammals suggests it may contribute to survival and reproductive fitness (Fry, 2005). The ethological study of RTP in non-human mammals began in the late 20th century, including specific behaviours such as wrestling, jumping, pushing away, and chasing, which lay the foundations for the study of strikingly similar behaviour in human children (Scott and Panksepp, 2003). Behavioural components of children's RTP include running, jumping, wrestling, and chasing, often alongside indicators of fun such as laughing, which are distinct from organised activities such as football or other sports and games. Although RTP in both humans and non-humans can include behaviours which may be seen as aggressive, such as wrestling or hitting, it is distinct from aggression in the following ways; neither party disperses at the end of the interaction (Jarvis, 2007); both parties will show signs of positive affect such as play-face, laughter, or other signals indicating non-aggression such as head-shaking (Blurton Jones, 1972; Pellis and Pellis, 1996); both parties will show role-reversals, switching from aggressor to defender (Power, 1999); and finally, actions are staged, restrained, stylised, or self-handicapped in order to prolong or facilitate playful interactions (Jarvis, 2007; Lutz and Judge, 2017). Although RTP can occur between adults, or between adults and juveniles (most notably between a parent and their offspring), it is most commonly associated with the juvenile period and interactions between peers (Flanders, Herman and Paquette, 2013), which is the form of RTP that I focus on in this thesis.

For a behaviour to have an adaptive function, it must have net survival and/or reproductive fitness benefits (Burghardt, 2005). Behavioural ecologists have long thought that RTP has adaptive functions as it persists even with high fitness costs which can include energy expenditure, time which could have been spent foraging or in other activities, and risk of injury and/or predation (Boulton, 1996; Smith, 2005). For an individual to continue to engage in RTP in the face of such costs suggests that the behaviour enhances relative fitness (Burghardt, 2005). There are many proposed functions of RTP, including the development of communicative and social abilities (Spinka, Newberry and Bekoff, 2001), learning and practicing dominance behaviours (Humphreys and Smith, 1987), the development of physical strength and skills in preparation for adult competition and aggression (Cenni and Fawcett, 2018), gaining knowledge about future competitors (Byers, 1980), developing predatory skills (Caro, 1981), learning to deal with unexpected situations within the individual's environment (Spinka, Newberry and Bekoff, 2001; Lutz and Judge, 2017), and developing peer relationships (Martin and Caro, 1985). These functions are not mutually exclusive, and it is likely that RTP has more than one function, which could vary by species, or by individual factors such as age or sex (Smith, 2005). These functions may have immediate benefits, such as gaining knowledge of the environment, but are more often seen as having delayed outcomes which benefit the individual in adulthood, such as building social relationships or physical development for aggression in adulthood (Burghardt, 2005).

RTP may also function as a form of social learning, which is particularly noted in studies of human children's play (Terashima and Hewlett, 2016). In hunter-gatherer societies, children's play has been shown to aid in learning the core values, skills and knowledge required for life in a subsistence society, particularly when engaging in social play with other children. As RTP is a form of play associated with childhood, it is suggested that it is necessary for child development, and is therefore likely to be a form of social learning (Boyette, 2016a). Smith (2005) suggests that human play may aid in the development of complex cognitive functions, including the facilitation of innovation and creativity, the development of perspective taking, and theory of mind skills (Flanders, Herman and Paquette, 2013), all of which are likely to be involved in preparation for the complex social lives of humans. During RTP, children may engage in the practice of social skills, experiencing both dominant and subordinate roles, and learning how to regulate aggressive behaviours (Storli and Hansen Sandseter, 2017).

The importance of the developmental benefits of play and other social interactions are further highlighted by play and social deprivation studies, in both humans and non-human mammals. Animals which are isolated during infancy have been shown to demonstrate higher levels of aggressive and fearful behaviours when introduced back into a social group, and are less likely to engage in social play compared to those that have not been isolated (Smith, 2005). This includes primate studies, where monkeys deprived of social interactions during the first 6 months of life are unable to engage in normal social functioning after this period, including being highly reactive to stress, unable to regulate aggression, and unable to send or decode emotional cues between peers (LaFreniere, 2011). When animals are deprived of play, they will compensate for this deprivation by increasing play when given the opportunity. For example, when peri-adolescent rats were deprived of opportunities to engage in RTP, they exhibited significantly higher levels of play in initial interactions with peers compared to those that have not been deprived, even when allowed to interact with peers in other ways such as via olfactory, visual, and gentle tactile interactions (Holloway and Suter, 2004). Similar effects are observed in human children, where American 5 to 9 year olds who were forced to be sedentary for a period of time engaged in more vigorous play for longer durations of time compared to those who were not deprived of exercise, with stronger effects shown for boys (Pellegrini, 2009). General reductions in time spent in play in children have been linked to negative mental health outcomes, including anxiety and depression (Gray, 2011), growing levels of health problems such as obesity, rickets, and attention deficit disorder (Gleave and Cole-Hamilton, 2012), and serious consequences for the physical, cognitive and social development of children (Whitebread et al., 2012). Therefore, it is clear that juvenile play is essential for typical development and functioning in childhood and beyond.

However, there is evidence that the time spent in RTP differs both across species (e.g. Iwaniuk, Nelson and Pellis, 2001) and across human cultures (e.g Fry, 2005), as well as within species or cultures, due to individual factors such as sex and gender (LaFreniere, 2011), which may suggest that the benefits of engaging in RTP also vary. In Chapters 3 and 4, cross-species analyses are used to investigate how sex biases in RTP are distributed across species, with the aim of considering the potential functions and adaptive benefits of RTP, and biological and ecological factors that may underpin sex differences in RTP. In Chapters 5 and 6, I use cross-cultural analyses to determine the extent to which boys and girls engage in RTP across human cultures, investigating cultural and environmental factors that may underpin variability in gender differences in RTP. I also take into account methodological factors that may further influence the results of studies concerning sex and gender differences RTP, and consider potential interactions between relevant biological, cultural, and contextual factors.

Juvenile RTP

Juvenile play is considered essential for typical development and functions, both throughout the juvenile period and into adulthood, in both humans and non-human mammals. Extended juvenile periods, which are particularly common in primate species including humans, are hypothesised to facilitate the acquisition of knowledge and skills in order to maximise future reproductive fitness (Kramer and Ellison, 2010), which may be obtained partly via RTP (Pellis and Iwaniuk, 2000). Therefore, understanding RTP among juveniles is of particular importance in the study of the origin and function of RTP. Play also occurs during infancy, often between infants and their mothers in the earliest stages of life (e.g. Hoff, Nadler and Maple, 1981; Palagi, 2018), and in adulthood (e.g. Zucker et al., 1986), but it is possible that the functions of RTP vary at different ages, particularly in different developmental stages. For example, adult RTP in orangutans compared to juveniles involves less locomotion such as chasing or following (Zucker et al., 1986), and adult RTP in harbour seals may only occur during the mating period (Renouf and Lawson, 1987). Furthermore, mother-infant play is likely to aid in the development and maintenance of the bond between the mother and her infant (Savage and Malick, 1977), and is more likely to be initiated and terminated by the mother, rather than the infant (Hoff, Nadler and Maple, 1981). This suggests engagement in RTP varies depending on age and context and may therefore have different functions in infancy and adulthood compared to play in the juvenile phase. Therefore, in this thesis I focus exclusively on juvenile RTP as a key adaptive behaviour during development.

The Comparative Method

This thesis centres around comparative methods, in both cross-species and cross-cultural analyses. I have chosen to use comparative methods to investigate sex and gender differences in RTP as there is evidence of variation in sex differences across species (Smith, 2005) and gender differences across cultures (Fry, 2005), and comparison could lead to the identification of factors which underlie sex and gender differences in RTP. Comparative methods are one of the fundamental methods in the study of human and non-human animal behaviour, where comparison across species or across cultures is used to infer evidence for adaptation and other evolutionary hypotheses (Cuthill, 2005; Nettle et al., 2013). There is also an emerging tradition of using cross-cultural comparisons to test hypotheses regarding the social and environmental factors that may explain variation in human behaviour (Mace et al., 1994), usually through the lens of cultural evolution (Mesoudi, 2016). As RTP is likely to be an adaptive behavioural trait, and shows considerable variation across species and cultures, it is therefore an ideal candidate for exploration through comparative methods. In this introduction, I first consider sex differences in RTP across species, focusing on how the principles of behavioural ecology, particularly life history theory, can be used to explore the adaptive functions of RTP. I focus on biological factors which may lead to evolved predispositions for males or females of a given species to engage in higher levels of RTP. I then go on to explore how gender differences in RTP vary across human cultures, thinking about possible adaptive functions in addition to cultural factors, such as marriage system or gender roles within a culture, which may interact with biological predispositions to determine rates of RTP for boys and girls. I explore cultural factors primarily through the lens of cultural evolution. Finally, I consider contextual factors, including variation in the physical and social environment, which may further promote or constrain RTP, and the interactions between biological, cultural, and contextual factors which may be associated with variation in sex and gender differences in RTP. I explore the application of the comparative method further in Chapter 2.

Sex Differences in RTP

First, I will consider the variation in sex differences in RTP across mammalian species through the lens of behavioural ecology. The core ideas of behavioural ecology, which were outlined in the 1960s and 70s, focus on simple adaptive models, where the relationship between environments and behaviour is considered in terms of evolution and natural selection (Owens, 2006). Central to behavioural ecology methods are optimality models, which capture the payoffs, trade-offs and constraints concerning an adaptive behaviour, and the balance which allows an animal to maximise reproductive fitness (Cuthill, 2005).

In particular, I will focus on life history theory as a framework for understanding biological influences on RTP, including its distribution across species and sex differences within species. Life history theory provides explanations for variations in behaviour involving trade-offs in the energy invested into age and size at maturity, reproductive investment, and lifespan in order to maximise reproductive fitness (Stearns, 2000). Energy and time are limited resources, so individuals must trade-off investment in current reproductive efforts against future reproductive efforts via growth or maintenance (Emery Thompson, 2017). Examples of factors which vary across species due to life history strategy include differences in gestation length, neonatal weight, litter size, age at weaning, age at sexual maturity, and longevity (Harvey and Clutton-Brock, 1985), where differences are shaped by extrinsic factors such as mortality risk from predation (Stearns, 2000). Life history traits can be split into stages of development, such as the juvenile phase, which is used as a period to develop skills which will be useful in adulthood, and the adult phase, in which the individual puts those skills to use to secure resources and mating opportunities, leading to reproductive success (Cenni and Fawcett, 2018).

Investment in RTP is a good example of life history trade-offs between developmental phases, where a juvenile individual should invest energy and time into RTP rather than growth if RTP is of sufficient ontogenetic importance, providing benefits in adulthood which lead to compensatory reproductive success, such as developing motor skills to aid with decreasing mortality risk and improving dominance rank in adulthood (Berghänel, Schülke and Ostner, 2015). The potential fitness benefits of the behaviour must be balanced against the associated risks, which can be physical, such as risk of injury (Heintz et al., 2017), or social, as the individual risks becoming too aggressive and being excluded from future play (Siklander, Ernst and Storli, 2020). The time and energy spent in RTP must also be balanced with the time and energy which could instead be dedicated to maintenance or growth (Miller and Byers, 1991), or, for humans, time spent in developing knowledge, technical skills, or contributing to society through economic activities such as agricultural or domestic labour (Larson and Verma, 1999). This balance between the benefits and costs of RTP is likely to be different both across species and across human cultures, due to the effects of specific ecological niches and/or cultural setting.

Sex, Activity Budgets, and RTP

Life history strategies often differ between biological sexes due to sexual selection, which may therefore help explain sex differences in the timing of and engagement in RTP. Sexual selection is a result of intrasexual competition for mates and breeding opportunities, leading to the evolution of behaviours which increase reproductive success, sometimes including pronounced secondary sexual characteristics, such as sexual size dimorphism (Clutton-Brock, 2004). These behaviours may be associated with factors such as social or mating system (Clutton-Brock, 2004), or differences in behaviour such as interactions with conspecifics, foraging behaviours, and sex-biased natal dispersal (Setchell and Lee, 2004). Levels of intrasexual competition in mammals tend to be higher between males, as they often compete for dominance rank and mating opportunities (Wright et al., 2019) which are typically more important for their reproductive success compared with females. For example, high levels of male competition are associated with polygyny and male-biased size dimorphism across mammalian species (Clutton-Brock, 2004). This is relevant to sex differences, as growth rates, attenuation of growth, timing of sexual maturity and reproductive investment are shaped by natural selection over the history of a species, in order to maximise reproductive success (Stearns, 2000).

There are also likely to be sex differences in mammalian activity budgets as a result of different reproductive strategies for males and females (e.g. Wojciechowski et al., 2019). According to predictions based on life history theory, adult females may invest relatively more in time spent foraging, in order to meet the energy demands of gestation and lactation, while adult males are predicted to minimise their time spent foraging relative to other activities that increase fitness, such as competition and mating (Nakagawa, 2000). Wedge-capped capuchins, for example, show strong differences in activity budgets across sex and age groups consistent with this suggestion; adult males devote less time to foraging and more time to scanning and resting compared with adult females and juveniles (Fragaszy, 1990). However, it is often the case that studies present mixed findings, or even a lack of sex differences. For example, silverback gorilla males show a greater proportion of time spent feeding than adult females, due to sexual size dimorphism, but the sex differences are reported to be small, and insignificant for other behaviours such as resting, moving, and social behaviours (Watts, 1988). Abondano and Link (2012) reported no sex differences in the time brown spider monkeys spent resting, moving, or socialising, but report that females spend more time feeding than males. Therefore, it is clear that sex differences in time and energy budgets differ across and within species, and that further investigation of variation in sex differences in RTP as part of wider energy budgets would be beneficial.

RTP is a component of physical activity generally and play in particular (Brockman, Fox and Jago, 2011), and animal studies suggest variability in sex differences in RTP across species. Studies have focused mainly on primates, showing a tendency for juvenile males to engage in higher rates of RTP compared to same-age females, including for tufted capuchins (Paukner and Suomi, 2008), rhesus macaques (Brown and Dixson, 2000), Japanese macaques (Hayaki, 1983), chimpanzees (Hayaki, 1985), vervets (Govindarajulu et al., 1993), and long-tailed macaques (van Noordwijk et al., 1993). Evidence of male biases in RTP is also found for other mammals including pigs (Brown et al., 2018), dogs (Ward, Bauer and Smuts, 2008) and rats (Meaney and Stewart, 1981). However, there are studies which show equal rates of RTP between males and females of the same species, or even female biases (e.g. Worch, 2010), and there has been no systematic attempt at capturing the extent to which male biases are consistent across species. The examination of cross-species sex differences in RTP could help to shed light on the functions of RTP and how the behaviour was shaped through natural selection (see Nunn, 2011). Furthermore, factors such as variation in measurement of RTP behaviour (such as the use of rates, durations, or initiations), components of RTP (where males may engage in more aggressive component of RTP e.g. (Owens, 1975)), and/or setting (such as captive versus wild populations, which may affect behaviours including RTP due to differences in energy constraints e.g. Fragaszy, Visalberghi and Fedigan (2004)) have not yet been explored systematically. Therefore, I aim to investigate biological and methodological factors affecting sex differences in RTP by considering the effects of sexual selection and life history strategies on variation in sex differences in engagement in RTP across non-human mammalian species.

Mechanisms of RTP

Having established that sex differences in RTP are expected to vary across species based on variation in sex differences in reproductive strategies and in the effects of sexual selection, it is important to consider proximate factors which may affect the expression of RTP, including morphological and/or physical traits which facilitate the expression of the behaviour. One potential biological mechanism is the endocrine system, as higher levels of juvenile RTP have been associated with higher levels of testosterone in both males and females, either through priming or organisational effects (prenatal or during early infanthood), or activating effects at puberty (Jarvis, 2007; Grebe et al., 2019). Neonatal exposure to testosterone by injection has been shown to increase the number of playful attacks by both female and male rat pups compared to controls (Pellis, Pellis and Kolb, 1992), and implanting testosterone directly into the amygdala of female rat pups resulted in a similar level of play-fighting to male rat pups, which was significantly higher than female controls (Meaney and McEwen, 1986). Also in rats, the castration of males soon after birth has also been shown to reduce levels of playfighting to female-typical levels (Taylor, Frechmann and Royalty, 1986). Similar results are found for rhesus monkeys, where increasing prenatal testosterone for female juveniles results in similar rates of RTP to control males (Goy and Phoenix, 1972). These findings suggest that the absence of testosterone results in female-typical development and therefore lower levels of RTP, and that the presence of testosterone is necessary for development of higher or male-typical levels of RTP (Pellis, 2002).

The same underlying mechanisms are expected to occur in humans, as testosterone has also been implicated in higher levels of RTP for humans. Girls with congenital adrenal hyperplasia (CAH), a genetic condition that results in increased exposure to androgens during early gestation, are reported to engage in more male-typed interests and play (Berenbaum and Beltz, 2011). Pasterski et al. (2011) reported that girls with CAH preferred a more rough-and-tumble play style to unaffected girls of the same age, but not to an equal level of unaffected boys. However, there are mixed findings, as Hines and Kaufman (1994) found that girls with CAH engaged in similar rates of RTP compared to unaffected girls. Knickmeyer et al. (2005) found that higher levels of amniotic testosterone were not correlated with play behaviours such as RTP for children of around 5 years of age, but do note that it is possible that there may be a period of development that is important for RTP that was outside of the window where amniotic testosterone levels were measured. Similarly, Sánchez-Martın et al. (2000) examined the play of 48 preschool children in Spain, and found that although serious aggression was positively correlated with levels of testosterone (measured by saliva sample), there was no association between RTP and testosterone, and reverse causality is also possible (where high levels of RTP could cause elevated levels of testosterone). There were also no significant differences between levels of testosterone for boys and girls, which again suggests that testosterone has limited effects on play behaviour, or that the effects of testosterone act on RTP at a different developmental period. Other reproductive hormones may also be involved in the expression of RTP. Female rat pups which were treated with oestradiol, a form of oestrogen, showed a significantly increased frequency of RTP compared to control females, engaging in RTP at similar levels to control males (Olesen et al., 2005). This effect was removed when pups were previously treated with an oestrogen receptor antagonist, suggesting that oestrogen may also be affecting rates of RTP. Although the endocrine system is likely to be one of the main mechanisms underlying the expression of RTP, the picture seems to be complicated, especially for human RTP.

Overall, although testosterone and other reproductive hormones are clearly involved to some extent in the expression of RTP, the picture is not clear and often requires experimental manipulation to uncover. As I wish to focus on RTP as it occurs naturally, and not under the effects of experimental manipulation, I have decided not to consider studies of hormonal effects directly in this thesis. Studies of hormonal effects on RTP are often on a limited number of species, such as primates or rodents, and for children often focus on small sample sizes in Western, industrialised societies. Therefore, in this thesis, I focus on using comparative methods to identify the adaptive functions of RTP, and to analyse the effects of other underlying biological and social factors.

Potential Functions of RTP

Thinking about play in terms of its adaptive functions originated with Karl Groos (1898), who argued that young animals have a critical period during juvenility in which to play, which serves as a method of developing and perfecting behaviours which are required for survival and reproduction in adulthood. Other early views on play included recapitulation theory, which argues that play is no longer necessary but only reflects behaviours which were important in earlier evolutionary history (mostly associated with G. Stanley Hall), and surplus energy theory, which presents the argument that animals are compelled to play to burn off surplus energy or 'vigour' (originally proposed by Friedrich Schiller, and further promoted by Herbert Spencer (see Burghardt, 2005)). However, modern evolutionary views on play focus on the various adaptive functions of play, including growth and development of various domains and skills, since play persists even when incurring high costs (Smith, 2005).

In behavioural ecology, a function of a behaviour refers to the adaptive value; any behaviour which is adaptive must enhance inclusive fitness at the individual (Cuthill, 2005) or, more controversially, group level (see Okasha, 2001). Where play does have an adaptive function, it follows that higher levels of engagement in play should lead to increases in reproductive fitness. RTP may have many functions, none of which are mutually exclusive (Burghardt, 2005), and may have consequences which are beneficial in the present or in the future (Pellegrini, 2002). Furthermore, the function of play and its role in individual development may differ based on a number of factors, including species, sex, age, group composition and relationships, context, and habitat (Cordoni and Palagi, 2011; Palagi, 2018).

As noted above, the adaptive function of a behaviour can change throughout development (Bateson and Laland, 2013), so the thesis focuses solely on juvenile RTP, and will take into account age differences where possible. Cross-species comparative analyses will be used to examine the extent to which each of these proposed functions helps to explain variation in sex differences across non-human mammalian species. Each potential function may be used to explain sex biases or a lack of sex differences in RTP. Where relevant, I also consider adaptive functions that may be relevant only to humans and gender differences in RTP, which will be considered further later in the chapter. The various proposed functions of play are explored below, and are summarised in Table 1.1.

Physical Development

Physiological Development

One proposed function of RTP is that of physical training, where RTP may aid in the development of muscular and skeletal strength, cardiovascular fitness, and general endurance (Byers and Walker, 1995; Nunes et al., 2004; LaFreniere, 2011). Longer, sustained bouts of RTP may result in aerobic and endurance training, whereas shorter, more vigorous bouts of RTP can increase anaerobic capacities and improve recovery between bouts of activity (Bekoff, 1988). For young animals, this physical training may be necessary in order to train the muscle groups used in escape, fighting, and/or reproduction (Fagen, 1976). The physical training effects of RTP may be both immediate and deferred, as early development of physical fitness can have long-term cumulative effects on endurance and the efficiency of actions used in predation, predator avoidance, territory defence, mating, and caregiving (Bekoff, 1988), which may contribute to fitness to different extents for males and females.

Motor Development

The neuromuscular system requires development to aid in the co-ordination of movement and maintaining equilibrium for life events such as dispersal, participation in social dominance hierarchies (Nunes et al., 2004), and competency in fight/flight reactions (Berghänel, Schülke and Ostner, 2015). The motor training hypothesis of play posits that the function of RTP is to develop the neuromuscular system in preparation for the same motor patterns in serious functional contexts during adulthood (Martin and Caro, 1985; Byers and Walker, 1995). RTP has been shown to predict neuromuscular development, as wild chimpanzee infants that spent more time in RTP achieved motor milestones, including riding dorsally and travelling independently, at earlier ages than their peers who engaged in less RTP (Heintz et al., 2017). Nunes et al. (2004) tested the motor skills of juvenile Belding's ground squirrels before and after a two week play period and found that juveniles who played more and had more play partners showed significantly greater improvement in motor skill development. Male biases in RTP for a number of mammalian species have been suggested to provide evidence for the motor training hypothesis, as species where males would benefit from more developed motor skills than females in order to compete in male dominance hierarchies have been shown to engage in higher levels of juvenile RTP (e.g. Assamese macaques (Berghänel, Schülke and Ostner, 2015), tufted capuchins (Paukner and Suomi, 2008), and gorillas (Maestripieri and Ross, 2004)). These studies, among others, show support for the motor training hypothesis, suggesting that one of the functions of RTP is to aid in the development of the neuromuscular system, which may be more beneficial to males compared to females. However, enhanced motor skills may also enable higher rates of RTP, so although there is a correlation between the two factors, a causal effect cannot be concluded (Berghänel, Schülke and Ostner, 2015).

Children's play, including balancing, dodging, climbing, throwing, and catching, is also associated with the development of motor skills (Hynes-Dusel, 2002), although the development of these abilities may not be specific to RTP. Palma et al. (2014) state that engaging in a diverse range of tasks and play activities is essential for developing sophisticated motor skills which are used throughout childhood and later adult life; to develop adequately, a child must engage in tasks that incorporate a variety of physical demands. Although children may develop fundamental motor skills through their own self-directed play, proficiency in motor development may require specific instructions and opportunities to practice motor skills, although evidence only includes children attending Western schools, who may have reduced opportunities to develop motor skills through free play (Barela, 2013). Sääkslahti and Niemistö (2021) state that although play is important for motor development, for optimal development to take place children must play in a range of versatile environments which challenge their current motor skills.

Fighting

Similar to the motor skills hypothesis, RTP may also assist with the development of specific physical skills such as fighting ability. RTP is a safer way to practice fighting compared to genuine aggression, as it provides opportunities to engage in the same motor patterns and skills used in fighting, but in a non-aggressive context (Boulton, 1996). Cenni and Fawcett (2018) propose a life history model in which individuals use the juvenile phase to engage in RTP and develop fighting skills, which is followed by the adult phase in which individuals use these skills in aggressive contests and therefore secure resources and mating opportunities, leading to reproductive success. For example, Berghänel, Schülke and Ostner (2015) found that for Assamese macaques, male juveniles played, acquired motor skills faster, and grew less than female juveniles, suggesting that investment in play is prioritised over investment in growth, displaying sex-differentiated life history strategies. However, Worch (2010) found that male and female red colobus monkeys engaged in similar levels of RTP, despite the fact that fighting skills would be of greater benefit to the more competitive males. Furthermore, in a longitudinal study of wild meerkats, Sharpe (2005) found no correlation between RTP and adult fighting success. Therefore, although the hypothesis that RTP serves as a method of training fighting skills is somewhat supported, the evidence is occasionally mixed and inconsistent.

Predation

Another motor skill that has been hypothesised to develop through engagement in RTP is, for predators, the individual’s ability to hunt. Animal RTP contains many of the same motor patterns and behaviours as adult predatory behaviour, such as holding, biting, and chasing (Caro, 1981). In a study of domestic kittens, Caro (1979) found that although some measures of play, such as approaching, pawing, holding, and biting were associated with improved adult predatory behaviours, other play behaviours such as rolled contact, arching, and chasing were not, suggesting that practice of specific play behaviours does not necessarily lead to successful execution of those behaviours in adult predatory behaviour. The development of predatory behaviour may be equally important for both male and female animals of the same species, as both must hunt. However, this is only limited evidence for the association between RTP and the development of predatory skills, which is challenged by other animal studies. Davies and Kemble (1983) found no association between RTP and efficiency of predation for northern grasshopper mice, and Vincent and Bekoff (1978) found that higher levels of RTP had no association with later predatory success in coyotes, which may again reflect the limitation of correlative studies. A similar picture is found in the human literature; there is a traditional view that RTP functions as safe practice for the development of hunting skills in hunter-gatherer societies, but there is little direct evidence that supports this hypothesis (Pellegrini and Smith, 1998b). If there is an association between RTP and the development of hunting skills, this could be associated with gender differences, as hunting is often traditionally associated with male behaviours (e.g. Wood et al., 2021).

Cognitive Development

A cognitive element of development that may be trained by RTP is behavioural flexibility. This is known as the ‘training for the unexpected’ hypothesis, where RTP is suggested to enable animals to develop a repertoire of behaviours in a safe environment, which can be applied to novel and/or unpredictable stimuli in future situations (Spinka, Newberry and Bekoff, 2001). RTP allows an individual to purposely lose control of a situation, often through self-handicapping, after which they must improvise new behaviours in order to recover quickly (Heintz et al., 2017; Lutz and Judge, 2017). These behaviours can be used in future social situations, and the individual also benefits from a reduced physiological reaction to future unexpected stressors (Spinka, Newberry and Bekoff, 2001). Learned responses can be applied to both environmental and social stimuli, ensuring that the individual learns to respond to a variety of situations (Pellegrini, Dupuis and Smith, 2007). Examples include acquiring a working knowledge of the environment which could be used in intraspecific competition or in predator avoidance (Smith, 2005), which could be more beneficial for the dispersing sex of a species (Li and Kokko, 2019). For humans, cognitive development in RTP is associated with developing social competence that allows children to solve social problems during play and conflict (Pellegrini, 1993, 1995), which would be important for both girls and boys.

Social Development

As RTP is a social behaviour, it is likely that it evolved in association with living in social groups, as it may allow individuals to learn about others within the group, and develop and maintain their relationships (Smith, 2005). The social skills developed during RTP may include the ability to read unpredictable social situations (Spinka, Newberry and Bekoff, 2001), the ability to demonstrate intent (e.g. demonstrating a play face to convey that the action is play rather than aggression (Koustourakis, Rompola and Asimaki, 2015)), learning how to cooperate and engage in fair play (Bekoff, 2001), turn-taking (Lee and Moss, 2014), regulation of emotional responses (Norscia and Palagi, 2016), and general communicative abilities (Smith, 2005), all of which are important skills for males and females. Male rats that are denied opportunities to play as juveniles do not develop the social skills necessary for adulthood, such as securing mating opportunities and avoiding intra-male competition (Pellis and Pellis, 2010), which suggests that RTP is fundamental to essential social development. Heintz et al. (2017) found that infant chimpanzees that engaged in greater amounts of RTP reached social milestones significantly earlier than their peers who engaged in less RTP, including greater spatial independence from their mother, grooming of non-maternal kin, and earlier mating attempts. Palagi, Antonacci and Cordoni (2007) suggest that RTP involves skills such as assessing the suitability of a play partner, gauging how roughly to play, and assessing space availability, all of which contribute to building social skills and relationships within a group. This suggests that RTP in animals may be fundamental for obtaining the necessary social competence for complex adult relationships and group living (Norscia and Palagi, 2016).

RTP may also play a role in the development of social skills for children, including more complex skills such as bargaining, manipulation, and the ability to redefine situations (Storli and Hansen Sandseter, 2017), as well as cognitive skills such as perspective taking (LaFreniere, 2011). Engagement in RTP peaks in middle childhood, which coincides with the establishment of social status within peer groups, and is associated with the ability to decode the emotional expressions and states of other children, and the child's own emotional states (Pellegrini and Smith, 1998b). Children who engage more frequently in RTP also show better social problem solving abilities, and score higher in social competence tests (Lindsey and Colwell, 2013). This suggests that there is a link between the development of social skills and engagement in RTP, although caution must be taken in determining the causality of the relationship; better social skills developed in other settings may lead to easier engagement in RTP (Pellegrini and Smith, 1998b).

Establishing Affiliative Bonds

Another potential social function of RTP is that it allows individuals to establish and maintain affiliative bonds within their social group, and improve the social cohesiveness of that group (Smith, 2005). Physical contact facilitates the building of social relationships, and RTP can be a method by which the individual induces positive affect states in conspecifics, leading to the establishment of social relationships (Pellis and Pellis, 2010). Expressions of playfulness, such as displaying a 'play face' for chimpanzees or laughter in humans, have been shown to be a method of advertising positive disposition between individuals, and are likely to increase the likelihood of engaging in positive social relationships (Cordoni and Palagi, 2011). In wolves, greater amounts of time spent in play has been shown to reduce aggression and increase other affiliative interactions such as grooming, both of which are associated with stable, positive group interactions (Cafazzo et al., 2018). For humans, there is evidence that boys who engage in higher levels of RTP compared to other boys tend to be more popular, have greater problem solving abilities, and show greater variety of social strategies for initiating and maintaining social interactions with their peers (Pellegrini, 2007). Children who are chosen as play partners more frequently than their peers are also more likely to be rated as closer friends, which implicates play in the development and maintenance of social bonds (Smith and Lewis, 1985).

On the other hand, social activities such as grooming may be a better form of establishing social bonds, as grooming is less energy intensive than RTP (Smith, 2005). For example, female geladas have been shown to stop playing at younger ages than males, and instead invest in grooming behaviour with other members of the social group (Barale, Rubenstein and Beehner, 2015). This would suggest that grooming behaviour may be more beneficial than RTP for female geladas compared to males. The role of RTP must be considered in relation to other strategies of establishing and maintaining social cohesion, and how these strategies may differ for males and females.

Establishing Dominance Hierarchies

In addition to establishing social bonds, juvenile RTP may also serve to establish the social ranks of individuals within a group, and therefore assist in the early formation of dominance hierarchies (Smith, 2005). The development of social rank and establishment of a dominance hierarchy can serve as a means of reducing aggression within a group, as it reduces the level of aggression that would otherwise be necessary in competition for resources (Smith and Boulton, 1990). RTP may allow individuals to establish dominance relationships in a safer context than through real aggression, which may serve to improve cooperation and cohesiveness within the social group, while allowing for the establishment of rank (Cafazzo et al., 2018). Similar dominance functions of RTP are suggested for humans, especially for boys, where physical prowess, affiliative skills, peer group status, popularity, and leadership abilities are associated with both RTP and dominance in Western populations (Pellegrini and Smith, 1998b). It is likely that RTP facilitates displays of prowess and strength, allowing individuals to evaluate their own strength and the strength of others, establishing the dominance hierarchy without aggression (Pellegrini and Smith, 1998b). However, Smith and Boulton (1990) suggest that the ability to assess strength may be limited due to the presence of self-handicapping behaviours, which limit the ability of individuals to accurately assess the strength of others. Furthermore, some studies provide evidence that direct aggression may play more of a role in the establishment of dominance hierarchies, such as in spotted hyena cubs, where dominance relationships are established through aggression at an early age (Cafazzo et al., 2018). Therefore, although RTP may assist in the formation of dominance hierarchies, it is likely that other methods of establishment such as direct aggression are also involved.

Innovation and Creativity

Play is often associated with creativity and behavioural flexibility, and has the potential to lead to innovations in behaviour where play creates novel experiences which provide learning opportunities (Carr, Kendal and Flynn, 2016; Kuczaj, 2017). This is particularly true for RTP, as interactions with a play partner demand higher levels of flexibility and improvisation compared to solitary play, which provides more novel situations and therefore greater opportunity for innovation (Fagen, 1993; Pellegrini, Dupuis and Smith, 2007). These opportunities for innovation are a result of play providing new insights and possibilities, which lead to novel behaviours without regard for the potential payoff (Smith, 2005). Children across cultures are reported to enjoy problem solving as part of play, and it is suggested that adults may encourage play where they wish to encourage innovation (Edwards, 2000). However, Montgomery (2014) suggests that non-social play may be more associated with innovation, as there are more consistent relationships between non-social play and behaviours such as tool use in a range of species, including primates, dolphins, and corvids. This may also be true for humans, where object play is more likely to be associated with the development of cognition and innovation (Riede et al., 2018). Therefore, although RTP may provide opportunities for creativity and innovation, it must be assessed in relation to other non-social behaviours such as object play or tool use.

Table 1.1 *Summary of potential functions of RTP, and potential hypotheses regarding sex differences in RTP.*

Potential Function	**Examples**	**Sources**	**Predicted Sex Differences in Non-Humans**
Physical development	Neuromuscular development	Martin & Caro, 1985 Byers & Walker, 1995	Males may engage in more RTP than females in species where males require greater motor development, physiological development, and physical skills, or display greater body mass. These could be required for male dispersal or higher levels of male competition and aggression.
	Muscular and skeletal strength Cardiovascular fitness Physical endurance	Byers & Walker, 1995 Nunes et al., 2004 LaFreniere, 2011	
	Fighting and aggression Predatory skills	Cenni & Fawcett, 2018 Caro, 1979	
Cognitive development	Training for the unexpected	Spinka et al., 2001	Males and females may engage in RTP at similar rates where both sexes require preparation for situations such as predator avoidance, hunting, and navigation of the environment. Males or females may engage in more RTP than the other sex where these skills are more beneficial i.e., if one sex disperses.
Social development	Reading unpredictable social situations Demonstrating intent Playing fairly Emotional regulation Communication	Spinka et al., 2001 Koustourakis et al., 2015 Bekoff, 2001 Norscia and Palagi, 2016 Smith, 2005	Males and females may engage in RTP at similar rates as both sexes require social skills to navigate living in a social group. Females may engage more in specific aspects of RTP for species where they are more reliant on social relationships.
Establishing affiliative bonds	Establish bonds and social cohesiveness	Smith, 2005 Barale et al., 2015 Pellegrini, 2007	Males and females likely to engage in more RTP for species where establishing affiliative bonds is more important for that sex.
Establishing dominance hierarchies	Reducing risk while establishing social rank	Cafazzo et al., 2018 Pellegrini and Smith, 1998	Males and females are more likely to engage in RTP for species with corresponding male or female dominance hierarchies.
Innovation	Problem solving and creativity	Pellegrini et al., 2007	Males and females equally likely to engage in RTP.

Gender Differences in RTP

I now move to considering cross-cultural variation in gender differences in RTP. A behavioural ecology framework based only in sexual selection and life history theory, as described previously when discussing cross-species variation in RTP, cannot simply be applied to cross-cultural variation in gender differences in RTP in humans. Humans are a single species with continuous phenotypic variation, with insufficient time and separation of lineages for different life history strategies to biologically evolve (Sear, 2020). Instead, the human brain has evolved to respond flexibly to a wide variety of different social and environmental conditions (Nettle and Frankenhuis, 2020). Therefore, when considering human life history strategies, it may be more important to consider life history trade-offs and their complex interactions with cultural and contextual factors (Sear, 2020). Although non-human mammals do have learned behaviour and, perhaps in some situations, cultural traditions (Laland and Janik, 2006), humans have much more complex cultural systems, including, crucially, social construction of gender due to factors such as self-identification (see Wood and Eagly, 2015) and social roles (see Eagly and Wood, 2012). Therefore, culture is considered much more important for human behaviour, and must be centred in the study of gender differences in behaviour, including RTP, as variation in human behaviour cannot be explained entirely in terms of evolutionary biology.

In this work, I rely on secondary analysis of data which uses a female/male binary approach to sex and gender, but this project will endeavour to be sensitive to both biological and social concepts of sex and gender which fall outside of this binary. The term ‘sex’ is usually used to refer to the biological differences between males and females in all sexually dimorphic species, such as anatomical and physiological differences, whereas, in humans, ‘gender’ tends to indicate an individual’s identification as a man, women, or other (such as non-binary) gender and the accompanying psychological, cultural, and social positioning within their society (see Muehlenhard and Peterson, 2011). As much as possible, sex will be used to refer to the chromosomal determination of sex and the resulting physiological differences, whereas gender will be used to refer to a person’s identification as male or female within their social and cultural context (Holdcroft, 2007). Therefore, the term ‘gender’ will not be used to refer to non-human animals, as gender identity cannot be modelled in animals who cannot express such concepts (Roselli, 2018). For the purposes of this document, this is how the terms ‘sex’ and ‘gender’ will be used, although there is an argument that sometimes the separation of the two terms is inappropriate, due to interactions between biological and social factors (Maccoby, 1988)., I also acknowledge that sex characteristics are not strictly binary, where intersex individuals can fall outside of the traditional male/female distinction due to variations in anatomy, hormones, and genetics (Sanz, 2017). Feminist, transgender, and intersex activists and scholars have been critical of the binary distinction between sex and gender, arguing that concepts of both sex and gender are a result of interactions between biology and culture, and that sex cannot be the foundation of gender as it is also socially constructed. In addition to this, concepts of gender often change based on cultural and historical contexts (Johnson, Greaves and Repta, 2009), which must be considered throughout this research, particularly when considering ethnographic data from diverse locations and time periods. It is also important to note that I do not assume that individual differences in human behaviours, including gender differences in RTP, can be entirely attributed to either biological or socially constructed factors, but rather to an interaction between biology and culture, and the associated evolutionary and cultural history.

Gender, Activity Budgets, and RTP

There is evidence of gender differences in activity budgets across human populations. Physical activity budgets, specifically, which include time spent in RTP, have been found to show robust differences across gender, age, and culture, with a pervasive concern about girls being less active than boys in societies in which low physical activity is a key risk factor for disease (Duffey et al., 2021). Japanese boys in primary and junior school had a significantly higher mean number of steps per day (Fukushima et al., 2016), American boys in grades one to twelve recorded significantly higher levels of overall activity through accelerometer counts (Trost et al., 2002), and Canadian boys consistently met physical activity guidelines at a significantly higher rate than girls (Colley et al., 2011). Adult men consistently report higher levels of objectively measured moderate-to-vigorous physical activity compared to women, in the UK (O'Connell, Griffiths and Clemes, 2014), Sweden (Ekblom-Bak et al., 2015), and the United States (Tucker, Welk and Beyler, 2011). Gender differences in physical activity have been attributed to a range of factors, including choices of physical activity during leisure time, time spent at work or in household tasks, engagement with organised sport, and knowledge and attitudes towards health and physical activity (Azevedo et al., 2007). Therefore, gender differences in RTP should be studied, with the aim of identifying the underlying factors which lead to differences and considering RTP as an element of physical activity.

There is already evidence that differences in cultural setting can lead to variations in the amount of RTP that children engage in. For example, Fouts and Lamb (2009) examined the play of children in two small-scale societies (Bofi farmers and foragers in Central Africa), and found that rough play was significantly more common for children in a farming community compared to those in a forager community, suggesting that setting, context, and the subsequent differences in cultural values can affect the rates of specific types of play. Furthermore, Fry (2005) examined the play behaviour of children in two communities in southern Mexico, finding that children in a community with higher incidences of physical punishment, adult fistfights, and homicide engaged in significantly higher rates of RTP and for longer bout durations than the community with lower rates of the above, which was attributed to differences in cultural values regarding aggression. There is also evidence of variation across societies in gender differences in RTP. A study of six cultures found that in India, Japan, Mexico, and the Philippines, boys up to the age of 11 participated in more RTP than girls of the same age, yet this pattern was reversed for children in Kenya, where girls engaged in more RTP (Whiting and Edwards, 1973). Although there is a common pattern of boys engaging in more RTP than girls, this does not appear to be universal (Fry, 2005), as no gender differences were found in rates of play aggression for Zapotec children (Fry, 1988). This is reflected in other forms of play, where girls in the Hadza and BaYaka hunter-gatherer groups were observed to engage in more pretend play involving playing house, playing with dolls, and foraging, whereas boys were more likely to play at hunting and collecting honey, both of which imitate adult behaviours according to gender roles in the respective cultures (Lew-Levy et al., 2019). This suggests that cultural factors such as subsistence style and adult behaviours can affect rates of RTP for children, and that this may further be affected by gender differences within that culture.

Cultural Evolution

I now move to considering cultural variation in gender differences in play through the lens of cultural evolution, in which the principles of Darwinian biological evolution are adapted to study cultural change and the transmission of social information (Richerson and Christiansen, 2013). The core principles of cultural evolution state that cultural traits exhibit variation, specific traits will vary in their rates of survival and reproduction, and that these traits are transmitted through processes of social learning, such as imitation or teaching (Mesoudi, 2016). Through observation and imitation, children can learn culturally appropriate behaviours and cultural scripts, including appropriate etiquette, social skills, and subsistence skills, which are used to be successful members of that specific culture (Lew-Levy et al., 2018). Comparative methods are also popular in the field of cultural evolution, where traits are compared across societies using phylogenies constructed typically from linguistic data to control for non-independence between cultures (Mace et al., 1994; Freckleton and Jetz, 2009). Gender differences in juvenile RTP are likely to have evolved through the process of both biological and cultural evolution, which I explore throughout the thesis, with a particular focus on cross-cultural comparisons and the contribution of social learning mechanisms.

Gender Roles

Gender roles are based on sets of expectations for behaviour based on a society's, group's, or individual's beliefs and values about gender (Blackstone, 2003), which can lead to cross-cultural variation in gender differences, such as a gendered division of labour (Alesina, Giuliano and Nunn, 2013), as cultural traits are transmitted by parents to their children (Hiller and Baudin, 2016). Eagly and Wood (2012) propose that the construction and performance of gender roles is the result of interactions between biological, psychological, and social mechanisms, where sexual dimorphism and hormonal fluctuations contribute to the occupation of different roles within society for men and women, and individuals internalise gender roles by assessing their own behaviour against self-standards and social regulatory mechanisms. Gendered behaviours are reinforced by social influences such as parents, who often encourage gender-typical behaviours, and later by the children's playgroup, where children begin to internalise the gendered expectations of the community (Lew-Levy et al., 2018). It is likely that play contributes to the foundations of cultural learning as children imitate cultural models and schema through their play activities, which may be heavily gendered (Boyette, 2016a). Furthermore, differences in gender roles across societies (where the varying employment and family roles held by men and women differ) can also lead to differences in accepted behaviours according to gender (Eagly and Wood, 2012), which in turn influence children's gendered play.

Furthermore, children's peer groups are often segregated by gender, which can lead to distinct gendered peer cultures and socialisation experiences, which often results in a higher likelihood of engaging in gender stereotyped activities (Fabes, Martin and Hanish, 2003). This is supported by evidence which suggests pre-school boys in Australia are likely to be more active, take up more space, and play in larger, more competitive groups, compared to girls who are more likely to be inclusive and cooperative, engaging in more passive games which require fewer players and less physical space, which is consistent with dominant models of gender roles in Australia (Chapman, 2016). This can lead to distinct preference for girls and boys, such as boys preferring RTP and girls preferring quieter, more structured activities (Smith and Inder, 1993). Therefore, I expect that gender roles could have a direct impact on RTP, where children would engage in RTP where it is deemed appropriate behaviour according to the child's gender, which could relate to children's peer groups and/or adult gender roles, and their corresponding accepted behaviours. Although I acknowledge that these differences may be in part biologically influenced, in Chapters 5 and 6 I focus on the impacts of more proximate social factors.

Mechanisms of Social Transmission

The mechanisms by which variation in gender roles and the subsequent gender differences in RTP occurs across cultures should also be considered. According to the principles of cultural evolution, any information that is socially transmitted can evolve by means of a Darwinian evolutionary process

(Mesoudi, 2016). Socially transmitted information can include beliefs, knowledge, skills, or practices, which suggests that engagement in RTP could differ between groups due to the processes of cultural evolution. Three principles are necessary for Darwinian evolution, either biological or cultural (Mesoudi, Whiten and Laland, 2004), as follows: the principle of variation, in which entities within a population vary in their characteristics; the principle of differential fitness, in which entities within a population vary in rates of survival and reproduction; and the principle of inheritance, in which entities' characteristics correlate between parents and their offspring (Lewontin, 1970). The mechanism by which cultural traits are passed between individuals is referred to as social transmission, when the behaviour of one individual influences the rate at which others acquire or perform the same behaviour (Jones and Rendell, 2018). Although original models of cultural evolution focused on inheritance of behaviour from parents to offspring, later models of cultural evolution were constructed which took into account not only vertical transmission (parent to offspring) but also oblique (an individual learning from members of their parent's generation), and horizontal transmission (peer to peer) (Mesoudi, 2016).

There are various mechanisms of social learning according to cultural evolutionary models, some of which create biases in the information which is socially transmitted (Mesoudi, 2016). Although social transmission is not unique to humans (with evidence in species such as bluehead wrasse, meerkats, rats, squirrels, and great apes (Hill, 2010)), cumulative cultural evolution, in which cultural changes exhibit the preservation of and improvements upon earlier traits, is almost entirely unique to humans, with potential rare possible exceptions in animals such as chimpanzees and New Caledonian crows (Caldwell, Renner and Atkinson, 2018). One of the crucial components of cumulative cultural evolution is that social learners are selective in what and who they imitate, as without this process social learning would be no more beneficial than asocial learning (Mesoudi, 2016). Social learning biases include payoff-biased social learning, in which an individual will copy those that receive the highest payoffs or benefits, and frequency-dependent bias, in which an individual will copy the most common behaviour within a group (Kendal, Giraldeau and Laland, 2009). Similarly, children may show biased social learning by choosing to copy individuals most similar to themselves, which can be beneficial as the individual being imitated is more likely to live in a similar environment and have relevant knowledge and experience of the social customs that individual will need to integrate and live successfully within that social group (Over and Carpenter, 2012). Therefore, I consider the transmission of engagement in RTP for boys and girls with respect to vertical and horizontal cultural transmission, and the potentially biased mechanisms of social transmission.

Vertical transmission refers to direct socialisation between parents and their offspring, where children gain socially transmitted information such as beliefs and behaviours (Mesoudi, 2016). Hiller and Baudin (2016) suggest that vertical cultural transmission can be a gendered process, where parents transmit their own culturally gendered traits onto their sons and daughters through gendered socialisation processes. This is likely to be reinforced by children's preferences for role models, as children are more likely to imitate adults and peers who share similar characteristics, such as the same gender (Draper, 1975). Play provides an environment in which children can practice cultural scripts through imitation, which often results in the recreation of behaviours such as gender-specific subsistence skills (Lew-Levy et al., 2018), which contributes to the development of the skills and knowledge necessary for adult hunter-gatherer life (Terashima and Hewlett, 2016).

Socially transmitted information is also passed between peers, where children learn about their culture and the associated behaviours and beliefs through social interactions with each other, in a process called horizontal transmission (Boyette, 2016b). Horizontal cultural transmission is most common between 5 and 12 years of age, where children spend much of their time in playgroups, observing and imitating others (Hewlett et al., 2011). As stated above, children are likely to imitate those that are most similar to them, as the learned behaviours are most likely to be relevant to their own current or future position within the social group (Over and Carpenter, 2012). Horizontal transmission occurs within cultures, where children within playgroups form their own sets of social norms and therefore influence each other's behaviours, but also between cultures (Nunn et al., 2010), where children from neighbouring cultures may transmit social norms of play. Therefore, I investigate horizontal cultural transmission by taking into account the dynamics of play groups within cultures, including choices of play partner and play activity, but also consider the spatial relationships between cultures in determining rates of RTP for boys and girls.

Finally, there are social learning biases that may be specifically relevant to gender and RTP. Children have demonstrated various preferences for imitation, including preferences for adult models of behaviour who are competent, older, and who demonstrate novel information, or peer models who present information which is familiar or related to play (Price, Wood and Whiten, 2017). The aims of a child who is imitating adults or peers may also change with age, as young children are likely to be using imitation to learn how to behave in particular circumstances, and older children may use imitation to form bonds with social partners through conforming with the social expectations of others and demonstrating that they are part of the group (Over and Carpenter, 2012). From around six years of age, children across cultures begin to identify with adults of the same sex and therefore are more likely to imitate adults of the same sex, learning to participate in gendered behaviours (Lew-Levy et al., 2018). Play has been found to be important for learning about various aspects of forager life, including politics, religion, and subsistence skills, with most play revolving around making a living, which often involves gendered tasks and behaviours (Terashima and Hewlett, 2016). Therefore, it is likely that children preferentially imitate adults and peers of the same gender, which would lead to pronounced gender differences in RTP where it is relevant to gendered adult social roles.

Contextual Factors and RTP

In additional to cultural factors, RTP in non-human mammals and humans may also be affected by environmental conditions, including changes to both physical and social environments. Contextual factors can change rapidly, on a much faster timescale compared to sexual selection or vertically inherited social norms such as gender roles. Behavioural flexibility allows an individual to respond to their environment, and changes in that environment can result in changes in behaviour to allow the individual to either exploit their environment or avoid risks within that environment (Barsbai, Lukas and Pondorfer, 2021). RTP has been shown to be sensitive to changes in the environment: the RTP of animals has been shown to be affected by contextual factors including temperature and weather (Yinhua Li et al., 2011), food availability (Moebius et al., 2019), and predator pressure (Smith, 2005). For non-human mammals, this is likely to be connected to energy availability, as suggested by findings that captive and food-provisioned groups, which do not have the constraints of having to spend energy on locating food or suffering from food scarcity (Fragaszy, Visalberghi and Fedigan, 2004), and are less likely to be spending energy on predator avoidance (Howell and Cheyne, 2019), usually show higher rates of RTP then animals living in the wild.

Context-dependent patterns of RTP are also evident in children. Previous research suggests boys consistently prefer outdoor play in order to engage in more vigorous activities, including RTP (Pellegrini, 1992), and teachers often restrict RTP to exclusively outdoor settings (Storli and Sandseter, 2015). Differences in engagement in RTP can also depend on the gender of peers and play groups. Boys and girls will often self-segregate, even in the absence of adult pressures (Smith and Inder, 1993). This may reinforce differences in activity, including engagement in RTP, where boys are more likely to group with other boys in contexts where RTP is more likely to happen, such as outdoor play settings (Pellegrini, 2004).

Interactions between Biological, Cultural, and Contextual Factors

Although I consider first behavioural ecology and biological factors underlying sex differences in RTP across mammalian species, then cultural evolution and cultural factors underlying gender differences in RTP across human cultures, I cannot ignore that there is almost certainly interaction between biological, cultural, and contextual factors in determining variation in sex and gender differences in RTP across both species and cultures. Although I have chosen to adopt two separate approaches to biological and cultural factors, it must be acknowledged that various evolutionary-based disciplines share considerable commonalities, and that insights and perspectives from each approach can potentially be synthesised given a critical approach (Laland, Brown and Brown, 2011), although this is challenging in practice. Within these frameworks, it is likely that biological factors will lead to a tendency for male biased RTP, and that subsequent variation in sex differences will be due to the influence on some combination of biological differences plus varying reinforcement due to cultural and/or contextual factors, particularly for humans where factors such as gender roles and norms differ. For an illustration of the potential interactions between these factors in determining rates of RTP, see Figure 1.1.

Although distinguishing between sex and gender, with sex focusing on biological differences between males and females, and gender focusing on identification as a man or woman (or other gender, such as non-binary), is convenient in exploring biological and cultural factors, in practice there are interconnections between culture and the body, and total separation of the two is difficult and unrealistic (Gove and Watt, 2004). However, there are some difficulties, particularly where common features of a theoretical standpoint are defined differently. For example, human behavioural ecologists tend to treat culture as an entity which is mostly dependent on the ecological environment and the evolved mechanisms of behaviour which adapt to that environment, whereas cultural evolutionists would consider culture to be created from socially transmitted information which is biased by adaptive learning rules and motivational priorities (Laland, Brown and Brown, 2011). Therefore, I aim to critically explore various evolutionary approaches which could be used to capture the interactions between potential factors which underlie adaptive variation in sex and gender differences in RTP, and recommend avenues for future research on this topic.

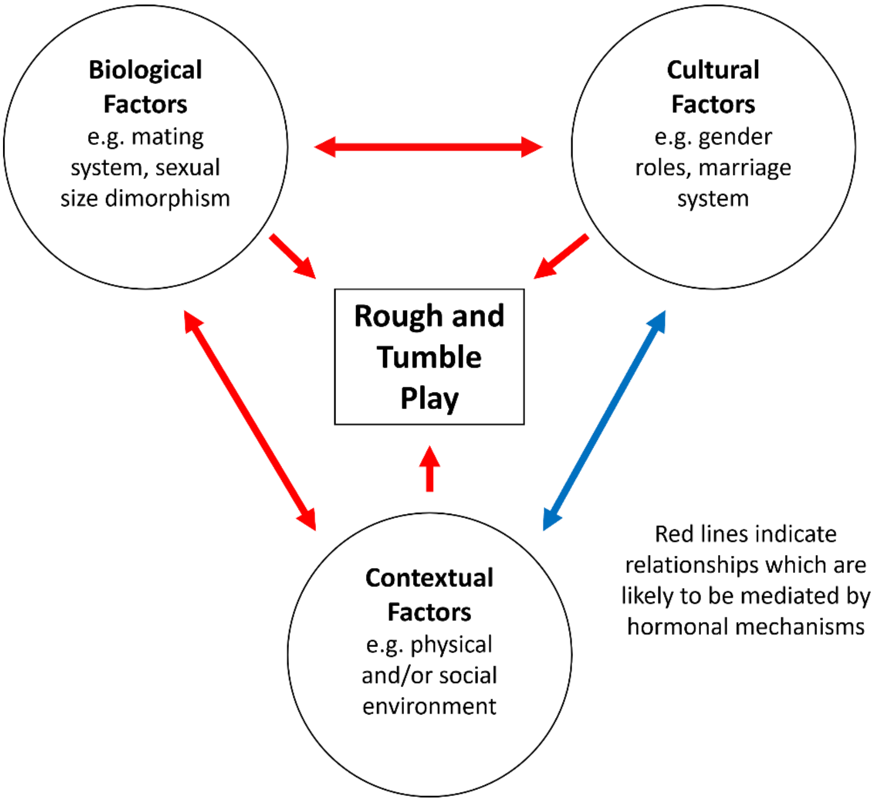

Figure 1.1. *Demonstration of the potential interactions between biological, cultural, and contextual factors in determining rates of RTP in humans.*

Significance of the Research

The prevalence of RTP suggests that it is an evolutionarily adaptive and important behaviour in the development of juvenile mammals, including humans. Therefore, the potential functions of the behaviour are worth investigating, as engagement in RTP could have important consequences for life history trajectories and ontogeny. Although there is a widespread view that juvenile male mammals tend to engage in more RTP than juvenile females (Smith, 2005), and that boys tend to engage in more RTP than girls (Pellegrini and Smith, 1998b), the consistency of these differences across species and human cultures is currently unclear. These findings could have implications for human health, as lower levels of activity are often found for young and adolescent girls (e.g. Vale et al., 2010; Bann et al., 2019; Tanaka et al., 2019), and there are calls for interventions to increase activity levels due to associated health benefits (Griffiths et al., 2013). I aim to clarify the extent and distribution of sex and gender differences in juvenile RTP, and investigate the biological, cultural, and contextual factors that may potentially contribute to such differences. I also aim to consider methodological factors in the study of RTP, and how these may affect the reporting of sex and gender differences across species and cultures. Therefore, this thesis should contribute to the current literature on sex and gender differences, by providing evidence to support or question current hypotheses, and to highlight avenues for further research by identifying which biological and cultural factors involved in determining levels of RTP require further investigation.

Summary and Aims

This thesis uses comparative methods to explore sex and gender differences in RTP, using both cross-species and cross-cultural data. In non-human mammals, the proposed functions and associated biological factors are explored in terms of behavioural ecology for mammalian species, focusing on sex-differentiated life history factors, while in humans, gender norms of engagement in RTP for boys and girls are explored using a framework from cultural evolution, focusing on variation in gender norms and mechanisms of social transmission. Table 1.2 shows the aims of each chapter of the thesis in more detail. The thesis concludes with a discussion of the findings, in which I summarise the findings of each chapter and assess evidence relating to the biological and social factors which may underlie sex and gender differences in RTP. I also consider potential methodological and contextual factors which may further influence rates of RTP, and potential interactions between biological and cultural factors. Finally, I consider the significance of the findings, and speculate on suitable directions for future research.

Table 1.2. *Summary of thesis chapters.*

Chapter	**Aims**
Chapter 2: Methods	- Describe the methodology of the study - Explore why comparative methods are suited to exploring variation in sex and gender differences in RTP across species and cultures
Chapter 3: A Systematic Review of Sex Differences in Rough and Tumble Play across Non-Human Mammals	- Evaluate the extent of male biases in RTP across non-human mammals, and identify patterns of sex differences in RTP across taxonomic groups - Highlight potential biological, contextual, and methodological factors underlying sex differences in RTP
Chapter 4: A Phylogenetic Comparative Analysis of Sex Differences in Rough and Tumble Play in Non-Human Mammals	- Use phylogenetic comparative methods to assess the distribution of sex differences in RTP across non-human mammals - Test hypotheses generated in Chapter 2 regarding potential contributors to sex differences in RTP, focusing on factors relating to male competition
Chapter 5: A Cross-Cultural Phylogenetic Comparative Analysis of Gender Differences in Rough and Tumble Play	- Evaluate cross-cultural variation in gender differences in RTP, including wrestling and chasing behaviours - Analyse the distribution of variation in RTP according to shared cultural history and spatial distribution - Investigate the extent to which certain cultural factors influence the presence of RTP for boys and girls across cultures, considering vertical and horizontal cultural transmission
Chapter 6: A Cross-Cultural Analysis of Ethnographic Data on Gender Differences in Play across Subsistence Societies	- Further investigate patterns of RTP within and across subsistence societies, using qualitative ethnographic data - Explore the potential functions of RTP in the context of gendered social roles and cultural context - Explore cultural and contextual factors which may interact with biological factors with regards to RTP
Chapter 7: Discussion and Conclusions	- Explore findings of the data chapters within the frameworks of behavioural ecology and cultural evolution - Discuss the significance of the research and explore potential avenues for future research

Chapter 2: Methods

Comparison is one of the fundamental methods of evolutionary anthropology, as it allows researchers to investigate biological and cultural diversity through generating and testing evolutionary hypotheses about the evolution of biological and behavioural traits (Nunn, 2011). A key assumption of the comparative method is that similarities between traits across species or across cultures result from responses to common selection pressures within the local environment (Barsbai, Lukas and Pondorfer, 2021), and/or as a result of shared evolutionary history (Freckleton and Jetz, 2009). I have chosen to compare both humans and non-human mammals, as the similarities in play between humans and non-humans are strong, and the potential universality of play suggests that the behaviour has deep evolutionary origins (Burghardt, 2005). This is particularly true for RTP, which has been observed to show similarities across mammalian species, including humans (Garcia et al., 2020), although the extent to which each species engages in play is known to vary (Iwaniuk, Nelson and Pellis, 2001). RTP is therefore likely to be an adaptive behavioural trait and is consequently an excellent candidate for exploration through comparative methods. In addition to cross-species comparisons, comparative methods can also be used to assess gender roles across cultures, with regards to shared mechanisms of social learning (Mesoudi, 2016), cultural history (Mace et al., 1994), spatial proximity (Freckleton and Jetz, 2009), and variation in cultural factors such as gender roles (Blackstone, 2003) and the gendered division of labour (Alesina, Giuliano and Nunn, 2013). This chapter considers the strengths and weaknesses of the comparative method, including phylogenetic comparative analyses, with respect to both cross-species and cross-cultural analyses.

Cross-Species Comparisons

I chose to focus on mammalian species as play has been suggested to be universal amongst mammals, compared to other orders such as birds or reptiles where evidence of RTP is less consistent (Bekoff and Byers, 1998). Locomotor play, which involves movement, is suggested to be ubiquitous across all mammals, but the extent to which animals integrate social play, such as RTP, is thought to vary (Haight and Black, 2001). RTP has been linked to life history traits which have strong phylogenetic signal, such as mating system (Koenig et al., 2013), which suggests that RTP will occur to similar extents in species which have a more recent common ancestor (Freckleton and Jetz, 2009). Animal social play requires the development and integration of cognitive, social, affective, and sensorimotor systems, creating a distinct behaviour through which an individual will explore their environment, form social relationships, and develop skills necessary for survival and reproduction (Haight and Black, 2001), with distinct courses of development according to species and sometimes sex (LaFreniere, 2011). As summarised in Chapter 1, there are various proposed functions of RTP, including development in physical (Martin and Caro, 1985; Byers and Walker, 1995), cognitive (Spinka, Newberry and Bekoff, 2001), and social domains (Smith, 2005), for which investment and development may differ by sex within a species. For RTP to occur, the benefits, either short- or long-term, must outweigh costs such as energy expenditure and risk of injury (Burghardt, 2005), which again may differ according to sex. Comparative methods are one way of exploring the various proposed functions of RTP, as comparing where sex differences in RTP occur can highlight the evolutionary factors which lead to increased levels of RTP where it is necessary for physical and/or social development according to sex.

Cross-Cultural Comparisons

There is also considerable cross-cultural variation in gender differences in RTP, which suggest that shared cultural history and social factors may influence variation in rates of RTP across human societies. Cross-cultural research is used by anthropologists to investigate cultural transmission, which describes the process of an individual acquiring cultural traits, such as behaviours and attitudes, through social learning (Smith et al., 2008). Cultural transmission can be vertical, where children learn from adults such as their parents, or horizontal, where children learn from their peers (Boyette, 2016b). Horizontal cultural transmission can take place within a culture, or can take place between neighbouring cultures, which highlights the role of spatial proximity in considering the relationships between cultures in cultural evolution (Lycett et al., 2013). For children in hunter-gatherer societies, the dominant mode of social learning is suggested to be vertical transmission until the age of 4 to 5 years, then as the child moves into the peer group and greater influence of their peers, horizontal transmission becomes more dominant between 5 to 12 years of age (Hewlett et al., 2011). Boyette (2016) suggests that if children's play does function as a method of cultural learning, then the decisions that children make about their play, including their choice of activity and playmates, should reflect their learning goals, which should reflect who they choose to learn from and the values which they learn. There are also various biases in social learning, which can affect the process of cultural transmission and select for certain traits and behaviours (Lew-Levy et al., 2018). Therefore, the process of cross-cultural comparison will be used in this thesis to assess where factors such as social learning mechanisms affect gender differences in RTP across cultures.

Although there are many common components of non-human and human RTP, including the behavioural components such as wrestling and chasing, and the social components such as role-reversals and self-handicapping behaviours (Scott and Panksepp, 2003), it must be acknowledged that the integration of language and other symbolic representations into locomotor and social play is unique to the human experience (Haight and Black, 2001). Brain size is associated with greater degrees of sociality and playfulness (in Rodentia, Marsupialia, and Primates, see Iwaniuk et al., 2001), so it is to be expected that humans, who have substantially larger brains compared to other primates, will display more complex play behaviours that have larger cognitive demands compared to other mammals (Smaldino et al., 2019). Therefore, when comparing RTP between non-human animals and human children, it is important to consider the context of play and environmental factors that may be affecting children's play. This is reflected in the choice to use both quantitative and qualitative analysis as a mixed methods approach to comparative methods, to capture this complexity and use rich detail to further explore results of quantitative analyses.

Focus on Subsistence Societies

To investigate the social and cultural factors which contribute to gender differences in RTP, I will examine differences in play between and within societies, with a focus on subsistence societies. I have chosen to focus on subsistence societies as the eHRAF database ('eHRAF : HRAF collection of ethnography', 1996) provides sources of rich description of play across cultures in a curated sample of ethnographic data, which is ideal for cross-cultural comparison. Generally speaking, in small-scale societies there is less strict separation between childhood and adult behaviours (Gray, 2012), children have more opportunities to observe adult behaviours and roles (Boyette, 2016a), and children may be free to dedicate more time to play (Gosso et al., 2005), although this is balanced against contributions to childcare, food production, and domestic work (Lew-Levy et al., 2021), as well as in some cultures the introduction of formal schooling. This is in comparison to high income, Western societies, where children are faced with declining opportunities to play (Jarvis, 2006; Flanders, Herman and Paquette, 2013), and RTP has, at least in the recent past, been seen as undesirable and consequently discouraged (Pellis and Pellis, 2007). Such constraints on children's behaviour makes it difficult to examine the underlying causes of a behaviour, and examining behaviour in an environment in which it is less constrained can be useful in investigating the potential benefits of RTP (Boulton, 1996; Lew-Levy et al., 2019).

Galton's Problem

A central issue with comparative methods is what is known as 'Galton's Problem', which states that in order to effectively carry out comparative research, one must take into account the adequate number of data points that will represent sufficient variation, yet at the same time take into account the relationships between individual cases where similarities may be a result of shared history or diffusion of a trait between groups due to proximity (Murdock and White, 1969). This applies to cross-cultural analyses, as cultures can share evolutionary histories and/or be in close proximity to each other in the present, which can lead to non-independence (Ember, 2009). It also applies to cross-species analyses, as species with more recent common ancestors are likely to share more traits, again leading to non-independence of data points (Thornhill and Fincher, 2013). There are a number of proposed methods to address Galton's problem, including using stratified samples to avoid clustering of data, such as the Standard Cross-Cultural Sample (SCCS) (Murdock and White, 1969), and using phylogenetic comparative methods which attempt to take into account evolutionary relationships between datapoints to avoid pseudoreplication and misleading results (Nunn, 2011). In this chapter, I discuss use of the SCCS and phylogenetic comparative analyses in order to address these problems in the data I used.

The Standard Cross-Cultural Sample

Cultures cannot be treated as independent data points (Mace et al., 1994), due to either shared cultural history, where cultures share a common cultural origin, and/or spatial proximity, where cultures are located close enough to each other for cultural traits to diffuse between the two cultures (Ember, 2009). The Standard Cross-Cultural Sample (SCCS) was designed by Murdock and White (1969) to address the non-independence of cultures in cross-cultural research by choosing a subset of 186 societies, which is designed to select cultures which have been described adequately for analysis, and which are not overly contiguous or similar based on spatial position or recent common origin. Therefore, by sampling from the SCCS a researcher can, to some extent, address Galton's problem.

Phylogenetic Comparative Methods

Phylogenetic comparative methods are specialist statistical techniques which can take into account the historical relationships between cultures or species. Performing comparisons for data points where traits may co-occur due to common ancestry, such as species or cultures, can lead to spurious results if the non-independence between data points is not taken into account, as Galton's problem states (Currie, Greenhill and Mace, 2010). A phylogeny is a hypothesised tree which represents the degree to which data points are related, which when taken into account during an analysis can theoretically solve the problem regarding independence of data (Nunn, 2011). Phylogenies can be used to take into account either the shared history or spatial proximity between data points (Thornhill and Fincher, 2013), which could be species or cultures.

For cross-species analyses, shared evolutionary history can be addressed by incorporating phylogenetic information into the analysis of the distribution of a trait (Harvey and Pagel, 1991). Cross-species phylogenies can be created using genetic or morphological data (Nunn, 2011), and allow for the adjustment of the structure of regression models, so that parameter estimates are adjusted for phylogenetic non-independence (de Villemereuil and Nakagawa, 2014). Phylogenetic correlation (or signal), which is the extent to which traits are correlated according to the shared ancestry of two or more species, is expected for any trait that is primarily vertically transmitted and evolved relatively gradually (Martins and Hansen, 1996). Behavioural traits may show lower levels of phylogenetic signal than biological traits, particularly when they are more labile and influenced by recent selective pressures (Blomberg, Garland and Ives, 2003).

For cross-cultural analyses, phylogenetic methods can incorporate language and genetic data, to take into account vertical transmission and the shared evolutionary history of cultures, or spatial proximity data, to take into account horizontal transmission between geographically neighbouring cultures (Nunn, Mulder and Langley, 2006). In cross-species analyses, phylogenetic methods concentrate on the distribution of (presumably) genetic traits, and in cross-cultural analyses the focus is instead on cultural traits, which are assumed to behave in an analogous manner as genetic traits (Nunn et al., 2010). However, cultural phylogenetic comparative analyses must also take into account horizontal cultural transmission, which can occur between individuals or between populations (Currie, Greenhill and Mace, 2010), and is likely much more common in cultural than biological evolution. As cultures and specific traits are subject to varying amounts of horizontal and vertical transmission, it is important to estimate using phylogenetic methods the extent to which each method of transmission is acting upon a specific trait. I expected sex differences in RTP in non-human mammals to have high levels of phylogenetic signal, due to its proposed adaptive functions and links to other slowly evolving traits, such as life history. I also expected gender differences in RTP in humans to show high levels of phylogenetic signal and spatial autocorrelation, due to factors such as gender roles and the biased nature of social transmission of these norms.

Addressing Criticisms of the Comparative Method

One major criticism of phylogenetic comparative methods is the argument that considerations concerning the validity of the data are often overlooked, and that some researchers do not take enough care to ensure that the data they use maps onto their research question (Gelman and Hill, 2006). Issues include the use of secondary data sources, in which there may be high amounts of missing values, variation in data quality, and weak comparability (Freckleton, 2009; Borries et al., 2016). One risk of using cross-species data include the risk of sampling error, which can arise as a result of biological error due to within-species variation, or methodological sampling error as a result of estimating mean values from inadequate sample sizes (Kelly and Price, 2004). Taking the mean value of an inadequate sample size, rather than the true mean which would result from sampling a larger proportion of each species can lead to sampling error and therefore invalid conclusions (Felsenstein, 2008). Errors within comparative data sets, which could be a result of sampling error or simply inaccurate data collection, can lead to invalid conclusions once such data is statistically analysed (Benton and Harper, 1999). Due to this criticism of comparative methods, I have endeavoured to collect as much data as possible, consequently carrying out a systematic review in order to comprehensively collect cross-species data, rather than rely on previous non-systematic reviews of such data. During the process of systematic review, I imposed strict inclusion and exclusion criteria on the assessed studies, in order to ensure that the data used within our analyses was reliable, accurate, and comparable. Furthermore, although caution must be taken when using comparative data sets, the risk of data error is not exclusive to this field, and do not justify avoiding such questions given that sufficient attention is given to such issues (Purvis and Webster, 1999). However, I have also used qualitative approaches to the same data used in the quantitative analyses, to further address issues by maintaining the context and richness of data, and considering issues with the classification of RTP.

There are also more specific criticisms of the assumptions underlying phylogenetic comparative methods. For example, De Bello et al. (2015) argue that phylogenetic relatedness is a signal that allows for different levels of evolutionary analysis, rather than a bias which must be corrected. Therefore, it has been argued that the inclusion of phylogeny where it is not appropriate could lead to over-correction. However, the phylogenetic models in this thesis measure the strength of signal in the model, then adjust the coefficients accordingly. Therefore, if phylogenetic signal is not present, the results are identical to those of a non-phylogenetic model, and therefore the inclusion of phylogeny in such analyses does not lead to over-correction.

Data Collection

Non-Human Data

To address some of the above criticisms of phylogenetic comparative methods, with regards to data quality (see Borries et al., 2016), I undertook a systematic review in order to collect and analyse data on sex differences in RTP for non-human mammals. This is a method that originated in the fields of education and psychology, and is now commonly used in the health sciences, with the aim of extensively documenting and appraising studies within a specific field (Littell, Corcoran and Pillai, 2008). I used a systematic review to document the range of studies on sex differences in RTP for non-human mammals, recording the methodological variation across studies and evaluating the findings of each study. The use of the systematic review method ensured that I was aware of the data quality throughout data collection, and that I could ensure I had comprehensively collected data for as many mammalian species as possible, maximising the sample size. Using the studies identified by the systematic review, I attributed a classification to each included species, including ‘no sex difference’, ‘males play more’, ‘females play more’, and ‘mixed evidence’. These classifications were used as data for subsequent analyses of phylogenetic signal and phylogenetically informed regression models (See Chapters 3 and 4 for more detail). I screened a total of 6308 sources of data, resulting in the inclusion of 121 sources of data regarding sex differences in mammalian species.

Data concerning predictor variables for non-human mammals were retrieved from existing databases, and supplemented by retrieving data from journal articles sourced from Google Scholar, Scopus, and Web of Science. Primarily, the database AnAge (De Magalhães and Costa, 2009) was used for information on litter size, a paper by Myhrvold et al. (2015) for male and female body mass data, and Mabry et al. (2013) for mating system and dispersal data. The mammalian phylogenetic tree was sourced from Vertlife, constructed using Bayesian inference with a combination of DNA data and birth-death models (Upham, Esselstyn and Jetz, 2019).

Human Data

Data concerning RTP in humans was collected from the eHRAF database, which is an online collection of ethnographies on past and present cultures, indexed so each paragraph is searchable by subject (‘eHRAF : HRAF collection of ethnography’, 1996). Within the eHRAF, cultures were limited to those within the SCCS (Murdock and White, 1969), to ensure that cultures were not overly similar and were therefore suitable for comparison. For the quantitative analysis of cross-cultural data (Chapter 5), I used the eHRAF to identify ethnographies which concerned play behaviour, using OCM identifiers (Outline of Cultural Materials, which index the subjects covered by material in the eHRAF database). I then coded each society according to whether wrestling or chasing were present for girls or boys. For the qualitative analysis (Chapter 6), a subset of these ethnographies was chosen, with those containing the richest description selected for further analysis.

Further data on predictor variables were sourced from D-PLACE, which is a database which has aggregated cultural, linguistic, environmental, and geographic information for over 1400 cultures (Kirby et al., 2016). The data collected included ‘marital composition’, ‘food stress or hunger’, ‘descent system’, ‘ideology of male toughness’, and ‘female age at marriage’, in addition to the latitude and longitude co-ordinates for each culture (see Chapter 5 for more details). The matrix of location data was converted into a rooted ultrametric tree format using the upgma function from the phangorn R package (Schliep, 2011), so that it was in the appropriate format to be included as a random effect in the regression models.

Analyses

Systematic Review and Narrative Synthesis

One method of qualitatively analysing data is narrative synthesis, which is used to synthesise findings from multiple studies when quantitative forms of synthesis such as meta-analysis is unsuitable (Popay et al., 2006). The aim of narrative synthesis is to qualitatively summarise and explain the findings of studies, which have often been collected for analysis by the process of systematic review (Popay et al., 2006). I carried out narrative synthesis on the non-human mammal data, which was collected by systematic review. Meta-analysis was not appropriate, due to a lack of reporting statistical information such as effect sizes, but also due to the variation in methods, most notably differences in how play was measured (e.g. rates, durations, and proportions of time) and large variations in samples (e.g. captive and wild populations and/or variation in sample sizes). The first aim of this review was to assess findings for each individual species, and then taxonomic group, to assess the extent to which male biases were present for RTP. The second aim was to identify common characteristics for species which showed the same sex differences in RTP, to highlight potential biological, ecological, and methodological factors that may underlie sex differences in RTP. During this process, I also assessed sample size, setting, age range of study animals and rigor of statistical testing across the studies included in the systematic review.

Quantitative Analyses

All quantitative analyses were conducted in R version 4.2.1 (Hornik and R Core Team, 2022). R code and data can be accessed at https://figshare.com/projects/A_Cross-Species_and_Cross-Cultural_Comparative_Analysis_of_Sex_and_Gender_Differences_in_Rough_and_Tumble_Play/161254.

Phylogenetic Signal and Spatial Autocorrelation

Phylogenetic signal is a measure of the tendency for species to resemble each other according to the degree to which they are evolutionarily related (Blomberg, Garland and Ives, 2003). Species which are more closely related are more likely to resemble each other, in traits such as behaviour, ecology, and life history patterns (Borges et al., 2019). Where phylogenetic signal is high, the distribution of a trait is likely to be strongly influenced by phylogenetic history (Münkemüller et al., 2012). Low phylogenetic signal can indicate that a specific trait is not affected by phylogenetic position for a number of reasons, such as trait saturation, where the trait is fast-evolving and therefore has evolved convergently in multiple distant lineages (Borges et al., 2019). Similarly, spatial autocorrelation is used to measure the spatial dependence between cultures, where cultures that are more closely located are more likely to resemble one another (Gangodagamage, Zhou and Lin, 2008). High levels of spatial autocorrelation indicate that geographically neighbouring cultures are likely to share similar traits, such as the distribution of the presence of RTP across cultures for boys and girls.

Phylogenetically Informed Regression Models

Further quantitative analyses were carried out using phylogenetically informed regression models in a Bayesian framework, to investigate the effects of various predictors variables on sex and gender differences in RTP. All analyses were carried out using the MCMCglmm R package (Hadfield, 2009). For the non-human mammal data, regression analyses were used to assess whether the presence of a male bias in RTP was associated with phylogenetic position, litter size, mating system, or sexual size dimorphism. For the cross-cultural analysis, phylogenetically informed regression analyses were used to assess the effects of phylogeny and various predictor variables (including phylogeny, marriage system, presence of food stress/hunger, age of girls at marriage, and descent system) on the presence of RTP for boys and girls across cultures. As part of these models, heritability (h^2) was also calculated, which is another measure of phylogenetic signal.

To assess the accuracy of the phylogenetically informed regression models, I carried out R^2 and AUC analyses for all models. R^2 is a measure of the good-of-fit of a model, and is presented as a proportion (0 to 1) which represents how much of the variance in the dependent variable that the model can explain (Nakagawa and Schielzeth, 2013). For each model, I calculated marginal R^2, which takes into account the variance of only the fixed effects, and conditional R^2, which takes into account both the fixed and random effects. Therefore, I focus on conditional R^2 values, but both are reported. As another method of assessing the fit of the models, I also calculated AUC values for each model, using the R package cvAUC (LeDell et al., 2022). AUC values represent the predictive accuracy of a model, typically ranging from 0.5, where the model performs no better than chance, to 1, where the model is completely accurate (Ling, Huang and Zhang, 2003).

Bayesian Methods

In this thesis, I use Bayesian methods for the phylogenetically informed regression models. Bayesian approaches to data analysis are based on estimating a posterior distribution, which tells us about the probability of the parameters included in a model, based on data, likelihood, and a prior distribution, which summarises our knowledge about the model or parameters before analysing the data (McElreath, 2015). Since the 1990s, Bayesian methods have gained popularity for certain types of problem (Nascimento, Reis and Yang, 2017), including phylogenetic methods and models with non-Gaussian data, where standard techniques may perform poorly (Hadfield and Nakagawa, 2010).

Therefore, as the analyses I wanted to perform concerned phylogenetic methods with categorical data, Bayesian methods were an appropriate choice over other, frequentist methods.

I chose to conduct the phylogenetically informed analyses using the R package MCMCglmm, as it is allows for phylogenetic mixed models with non-Gaussian dependent variables (Hadfield, 2010). Markov chain Monte Carlo (MCMC) is a numerical technique used for computing posterior distributions in Bayesian methods, and has been shown to be able to handle highly complex models (McElreath, 2015). The MCMC method relies on drawing samples from the posterior distribution, resulting in frequencies of parameter values which are analysed against prior plausibilities, which are used to compute the posterior distribution. The number of MCMC iterations are set manually, alongside thinning intervals, in which the output is taken from a set number of intervals, and burn-in period, in which the parameter values which are samples before reaching the stationary phase are discarded (Nascimento, Reis and Yang, 2017). Model outputs give 95% credible intervals (CIs), which represent the range in which the true value of a parameter lies, with a probability of 0.95 (Nascimento, Reis and Yang, 2017). Potential issues in the use of MCMCglmm algorithms are the risk of slow convergence, in which the chain struggles to move to high-posterior regions of the parameter space, and poor mixing, in which the chain inefficiently traverses the posterior once reaching the stationary distribution (Nascimento, Reis and Yang, 2017). Both of these issues can be diagnosed by examining trace plots, which are discussed after each analysis, and can be found in the Appendices (B and G for Chapters 4 and 5 respectively).

Qualitative Analysis

Finally, I carried out qualitative analysis on a selection of ethnographies, to qualitatively assess RTP in the wider context of play across cultures. I chose to use qualitative analysis to analyse this data as ethnographies vary in context, setting, time period, author, and methodology. When coding the ethnographic data for quantitative analysis, I noticed that the richness of the data was being lost, and decided that qualitative analysis would be a good method for exploring the fullness of the data, ensuring that RTP was understood within the context of wider play behaviours and the changing environments in which it was taking place. Qualitative analysis was particularly well suited to examining play behaviour, as ethnographers recorded play in different ways; for example, one author described rates and durations, whereas others described organised games in detail, mentioning elements of RTP. In the process of this qualitative analysis, I identified common topics and factors which were associated with play, particularly RTP, including choice of play activities, imitation of gendered adult roles, factors preventing engagement in play, choice of play partners, and settings in which play took place. The qualitative analysis was an iterative process, where topics were identified, and ethnographies continuously re-analysed to further identify information on these themes. The overall aim of this analysis was to summarise gender differences in play across cultures and identify potential reasons for variation in gender differences in RTP within the wider context of play and gender within each culture, taking into account the rich complexity of this behaviour.

Summary

Overall, data were collected from multiple sources, including through systematic review and a range of existing databases and sources. Data were analysed using a range of quantitative methods, including phylogenetic signal analyses and regression models, and qualitative methods including narrative synthesis. The mixed methods approach was taken in order to sufficiently address the complexity of RTP and wider play activities, and the variation in methods across non-human species and cross-cultural human contexts. This is particularly important for studies using comparative methods, as often studies can lead to erroneous conclusions when assumptions are made about cross-species or cross-cultural data (Cooper, Thomas and Fitzjohn, 2016). By using both quantitative and qualitative analysis, I have ensured this thesis is comprehensive, and therefore unlikely to miss key details or be influenced by inaccurate data. Further details of the methods are presented in the relevant chapters.

Chapter 3: A Systematic Review of Sex Differences in Rough and Tumble Play across Non-Human Mammals

This chapter is based on the publication ‘A systematic review of sex differences in rough and tumble play across non-human mammals’ (Marley, Pollard, Barton and Street, 2022), which was published in Behavioural Ecology and Sociobiology, and has been reformatted to match university guidelines.

In mammals, RTP consists of physically active social behaviours such as chasing and playfighting (Burghardt, 2005). Typically in RTP, threats are absent, animals signal via play faces or vocalisations that they are not acting aggressively, roles frequently reverse, and sequences of constituent behaviours vary (Fry, 2005). The actions involved in RTP of juveniles are similar to those exhibited by adults in ‘serious’ contexts of competitive, aggressive, and social encounters (Panksepp et al., 1984), which, together with specialised behaviours to communicate benign intent, suggests that RTP in early life is used to develop skills for social and environmental challenges in adult life (Norscia and Palagi, 2016).

Variation in sex differences in RTP across species could shed light on evolutionary drivers of play, but has not yet been systematically investigated. In mammals, it is generally believed that juvenile males typically engage in higher levels of RTP than females (Graham and Burghardt, 2010), which has been linked to adult behavioural sex differences in physical aggression and competition; male mammals generally engage in more fighting, dominance, and defence behaviours than females (Paukner and Suomi, 2008). In contrast, immature females are considered more likely to invest in lower intensity forms of RTP (Berghänel et al., 2015), or other social behaviours such as grooming (Young et al., 1982). One source of evidence suggesting that RTP should be male biased concerns the role of androgens, which have been demonstrated to influence behaviours and ‘masculine’ traits such as aggression, dominance, and RTP (Grebe et al., 2019). However, there are indications that higher levels of RTP in males than females may not be distributed as expected, and variation may correlate with socioecological factors (Smaldino et al., 2019). For example, frequent, high-intensity female RTP may also be expected for species with high levels of female-female competition, a possibility which has so far been largely overlooked (Stockley and Campbell, 2013). Our ability to propose well-informed hypotheses concerning the evolutionary origins of RTP would therefore be improved by first establishing the phylogenetic distribution of sex differences, which is currently unknown.

Proposed Adaptive Functions of RTP

Life history theory posits that growth rates, age and size at sexual maturity, and reproductive investment are shaped by natural selection to maximise reproductive success (Emery Thompson, 2017; Stearns, 2000). Due to sex differences in type and extent of investment required for reproduction, male and female mammals typically differ in their mating/reproductive strategies (Gittleman and Thompson, 1988; Pontzer, 2015). Male mammals typically bear high costs of intrasexual competition to secure mates and maximise reproductive potential, whereas females bear costs of gestation and lactation, investing more time and energy in individual offspring (Key and Ross, 1999; Kokko and Jennions, 2008). Typically, it is argued that males are more likely to invest in and bear the costs of RTP to maximise their competitive ability and reproductive success in later life, whereas females focus on early maturation to maximise time spent reproducing (Charnov, 1991). This hypothesis emphasises the importance of juvenile RTP for the development of motor control (Byers and Walker, 1995), and muscular strength (LaFreniere, 2011), both of which would aid in adult intrasexual competition. However, so far this idea has not considered variation in the extent to which adult males and females invest in mating competition or parental care across species (Clutton-Brock et al., 2006).

RTP may also be crucial preparation for dominance interactions over other resources, such as food, and to build alliances, both during immaturity and in adulthood (Maestripieri and Ross, 2004). If so, sex differences in RTP should depend on the social system and foraging ecology of the species, as these affect the importance of aggressive competition in the two sexes. According to this hypothesis, sex differences in RTP are not expected when adult males and females have similar social and foraging behaviours. This may be the case in some carnivorous species, for example, where developing hunting skills through play is of equal importance to males and females (Lewis, 2003). Similarly, there may be minimal sex differences in RTP where adult males and females both require sophisticated social skills, as communication of intent is a fundamental component of RTP (Palagi et al., 2016). Quantifying the extent of variation in sex differences in RTP across mammalian species is, however, required before such hypotheses can be formally developed and tested in comparative analyses.

Energy Constraints and Sex Differences in RTP

Energetic trade-offs may also be important for understanding variation in sex differences in RTP both across and within species. Life history theory concerns how animals allocate energy over the lifespan in order to maximise fitness (Emery Thompson, 2017). Energy can be used for maintenance and repair, growth, or reproduction, and males and females are likely to differ in how they invest the energy they harvest from the environment as they have different energy requirements for reproduction and maintenance (Hill, 1993; Lappan, 2009). Energy budgets can be affected by environmental and seasonal factors, and variation in the availability of food sources has direct effects on energy intake (Emery Thompson, 2017). This could affect within-species variation in time spent in

RTP, as animals reduce time spent in play when resources are scarce (Krachun et al., 2010; Held and Špinka, 2011). Under such conditions, RTP rates should be conserved in the sex for whom it has most direct fitness benefits, or the sex where it contributes greater survival benefits. As animals are unlikely to experience constraints on food availability in captivity (Howell and Cheyne, 2019), sex differences should therefore be less pronounced in captive groups. However, females may still continue to invest in growth and early reproduction, which can lead to earlier reproduction and obesity in captive females (Charnov, 1991), which may also affect rates of RTP.

Objectives of the Systematic Review

I undertook a systematic review to investigate the within- and across-species variation in sex differences in RTP in non-human mammals. The aims of the review were to (i) evaluate the ubiquity of male-biased RTP in non-human mammals; (ii) identify variation in sex differences in RTP within and across taxonomic groups; and (iii) highlight potential biological, social, ecological, contextual and methodological factors underlying variability in sex differences in RTP to be investigated by future studies. I used narrative synthesis (Popay et al., 2006) to summarise the literature and identify variables which may be associated with sex differences, with a focus on factors relevant to life history and sexual selection including mating system, sexual size dimorphism, male competition, dispersal, and sexual segregation. Employing narrative synthesis allowed us to assess quantitative and qualitative evidence, including the quality and variation of methodology (Howell and Cheyne, 2019). This is particularly relevant to studies on play, which can be highly methodologically heterogenous. Play can be measured by rates, initiations, and time budgets, and studies of play also vary widely in sample sizes, contexts, and statistical approaches, all of which can be evaluated holistically using narrative synthesis. Where possible, I complemented qualitative discussion of patterns in the literature with quantitative analyses, including an analysis of taxonomic bias (Clark and May, 2002) to assess the extent to which data were biased towards specific mammalian orders due to greater research interest, and a comparison of sample sizes between studies with different findings to see if unusual findings were more common in lower-powered studies.

Methods

Pre-registration

A protocol for the systematic review methodology was pre-registered using the Open Science Framework (see Foster and Deardorff, 2017), to ensure that the research is credible, transparent, and replicable (https://osf.io/a2q98/).

Information sources

Sources were identified using Scopus, Web of Science (Core Collection and Zoological Record) and ProQuest (Dissertations & Theses). Further texts were identified by searching reference lists of relevant results. Sources of information were all identified in April 2021.

Search Strategy

For RTP, the following search terms were selected: “social play”, “play activit*”, “play fight”, “play pattern”, “play behav*”, “rough and tumble”, “wrestling”, “play partner”, “playmate”, “play solicit*”, “playful interact*”, “aggressive play”, and “play and playthings”. Search terms were selected by identifying key words which were used to refer to RTP in the known literature, other than ‘play and playthings’, which was suggested by Scopus. The terms ‘play’, ‘social interactions’ and ‘social behaviour’ were excluded as they introduced large numbers of irrelevant results. A term for ‘sex differences’ was not included as studies were often not tagged as such, which may unintentionally exclude relevant results.

For Scopus, Web of Science Core Collection, and ProQuest, results were limited to non-human animals with the terms “nonhuman”, “non-human”, “animal*”, “juvenile”, “infant”, “yearling”, “young”, “immature”, or “species”, and excluding the term “child*”. Excluding ‘human’ resulted in many relevant studies being excluded, so the term ‘child*’ was used as an alternative. For the Zoological Record, these terms were not used, as the database only contains non-human studies. As RTP is rare in non-mammalian animals and the literature has focused on RTP in mammals (Burghardt 2005), specific non-mammalian species were not excluded using filters, as few results were expected and could be removed manually. See Table 3.1 for the final search strategies.

Additional sources were identified by searching the reference lists of eligible papers identified by these searches, as well as those of other relevant sources such as review papers.

Table 3.1 *Search strategies*

Database	Search Strategy	Number of Results
Scopus	TITLE-ABS-KEY (("social play" OR "play activit*" OR "play fight*" OR "play pattern*" OR "play behav*" OR "rough and tumble" OR wrestling OR "play partner" OR playmate OR "play solicit*" OR "playful interact*" OR "aggressive play" OR "play and playthings") AND (nonhuman OR non-human OR animal* OR juvenile OR infant OR yearling OR young OR immature OR species) AND NOT (child* OR lab OR laboratory))	2468
Web of Science Core Collection	TS=(("social play" OR "play activit*" OR "play fight*" OR "play pattern*" OR "play behav*" OR "rough and tumble" OR wrestling OR "play partner" OR playmate OR "play solicit*" OR "playful interact*" OR "aggressive play" OR "play and playthings") AND (nonhuman OR non-human OR animal* OR juvenile OR infant OR yearling OR young OR immature OR species) NOT (child* OR lab OR laboratory))	1339
Web of Science Zoological Record	TS=(("social play" OR "play activit*" OR "play fight*" OR "play pattern*" OR "play behav*" OR "rough and tumble" OR wrestling OR "play partner" OR playmate OR "play solicit*" OR "playful interact*" OR "aggressive play" OR "play and playthings") NOT (child* OR lab OR laboratory)) AND (ST = mammalia)	509
ProQuest	("social play" OR ("play activities" OR "play activity") OR ("play fight" OR "play fighting") OR ("play patterns") OR ("play behavior" OR "play behaviour") OR "rough and tumble" OR wrestling OR "play partner" OR playmate OR "play solicit*" OR "playful interact*" OR "aggressive play" OR "play and playthings") AND (nonhuman OR non-human OR animal* OR juvenile OR infant OR yearling OR young OR immature OR species) NOT (child* OR lab OR laboratory)	1992

Eligibility Criteria

Texts were deemed relevant if they contained comments or data on intraspecific RTP carried out by non-adult members of a species, which was split by sex, or the authors had carried out a statistical test which identified if sex had a significant effect on level of RTP. Texts were limited to those focusing on play between peers, as mother-infant play, or play with other adult members of a group may have different functions to RTP with same-age peers. This resulted in exclusion of some studies that focused on infants, as the majority of their play is with the mother. Texts were excluded if they did not contain relevant data, were not written in English, concerned interspecific or adult-only play, involved animals which had undergone experimental or physical manipulation or were placed into pairs for observation, or had definitions of RTP that included aggression and/or individual play.

For synthesis, studies were grouped by mammalian order, and further by family for the primates given the large number of studies identified from this order.

Selection Process

Texts identified as potentially relevant were first screened by title and abstract, and then by reading the full paper. The process was mostly carried out by the first author, with discussion between authors for difficult cases. The selection process was carried out using Covidence software (Veritas Health Innovation, 2019).

Data Collection

Data were collected by the first author. Any data that matched the inclusion criteria were recorded, including data collected at multiple time points and/or for different groups. Information was recorded in a spreadsheet, where additional information on Author, Year Published, Document Type, Journal/Book Name, Title, Species, Order, Location, Habitat, Sample Information, Age, Sexual Dimorphism, Mating System, Social System, Diet, Definition of RTP, Method, Duration of Study, Captive/Wild, Results, Analysis, Direction of Sex Difference in RTP, and General Notes was included. No assumptions were made for any missing or unclear information.

Taxonomic Bias

A potential source of literature bias particularly relevant to the present study is taxonomic bias, in which certain species attract more research than is proportionate to their frequency in nature (Clark and May, 2002). Research effort may be influenced by how easy it is to observe a species, which traits are of interest, and/or phylogenetic position (Ducatez and Lefebvre, 2014). The bias introduced by research effort is reinforced by taxonomic chauvinism, in which papers concerning ‘unpopular’ species are less likely to be published due to perception of less interest (Bonnet et al., 2002).

I carried out an analysis of taxonomic bias using a permutation approach (as used in e.g. Blackburn and Cassey, 2007), to test for differences between the observed number of species in each order with data on RTP, and the number that would be expected if the sample was representative of mammalian diversity. I took 10,000 random samples of mammalian species of the same size as the sample with data on RTP, to compare the number of species with RTP information in each order against the number that would be expected without taxonomic bias. For each iteration of the simulation, a sample of 66 species (representing the sample size included in the systematic review) were chosen at random, without replacement, from the total number of mammalian species, and the sum of species chosen for each order was calculated, which represented the expected value. Medians and 95% intervals were then computed for the expected number of mammals in each order across the samples, to judge if the observed number of species within each order was significantly different from that expected under random sampling.

Sample Size

To analyse the extent to which the sample size of a study could bias the findings, I compared the sample size of studies between those finding male-biased RTP, female-biased RTP and no sex differences. I was particularly interested to see whether studies reporting rarer outcomes were more likely to have smaller samples and therefore a greater risk of spurious findings. Since data did not meet parametric assumptions, I used a Kruskal-Wallis test to compare median sample sizes between the three groups.

Effect Measures

For each study, the direction of sex differences in RTP was recorded; this could be in the form of effect sizes, significance tests, reporting of group means and/or frequencies, or verbal summaries, where available. If results were split by age, population, time, or specific behaviour (e.g. split into chasing or wrestling) this was also recorded.

Synthesis Methods

Texts were grouped by mammalian order for narrative synthesis. Within each order, studies were initially grouped by their findings (male bias, female bias, or no sex difference). Then, common characteristics of species were identified within these groups, to identify potential predictors of sex differences in RTP for investigation in future comparative analyses. Strength of evidence for sex differences was assessed qualitatively based on sample size, setting, age range of study animals, and rigor of statistical testing, with more weight given to studies which were deemed higher quality. Results were summarised in tables, including information on these methodological categories. Quantitative synthesis (e.g. meta-analyses) could not be carried out due to high methodological heterogeneity between the studies, particularly in terms of the definitions and measures of RTP.

Results

Study Selection

The systematic search initially found 4970 results after duplicates were removed, which were screened by title and abstract, identifying 549 sources for full-text screening. I could not access 22 studies, which were excluded at this stage. 452 results were excluded as the full text did not meet the criteria. Exclusion criteria were the following: the text did not contain relevant data, was not written in English, concerned interspecific or adult-only play, involved animals which had undergone experimental or physical manipulation, involved animals which were placed into pairs for observation, or had definitions of RTP that included aggression and/or individual play. The majority of papers which were excluded were unsuitable due to animals having undergone experimental manipulations such as hormone treatments or gonadectomies. 97 texts were deemed relevant from the initial systematic search. 113 further texts were identified through reference list searching, 22 of which were suitable for inclusion. 2 further sources were identified by study referees. Thus, a total of 121 sources were included for narrative synthesis. See Figure 3.1 for a flow chart of the screening process.

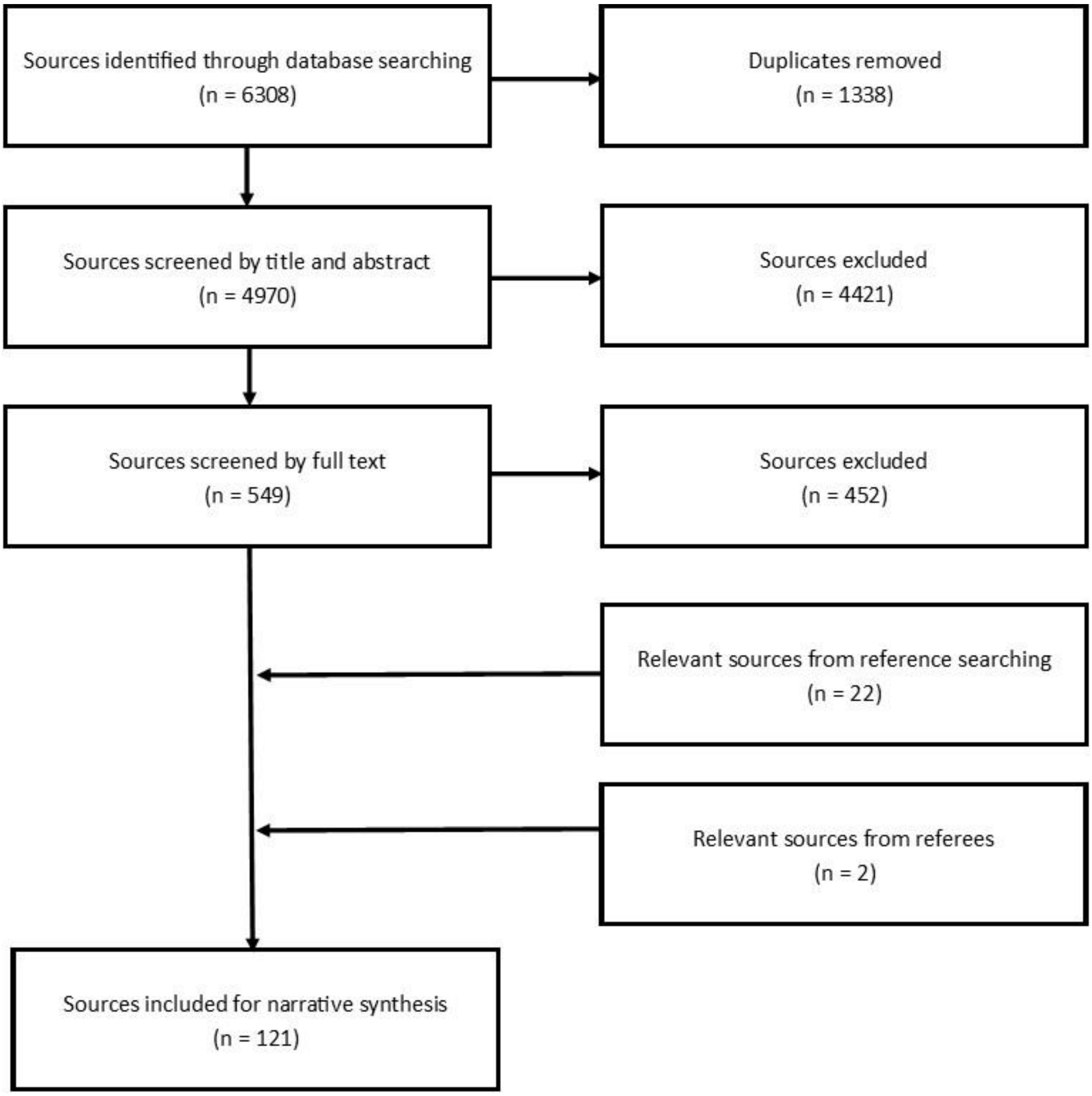

Figure 3.1. *Screening process showing stages of exclusion.*

Sources of data ranged from the year 1967 to 2020, and consisted of 104 journal articles, 4 book chapters, 1 meeting abstract, and 10 theses. 73 of these sources contained data on primates, 16 on carnivora, 11 on artiodactyla, 10 on rodentia, 5 on perissodatyla, 2 on proboscidea, and 1 each for chiroptera, dasyuromorphia, and diprotodontia.

59 studies showed a male bias in RTP, 3 studies a female bias, and 41 reported no sex differences in RTP. All studies concerned RTP, but some looked at specific component behaviours of RTP. For example, some studies such as Fragaszy et al. (2004) and Paukner and Suomi (2008) make a distinction between sub-types of RTP, such as wrestling and chasing. Other studies specify a particular measure of RTP, such as initiations, rates, or total times. Although all discussed results concern RTP, I have maintained the use of the phrases used in each study so that results cannot be misconstrued or over-generalised. Where measurements of RTP concern rates and/or durations, I have made the distinction clear, and do not weight one in favour of the other.

61% of studies were on captive populations, 36% wild, and 3% wild but provisioned. For studies which reported sample size, samples ranged from 3 to 213 individuals, with a median value of 18. The median sample size was 15 for captive groups, 27 for wild, and 20 for provisioned. Further details and a summary of the results of each text can be found in Table 3.2, and the phylogenetic distribution of results is shown in Figure 3.2. Figure 3.3 shows the distribution of results by order.

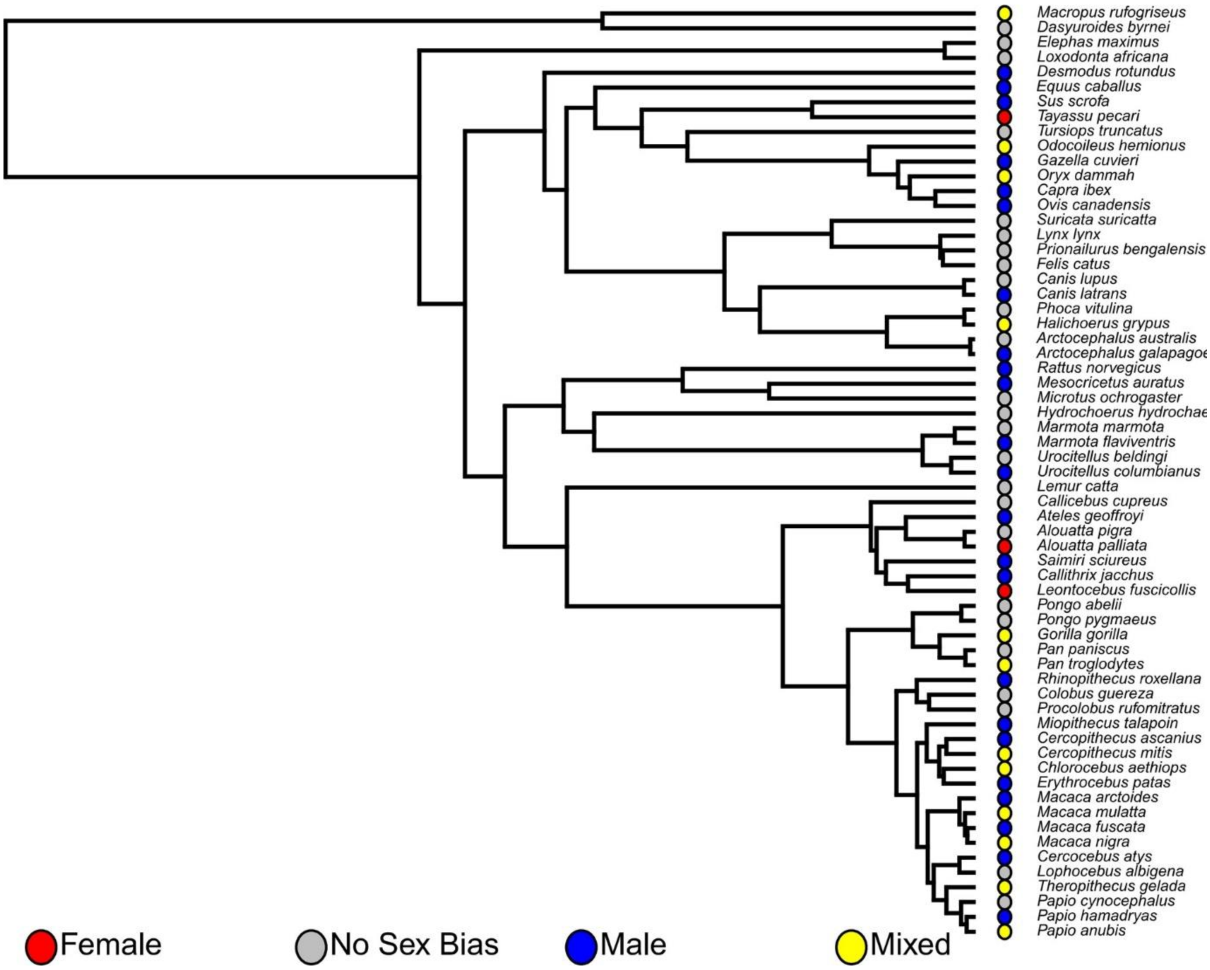

Figure 3.2. *Plot showing phylogenetic distribution of sex differences for RTP (rough and tumble play).*

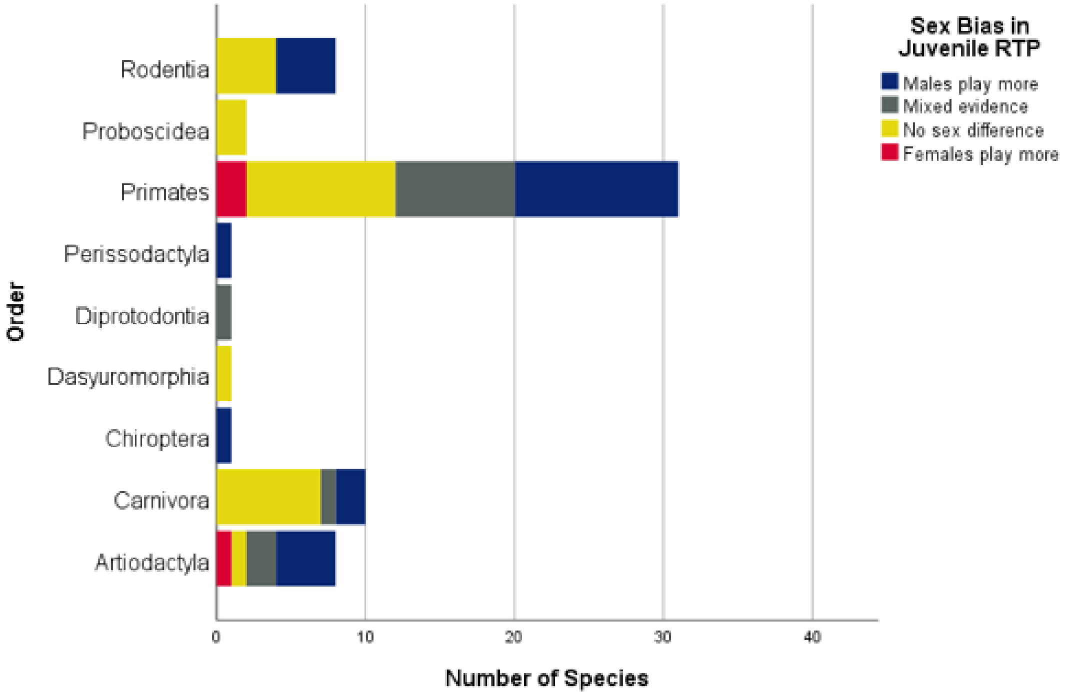

Figure 3.3. *Stacked bar plots showing distribution of sex biases in RTP (rough and tumble play) by order.*

Taxonomic Bias

As seen in Figure 3.4, primates were hugely overrepresented within the sample ($p<0.05$), with 33 relevant species, compared to the five predicted based on the size of the primate order. Other significantly over-represented orders ($p<0.05$) included the carnivora (11 relevant species compared to 3 predicted) and the proboscidea (2 relevant species compared to 1 predicted). The dasyuromoprhia, diprotodontia, and perissodactyla were represented in line with expectations, not differing significantly from the expected value.

Most other orders were under-represented, most notably the rodentia (with 8 relevant species compared to a predicted 27), and the chiroptera (with 1 relevant species compared to a predicted 15) ($p<0.05$). 18 mammalian orders were not represented at all within the sample.

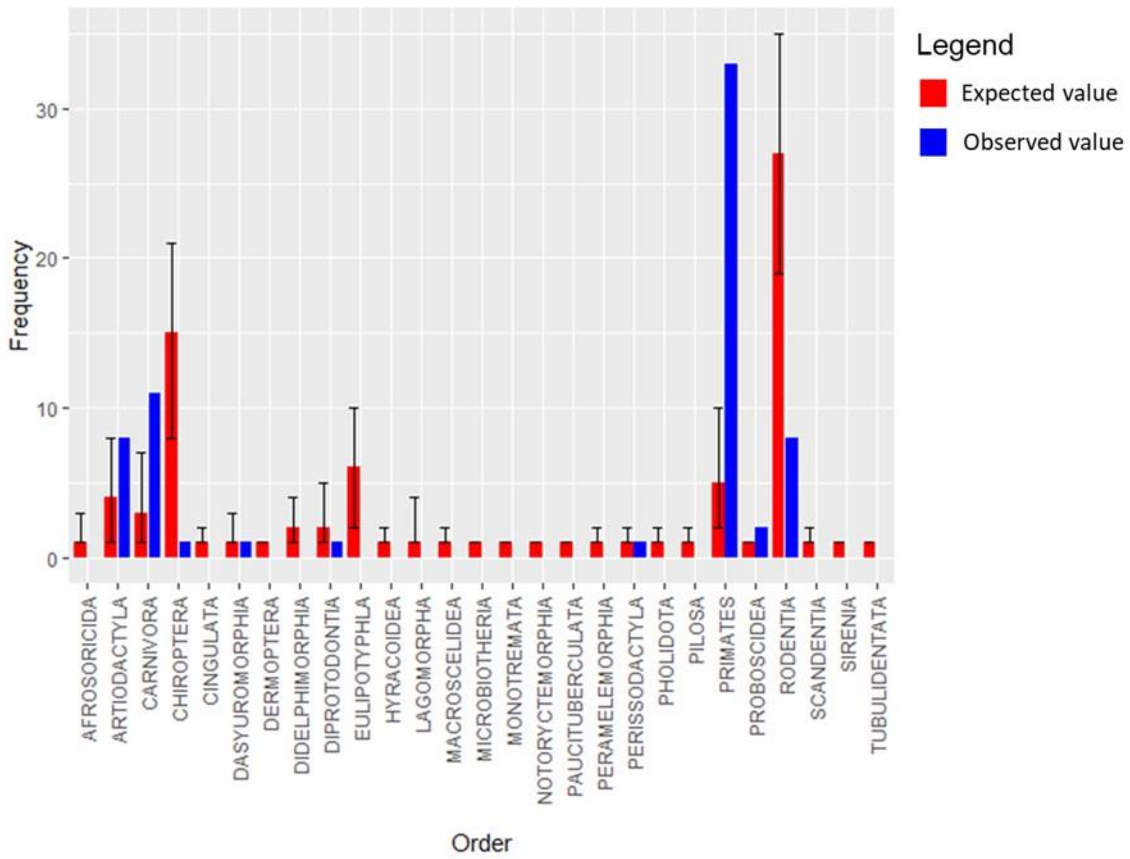

Figure 3.4. *Analysis of research effort, displaying expected and observed values of species included in the systematic review. Error bars represent 95% intervals.*

Sample Size

The sample size for studies that showed a female bias in RTP was lower than those that showed a male or no bias, with medians of 9.5, 18, and 19 respectively (Figure 3.5). However, a Kruskall-Wallis test showed that these differences were not statistically significant, H(2) = 2.2051, p = 0.332. This suggests that findings were unlikely to be biased by sample size of the individual study.

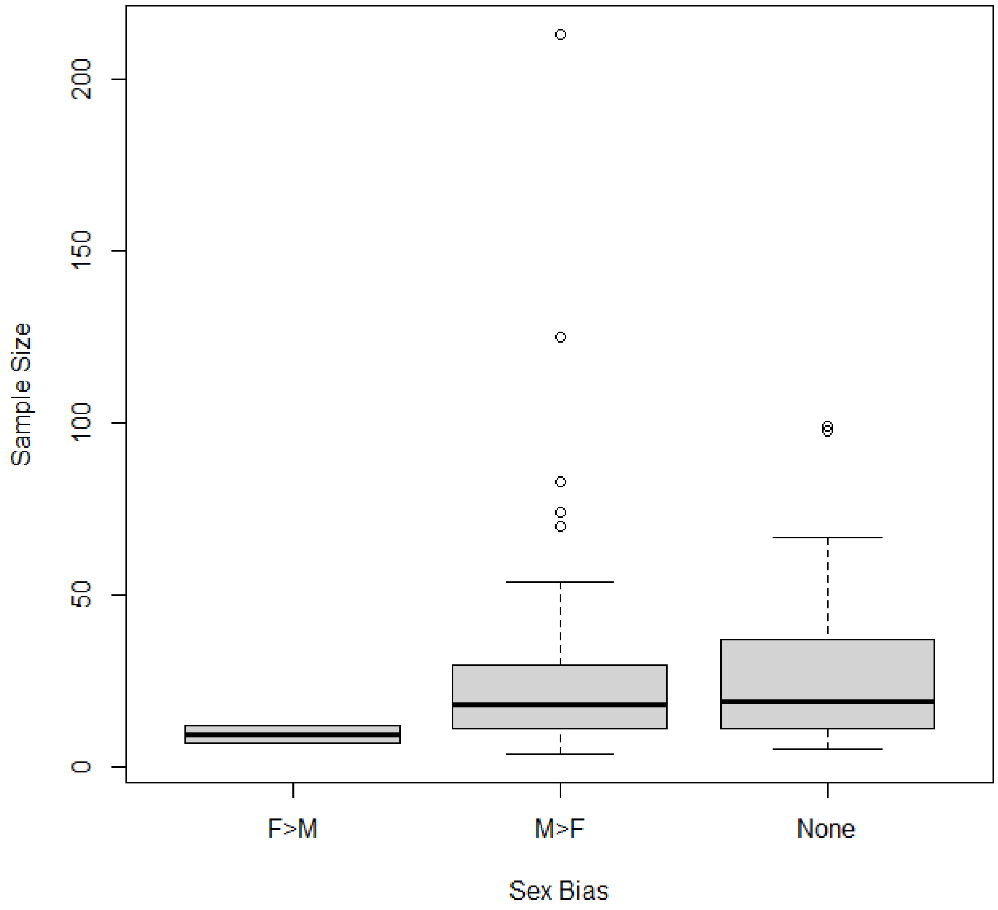

Figure 3.5. *Distribution of sample size between studies that found a female bias, male bias, or lack of sex bias in RTP (rough and tumble play). Error bars represent 95% intervals. Dots represent outliers.*

Artiodactyla (even-toed ungulates)

Artiodactyla is one of the most diverse orders of mammals, consisting of primarily omnivorous or specialised herbivores (Macdonald, 2014). There tends to be male-biased sexual dimorphism in artiodactyl species, which is associated with sexual segregation, sex differences in habitat use, polygynous mating systems, and high levels of male competition (Pérez-Barbería and Gordon, 2000). All studies for this order involved captive or domestic populations.

The domestic pig, *Sus scrofa,* had three relevant texts. Dobao, Rodrigañez and Silio (1985) found that sex had a significant effect on the number of observed play bouts, with male piglets participating in a greater mean number of bouts than females. Brown et al. (2018) found that sex had a significant effect on levels of social play and non-harmful fighting, with males performing significantly more social play. Brown et al. (2015) supported these findings, reporting that male piglets engaged in significantly more total social play behaviours than females. They also reported that piglets displayed sex differences in the percentages of social rather than individual play performed (41 % of male piglets' play was social, compared to 31% of females' play) and that male piglets were more likely to initiate social play.

Two relevant texts were found concerning the Siberian ibex, *Capra ibex sibirica,* both concerning the same population of animals (Byers, 1977, 1980). Byers (1977) reported that male ibex kids engaged in significantly more social play interactions than female kids. Byers (1980) reports that male ibex were more likely to initiate social play bouts than females, and were more likely to initiate play with related males.

Male-biased RTP was also reported for the Cuvier's gazelle (*Gazella cuvieri)*, Scimitar-horned oryx (*Oryx dammah)*, and Bighorn sheep (*Ovis canadensis)*. Gomendio (1988) reports that male Cuvier's gazelle calves engaged in significantly more play-fighting than females, although both sexes showed a similar developmental curve where RTP peaked as the individual entered the larger social group. Similarly, Hass and Jenni (1993) report that for Bighorn lambs both sexes displayed a peak of RTP at 9 to 11 weeks of age, although males consistently played at significantly higher rates. For the Scimitar-horned oryx, Pfeifer (1985) reported that significantly more bouts of social play were initiated by male calves. Neither sex displayed a significant preference for partners of the same sex, and there was no significant sex difference in the duration of social play bouts.

Three species of artiodactyla did not show a strong male bias for RTP. Sachs and Harris (1978) found that male domestic lambs (*Ovis aries*) were significantly more likely to engage in mounting and one-way butting behaviours, but there were no significant sex differences in displays of reciprocal butting. Miller (1975) also found mixed results for black-tailed deer (*Odocoileus hemionus columbianus*), with no apparent sex differences in chasing. However, playfighting was observed on 10 occasions, with only one occasion involving a female immature. For the white-lipped peccary (*Tayassu pecari*), immature females were found to engage in significantly more social play interactions than males (Nogueira et al., 2011).

Carnivora (carnivores)

There is a large discrepancy in the energy requirements for male and female carnivorans, particularly in the breeding season, as females provide food for their young (Kidawa and Kowalczyk, 2011). Male carnivorans tend to be larger, often attributed to their polygamous or promiscuous mating system (Derocher et al., 2005), which may be reflected in higher rates of RTP compared to females.

Pinnipeds, such as seals, typically display high levels of sexual size dimorphism (Lindenfors, Tullberg and Biuw, 2002). Two texts contained data on grey seals (*Halichoerus grypus*), with potentially conflicting results. Cairns (2013) concluded that there were no significant sex differences between male and female pups for mean time spent in social play, although there was a trend for females to engage in more social play than males. Contradictorily, Surviliene et al. (2016) reported that subadult male grey seals were more often engaged in dyadic play bouts than females (61.76 vs 13.53%). Harcourt (1991) reports no sex differences in the play of South American fur seals (*Arctocephalus australis*) and Renouf and Lawson (1987) report no significant sex difference in the chasing behaviour of harbour seals (*Phoca vitulina*). Arnold and Trillmich (1985) report that male Galapagos fur seal pups (*Arctocephalus galapagoensis)* engage in play fighting bouts that are, on average, almost twice as long as female bouts. All studies were carried out on wild populations, but the reliability of the results is hindered by small sample sizes.

Canine species for which relevant data were found included dogs (*Canis familiaris*), coyotes (*Canis latrans*), wolves (*Canis lupus occidentalis*), bush dogs (*Speothos venaticus*), crab-eating foxes (*Cerdocyon thous*), and maned wolves (*Chrysocyon brachyurus*). For domestic dogs, male puppies initiated play more often than females, but only significantly at weeks 7 to 8 (Lund and Vestergaard 1998), and males initiated play more often in mixed-sex dyads (Ward et al., 2008). However, for overall rates of social play, Koscinczuk et al. (2015) found no significant sex differences. For free-ranging dogs, male puppies were found to initiate RTP with a greater frequency than females (Pal, 2010), and were found to engage in RTP at a higher frequency per hour than females (Pal, 2008), in contrast to domestic dogs. Vincent and Bekoff (1978) reported that male coyotes showed slightly higher frequencies of play than females. For wolves, no sex differences were found for rates of RTP (Cafazzo et al., 2018), and there were no sex differences in frequency of social play behaviours for bush dogs, crab-eating foxes or maned wolves (Biben, 1983).

For the Felidae, data were found for the Eurasian lynx (*Lynx lynx*), Far-Eastern wild cat (*Prionailurus bengalensis euplilurus*), and domestic cat (*Felis catus*). Antonevich et al. (2019) report that sex did not have a significant effect on rates of social play for all three species, based on captive populations. Alekseeva et al. (2014) found no sex differences in the social play of the Eurasian lynx, and Caro (1981) found no sex differences in social play of domestic kittens. Provisioned meerkats (*Suricata suricatta*) were also reported to display no sex differences in rates of social play (Sharpe and Cherry, 2003).

Primates

Many group-living primate species are characterised by the presence of a dominance hierarchy in males and/or females, and in most primate species males disperse from the natal group (Lonsdorf, 2017). Primates are unique in the length of their juvenile period relative to body size, with small litter sizes, long inter-birth intervals, extended lifespans and high levels of investment in offspring (Joffe 1997). This long juvenile period is associated with high levels of play.

Lemuroidae (lemurs)

Data on sex differences in RTP was found for only one species of lemuroidae, the ring-tailed lemur (*Lemur catta*), with four relevant texts. Two texts concerned the same study of a free-ranging group, in which female infants tended to engage in social play slightly more frequently than males (Gould, 1989, 1990). Meredith (2018) found no significant sex difference for time spent in social play for wild ring-tailed lemurs, and Grebe et al. (2019) reported no overall sex difference in rates of play initiation, but did note a significant interaction between age and sex, with females ceasing to play at earlier ages than males, in a captive group.

Atelidae

Three texts were relevant for the family Atelidae, all concerning wild populations. For the black-handed spider monkey (*Ateles geoffroyi*), males were reported to play on more occasions than females, and were more likely to be involved in play bouts (McDaniel, 1994). However, in a howler species of the same family, the Yucatán black howler monkey (*Alouatta pigra*), sex differences were not found in the time immatures spent playing (Rizzo, 2004). Zucker et al. (1992) reports that in the mantled howler monkey (*Alouatta palliata*), the two male infants in the study played very little compared to the older females.

Callitrichidae

Two texts were relevant for the Callitrichidae, both involving small captive groups. For the common marmoset (*Callithrix jacchus)*, males were reported to play more than females (Box, 1975). For the saddle-backed tamarin (*Saguinus fuscicollis)*, females were reported to play more than males (Vogt, 1978).

Cebidae

Five relevant texts were found for capuchins, all involving captive groups. For an unspecified species of capuchin, Fragaszy et al. (2004) report that males spent slightly more time in wrestling play, chasing, and overall social play than females. This is supported by Visalberghi and Guidi (1998), who reported that sex and age did not affect levels of engagement in play for immature tufted capuchins (*Cebus apella*). However, Paukner and Suomi (2008) found that infant male tufted capuchins spent significantly more time in wrestle and chase play than females. In the black-capped capuchin (also *Cebus apella*), male infants were reported to exhibit higher frequencies of social play behaviour compared to females (Welker et al., 1987, 1990).

Two relevant texts were selected for the squirrel monkey (*Saimiri sciureus*). Biben (1986) reported that immature males had significantly higher rates of social play and significantly longer social play bouts compared to females, in a captive group. In a later study, Biben (1989) again reported that males played at a higher rate than females.

Pitheciidae

Chau et al. (2008) reported that for captive coppery titi monkeys (*Callicebus cupreus*), sex did not have a significant effect on contact play, chasing, or pulling on tails.

Macaques

17 texts had relevant data for macaques, with 7 focusing on Japanese macaques (*Macaca fuscata*). For most captive populations, immature males engaged in social play significantly more frequently than females (Eaton et al., 1985, 1986; Glick et al., 1986). Petit et al. (2008) reported that although sex did not have a significant effect on hourly frequencies of overall social play, males did wrestle more frequently and for longer durations than females. Findings for wild groups of Japanese macaques are more varied. Koyama (1986) reported that although the mean frequency of chasing and wrestling is significantly higher for males than females, the difference only becomes apparent after four years of age. Nakamichi (1989) reported that the median percentage of time spent in social play was higher for males than females in 10 of 17 age periods. However, Shimada and Sueur (2018) reported that for juvenile Japanese macaques, sex was not significantly correlated with the ratio of time spent in social play.

Another commonly studied macaque species was the rhesus macaque (*Macaca mulata*), with seven relevant texts. Wooddell et al. (2017) reported that male immatures initiated and participated in social play more frequently than females, Lovejoy and Wallen (1988) reported that males initiated and received rough play significantly more frequently than females, and Gard and Meier (1977) reported that males performed significantly more social and rough and tumble play than females. However, although Yanagi and Berman (2017) reported that males engaged in a significantly higher number of overall play bouts and had a higher percentage of successful play bouts (bouts which were accepted by the receiving partner leading to play) compared to females, no significant sex differences were found in the number of initiations or durations of social play bouts. Ehardt and Bernstein (1987) reported no sex differences in the amount of social play of infants, but male juveniles engaged in significantly more amounts of social play than female juveniles. Hinde and Spencer-Booth (1967) report that although males showed higher median levels of initiating RTP bouts, the sex difference was never significant. Tartabini (1991) reported that infants show no significant sex differences in initiations of play.

Data were also found for stumptail (*Macaca arctoides*) and crested (*Macaca nigra*) macaques. Bernstein (1980) reported that males played significantly more often than females, and Nieuwenhuijsen et al. (1988) reported that males had higher social play frequencies than same-aged females. For the crested macaque, sex did not have a significant effect on hourly frequencies of play, although males did wrestle more frequently and play for longer sessions than females (Petit et al., 2008).

Baboons

Six texts were found for baboons. For the Yellow baboon (*Papio cynocephalus*), Young and Hankins (1979) reported no significant sex difference in a captive group, and Cheney (1978) reported that wild male and female juveniles devoted roughly similar amounts of time to RTP. For the captive Hamadryas baboon (*Papio hamadryas*), male juveniles engaged in higher levels of dyadic play compared to female juveniles (LeResche, 1976). However, all three studies of the Olive baboon (*Papio anubis*) report a significant sex difference, with provisioned males engaging in a higher median percentage of mouth-and-wrestle play (Chalmers, 1980) and wild males engaging in higher levels of social and aggressive play (Owens, 1975a, b).

Geladas

Three texts were relevant to geladas (*Theropithecus gelada*). Mancini and Palagi (2009) reported that captive immature males and females showed no significant difference in the frequency of contact play or the frequency of initiating play sessions. However, in a wild population, male geladas spent significantly more time in social play than females between the ages one to five (Barale, 2015; Barale et al., 2015). Between six months and one year, infants engaged in similar amounts of social play, and by six years of age neither males nor females played enough to detect a sex difference, although female play declined faster (Barale, 2015).

Vervets

Four texts were relevant to the vervet (*Cercopithecus aethiops*). Raleigh et al. (1979) reported that juvenile males engaged in RTP at a significantly higher rate than females, and Fedigan (1972) reported that males initiated higher levels of aggressive play, both for captive groups. Govindarajulu et al. (1993) reported that play frequencies did not differ by sex in a wild population. Bramblett (1978) reported that the sex differences in play change with age. Males had a higher mean rate of social play compared to females between months 1 and 47, but females had a higher mean rate of social play between months 48 and 61. Males performed the majority of their social play between 9 and 34 months.

Guenons

Guenons also showed a male bias in RTP, in both wild and captive populations. This includes the samango monkey (*Cercopithecus mitis erythrarchus*), for which males played significantly more often than females (Macleod, 2000), and the talapoin (*Miopithecus talapoin*), for which males engaged in significantly more social play (Wolfheim, 1977). For patas (*Erythrocebus patas*) infants, males spent more time in social play than females, with males playing in longer bouts and showing chasing behaviours more often than females (Rowell and Chism, 1986). A significant male bias in RTP was found for the redtail monkey (*Cercopithecus ascanius*) when all immatures were included in the analysis (Lucci and Rothman, 2020). For the blue monkey (*Cercopithecus mitis stuhlmanni*), males engaged in a significantly higher proportion of RTP, and for longer bout durations, although females engaged in a significantly higher proportion of chasing behaviour (Förster and Cords, 2005).

Mangabeys

Captive male sooty mangabeys (*Cercocebus atys*) were reported to play significantly more often than females (Bernstein, 1976). However, Lucci and Rothman (2020) reported no sex difference in the frequency of RTP for immature grey cheeked mangabeys (*Lophocebus albigena*) in the wild.

Colobines

Lucci and Rothman (2020) reported no sex differences in the frequency of RTP for wild black-and-white colobus monkeys (*Colobus guereza*) or red colobus monkeys (*Procolobus rufomitratus*). Worch (2010) also reports that male and female red colobus engaged in equal amounts of RTP. However, the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) displayed a male bias in frequency of RTP (Li et al., 2011), in a provisioned group.

Gorillas

Six relevant texts concerned sex differences in RTP for gorillas (*Gorilla gorilla*), all concerning captive populations. Brown (1988) reported no sex differences in preference for type of play, Mallavarapu (2002) reported no significant differences in time spent in social play, and Maple and Zucker (1978) reported no sex differences in engagement in RTP. However, in a study of four infant gorillas from 15 to 24 months, the male infant participated in 808 play interactions, compared to the 449, 497, and 394 play interactions of his female conspecifics (Gomez, 1988). Palagi et al. (2007) reported that although there was no sex difference for gentle social play, juvenile males recorded a higher mean hourly frequency of rough social play compared to females. Hoff et al. (1981) reported a strong and consistent male bias in active social play (chasing and vigorous wrestling), but inconsistent and small sex differences in moderate social play (light bouncing and pulling).

Chimpanzees

Eleven relevant texts were selected for chimpanzees (*Pan troglodytes*). Bloomsmith et al. (1994) reported that males showed higher levels of social play than females, Nadler and Braggio (1974) reported that male immatures showed a greater proportion of RTP compared to females, and Moebius et al. (2019) reported that wild male juveniles engage in social play almost twice as much as females, and infant males engage in around 1.2 times more social play than females. Hayaki (1985) and Markus and Croft (1995) report a male bias in frequency of RTP for captive and wild groups respectively, and Montedoro et al. (2017) report a male bias in time spent in social play for wild juveniles.

In two studies at the Arnhem zoo and TNO primate centre, Spijkerman et al. (1994, 1996) report that immature chimpanzees do show male bias in time spent in social play, although the extent of this is affected by age, component of play, setting, and peer group. In the zoo, where chimpanzees are raised in a family group, adolescent males played significantly more than females, with longer gnaw-wrestle bouts but no sex difference in chasing play (Spijkerman et al., 1994). Sex differences were not significant in other juvenile age classes, or for those raised in peer groups. Spijkerman et al. (1996) elaborates on these results, reporting that the male bias in RTP for adolescent family group chimpanzees is mainly due to longer duration of wrestling compared to females, and the increased likelihood for males to play longer than females when wrestling play was more aggressive. For younger chimpanzees, Spijkerman et al. (1996) reported a higher frequency of chasing for males, but only in the family group. The only significant sex difference for chimpanzees in both the family and peer groups was tickling, which was shown more often by females than males below three years of age.

In contrast, three texts suggest that there are no sex differences in social play for immature chimpanzees. De Lathouwers and Van Elsacker (2006) report no main effect of sex for time spent in social play for chimpanzee infants, and Mendoza-Granados and Sommer (1995) report that although chasing was significantly over-represented in male immatures, frequencies and durations of play bouts did not show a significant sex difference. For a wild chimpanzee group that had been provisioned in the past, Pusey (1990) reported no sex differences in rates of play.

Bonobos

De Lathouwers and Van Elsacker (2006) reported that sex did not have a significant effect on time spent in social play for captive infant bonobos (*Pan paniscus*).

Orangutans

Four relevant texts concerned various species of orangutan (*Pongo* sp.), with only one reporting a significant male bias. Nadler and Braggio (1974) reported that captive male juveniles showed a greater proportion of RTP than females, but no significant sex difference was found for chasing. However, Maple and Zucker (1978) report no sex differences in any component of RTP for another captive population of orangutans. In wild populations, both Frohlich et al. (2020) and Kunz (2015) report that sex did not have a significant effect on the occurrence of social play, for Sumatran (*Pongo abelii*) and Bornean (*Pongo pygmaeus wurmbii*) orangutans.

Rodentia (rodents)

10 relevant texts contained RTP data for rodents, with most studies reporting no significant sex differences, or inconclusive results. Chau et al. (2008) reported that sex did not have a significant effect on total play rate for captive prairie voles (*Microtus ochrogaster*) and Congdon (2007) reported no sex difference in the frequency of play bouts for wild capybaras (*Hydrochoerus hydrochaeris*). Wild alpine marmots (*Marmota marmota*) displayed no significant sex differences in RTP (Perrin et al. 1993), but wild yellow-bellied marmots (*Marmota flaviventris*) showed a trend towards higher levels of participation in play bouts for male yearlings compared to females (Armitage, 1974).

Mixed results were found for ground squirrels, all of which concerned wild populations. Festa-Bianchet and King (1984) reported a significant male bias for participation in playful social interactions for two of the three years studied, which is supported by Waterman (1988), who reports that juvenile and yearling male Columbian ground squirrels (*Spermophilus columbianus*) initiate play more often than females, and that male-male play bouts have a significantly longer duration. However, in an earlier study, Waterman (1986) reported that both sexes spent similar amounts of time in play. Marks et al. (2017) reported no significant sex differences in the rate or duration of social play for the Belding's ground squirrel (*Urocitellus beldingi*).

Mixed results were also found for captive golden hamsters (*Mesocricetus auratus*), in which immature males engaged in significantly more playfighting than expected based on the sex ratio in four of eight litters, but female-female play was lower than expected in all litters (Goldman and Swanson, 1975). A significant male bias was found for captive hooded rats (*Rattus norvegicus*), for which males displayed significantly more play initiations than females for all but the first age period studied (Meaney and Stewart, 1981).

Other

Cetaceans (whales and dolphins)

In a study of bottlenose dolphins (*Tursiops truncatus*), Walker et al. (2017) reported similarly low levels of social play, with no sex difference between calves.

Chiroptera (bats)

One relevant text contained data on the common vampire bat (*Desmodus rotundus*). Park (1990) reported that immature male bats seemed to initiate social play more often than females, in a captive group.

Dasyuromorphia (carnivorous marsupials)

The only relevant text for the dasyuromorphia concerned the kowari (*Dasyuroides byrnie*). Meißner and Gansloßer (1985) report no obvious sex differences in levels of RTP for captive immature kowaris, but do comment on the difficulty of separating grooming and play behaviours.

Diprotodontia (marsupials)

Only one relevant text was found to contain data on diprotodontia, which concerned captive red-necked wallabies (*Macropus rufogriseus banksianus*). Watson and Croft (1993) reported that playfights were rare for immature female wallabies, with only three out of nine females engaging in any RTP, at a significantly lower rate than males. However, the median duration of playfighting bouts did not differ significantly between male and female wallabies.

Perissodactyla (odd-toed ungulates)

Five relevant texts were found concerning RTP in perissodactyla, all of which focused on horses (*Equus caballus*). Rho et al. (2007) reported that male Jeju pony foals were more likely to play-fight than females, although this was only recorded in relation to behaviour after mutual grooming. Sigurjonsdottir et al. (2003) report that subadult male Icelandic horses engaged in dyadic play significantly more than females, and Crowell-Davis et al. (1987) reported that male Welsh pony foals engaged in interactive play bouts significantly more often, for longer durations, and for a higher proportion of total play compared to females. Similar trends were found for the Camargue horse, for which male yearlings played significantly more often, and a similar male bias was found for younger foals, although not statistically significant (Wells and von Goldschmidt-Rothschild, 1979). In feral horses, males had higher levels of involvement in fighting play than females (Cameron et al., 2008).

Proboscidea (elephants)

A PhD thesis and journal article were found containing data on RTP in elephants, although both concerned the same study. Although male calves played more than females at all ages, age and sex did not have a significant effect on overall rates of RTP for African and Asian elephants (Webber, 2017; Webber and Lee, 2020). However, there was a significant interaction effect between calf sex and context, as a slight male bias in RTP was more pronounced in captivity compared to wild animals.

Table 3.2 *Summary of results.*

Order	Species	Text	Age of animals	Observation Period (Approximate)	Sample size	Outcome measure	Findings		
							M>F	F>M	No sex difference
Artiodactyla	Domestic pig, *Sus scrofa*	Dobao et al. 1985	50-68 days	18 days (130 minutes per individual)	32	Mean number of play bouts	○		
		Brown et al. 2018	0-8 weeks	8 weeks	83	Social play	●		
		Brown et al. 2015	1 week to weaning	1 week to weaning age	70	Total social play behaviours	●		
	Siberian ibex, *Capra ibex sibirica*	Byers 1977	Immature	>50 hours	14	Total social play patterns	●		
		Byers 1980	Immature	-	20	Initiation of social play bouts	○		
	Cuvier's gazelle, *Gazella cuvieri*	Gomendio 1988	Immature	8 months	16	Play-fighting	●		
	Scimitar-horned oryx, *Oryx dammah*	Pfeifer 1985	Immature	135 days (644 hours total)	8	Number of social play bouts	●		
						Duration of social play bouts			●
	Bighorn sheep, *Ovis canadensis*	Hass and Jenni 1993	Juveniles	27 months (635 hours total)	10	Rate of play	●		
	Domestic sheep, *Ovis aries*	Sachs and Harris 1978	0-10 weeks	Two lambing seasons	147	Reciprocal Butting			●
						One-way butting	●		
						Mounting	●		
	Black-tailed deer, *Odocoileus hemionus columbianus*	Miller 1975	Yearlings and fawns	5 months (1411 hours total)	15	Chasing			○
	White-lipped peccary, *Tayassu pecari*	Nogueira et al. 2011	Juveniles and subadults	12 weeks (160 hours total)	12	Number of social play interactions		●	
Carnivora	Grey seal, *Halichoerus grypus*	Cairns 2013	6 months to 5 years	3 breeding seasons	10	Mean level of social play			■

		Surviliene et al. 2016	Juveniles and subadults	3 months (107 hours total)	-	Number of dyadic play bouts	□		
	South American fur seal, *Arctocephalus australis*	Harcourt 1991	1 to 25 months	1 year (2523 hours total)	36	Play			■
	Harbour seal, *Phoca vitulina*	Renouf and Lawson 1987	-	3 months (>70 hours)	Approximately 300	Chasing			■
	Galapagos fur seal, *Arctocephalus galapagoensis*	Arnold and Trillmich 1985	18-37 days	3 months	6	Length of playfighting bouts	□		
	Dog, *Canis familiaris*	Lund and Vestergaard 1998	0-8 weeks	8 weeks	22	Initiations of social play	●		
		Ward et al. 2008	3-40 weeks	7.1 hours	19	Initiations of play in mixed-sex dyads	●		
		Koscinczuk et al. 2015	40-45 days	-	32	Social play activity			●
		Pal 2010	0-12 months	1 year	24	Initiations of play fighting	■		
		Pal 2008	0-4 months	1 year	35	Frequency of social play per hour	■		
	Coyote, *Canis latrans*	Vincent and Bekoff 1978	20-35 days	15 days (180 hours total)	4	Frequency of play	○		
	Wolf, *Canis lupus occidentalis*	Cafazzo et al. 2018	3-5 months	15.6 hours	12	Competitive social play			○
						Relaxed social play			○
	Eurasian lynx, *Lynx lynx*	Antonevich et al. 2019	30-90 days	1654 hours	50	Contact social play			●
		Alekseeva et al. 2014	30-90 days	1491 hours	46	Social play			●
	Far-Eastern wild cat, *Prionailurus bengalensis euplilurus*	Antonevich et al. 2019	30-90 days	582 hours	14	Contact social play			●
	Domestic cat, *Felis catus*	Antonevich et al. 2019	30-90 days	479 hours	37	Contact social play			●
		Caro 1981	1-12 weeks	8 weeks	21	Social play			○
	Meerkat, *Suricata suricatta*	Sharpe and Cherry 2003	4-10 weeks	16 months	40	Rate of social play			▲
	Bush dog, *Speothos vanaticus*	Biben 1983	3-6 weeks and 15-18 weeks	150-200 minutes per week	12	Social play (Roll Over, Stand Over, Grapple, Chasing, Biting)			●

	Maned wolf, *Chrysocyon brachyurus*	Biben 1983	3-6 weeks and 15-18 weeks	150-200 minutes per week	8	Social play (Roll Over, Stand Over, Grapple, Chasing, Biting)			●
	Crab-eating fox, *Cerdocyon thous*	Biben 1983	3-6 weeks and 15-18 weeks	150-200 minutes per week	9	Social play (Roll Over, Stand Over, Grapple, Chasing, Biting)			●
Primates	Ring-tailed lemur, *Lemur catta*	Gould 1989, 1990	0-16 weeks	6 months (260 hours)	11	Social play			☐
		Meredith 2018	0-23 months	-	53	Time spent in social play			☐
		Grebe et al. 2019	3-30 months	315 hours	18	Rates of play initiation			●
	Black-handed spider monkey, *Ateles geoffroyi*	McDaniel 1994	Infants and juveniles	8 months	31	Number of play bouts	☐		
						Involvement in play bouts	☐		
	Howler monkey, *Alouatta pigra*	Rizzo 2004	Infants and juveniles	4 months (2021 hours)	-	Time spent playing			☐
	Mantled howler monkey, *Alouatta palliata*	Zucker et al. 1992	0-80 weeks	22 months (529.2 hours)	7	Number of play bouts		☐	
	Marmoset, *Callithrix jacchus*	Box 1975	143-291 days	-	6	Play	○		
	Saddle-backed tamarin, *Saguinus fuscicollis*	Vogt 1978	-	14 months	-	Play		○	
	Capuchin, *Cebus apella*	Fragaszy et al. 2004	Infants and juveniles	-	18	Wrestling	○		
						Chasing	○		
						Overall social play	○		
		Visalberghi and Guidi 1998	12-60 months	3 months	9	Play			○
		Paukner and Suomi 2008	2 to 5 years	5 months (132 hours)	11	Wrestling	●		
						Chasing	●		
		Welker et al. 1987	0 to 6 months	6 months	14	Frequency of social play behaviour	●		
		Welker et al. 1990	6 to 12 months	-	15	Frequency of social play behaviour	●		
		Biben 1986		5 months	10	Rate of social play	●		

	Squirrel monkey, *Saimiri sciureus*		Approx. 10 months			Social play bout duration	●		
		Biben 1989	9 to 15 months	40 hours per individual	28	Rate of play	○		
	Coppery titi monkey, *Callicebus cupreus*	Chau et al. 2008	0 to 6 months	6 months	10	Contact play			●
						Chasing			●
						Tail pulling			●
	Japanese macaque, *Macaca fuscata*	Eaton et al. 1985	0 to 1 year	1 year	22	Frequency of social play	●		
		Eaton et al. 1986	1 to 2 years	3 months	18	Frequency of social play	●		
		Glick et al. 1986	12 to 24 months	5 months	18	Frequency of social play	●		
		Petit et al. 2008	1.5 to 5 years	4 months	20	Frequency of wrestling bouts	●		
						Duration of wrestling bouts	●		
						Hourly frequency of social play			●
		Koyama 1986	<5 years	6 months	125	Frequency of chasing	■		
						Frequency of wrestling	■		
		Nakamichi 1989	0 to 4 years	4 years (656 sessions)	20	Median percentage of time spent in social play	□		
		Shimada and Sueur 2018	1 to 4 years	2 seasons (322.9 hours)	11	Ratio of time spent in social play			■
	Rhesus macaque, *Macaca mulata*	Woodell et al. 2017	1 to 5 months	5 months (37 hours)	17	Initiations of social play	■		
						Frequency of social play	■		
		Lovejoy and Wallen 1988	12 to 16 months	12 weeks (5 hours per individual)	11	Initiating social play	●		
						Receiving social play	●		
		Gard and Meier 1977	8 to 30 months	8 weeks	11	Social and rough play	○		
		Yanagi and Berman 2017	<4 years	10 months (344 hours)	20	Number of play bouts	▲		
						Initiation of play bouts			▲
						Duration of play bouts			▲
		Ehardt and Bernstein 1987	<5.5 years	484 observations	>68	Social play (infants)			●
						Social play (juveniles)	●		

		Hinde and Spencer-Booth 1967	0 to 2.5 years	2.5 years	16	Active social play			○
						Passive social play			○
		Tartabini 1991	3 to 6 months	3 months	17	Initiations of play			●
	Stumptail macaque, *Macaca arctoides*	Bernstein 1980	Infants	4 years	31	Play	●		
		Nieuwenhuijsen et al. 1988	-	>1000 hours	-	Frequency of social play	○		
	Crested macaque, *Macaca nigra*	Petit et al. 2008	1.5 to 5 years	2 months	10	Hourly frequency of play			●
						Frequency of wrestling	●		
						Duration of play sessions	●		
	Common baboon, *Papio cynocephalus*	Young and Hankins 1979	0-3 months	>128 hours	25	RTP			●
		Cheney 1978	0 to 48 months	-	20	Time spent in play			□
	Hamadryas baboon, *Papio hamadryas*	Leresche 1976	11 to 37 months	2.5 months (>170 hours)	4	Dyadic play	○		
	Olive baboon, *Papio Anubis*	Chalmers 1980	1 to 52 weeks	6 months	40	Median percentage of mouth-and-wrestle play	▲		
		Owens, 1975a/b	-	13 months	-	Social play			■
						Aggressive play	■		
	Gelada, *Theropithecus gelada*	Mancini and Palagi 2009	Non-adult	6 months (513 hours)	11	Frequency of contact play			●
						Initiation of play sessions			●
		Barale 2015, Barale et al. 2015	0 to 6 years	2 years (820 hours)	74	Time spent in social play	■		
	Vervet monkey, *Cercopithecus aethiops*	Raleigh et al. 1979	Infants and juveniles	4 months (15 hours per individual)	11	Rate of RTP	●		
		Fedigan 1972	1 to 4 years	-	10	Aggressive play	●		
		Govindarajulu et al. 1993	0 to 30 weeks	8 months	7	Play frequency			■
		Bramblett 1978	Subadults	-	18	Mean rate of social play at months 1-47	●		

						Mean rate of social play at month 48-61		●	
	Sooty mangabey, *Cercocebus atys*	Bernstein 1976	Non-adults	3 years	-	Play	●		
	Samango monkey, *Cercopithecus mitis erythrarchus*	Macleod 2000	Infants and juveniles	2 years (1506 hours)	27	Play	■		
	Talapoin, *Miopithecus talapoin*	Wolfheim 1977	1 to 3 years	1 year (117 hours)	7	Social play	●		
	Patas monkey, *Erythrocebus patas*	Rowell and Chism 1986	1 to 3 years	-	20	Social play	●		
						Duration of play bouts	●		
						Chasing	●		
	Redtail monkey, *Cercopithecus ascanius*	Lucci and Rothman 2020	Infants and juveniles	100 days	-	RTP	■		
	Sichuan snub-nosed monkey, *Rhinopithecus roxellana*	Li et al. 2011	Infants	11 months	7	Play	△		
	Blue monkey, *Cercopithecus mitis stuhlmanni*	Forster and Cords 2005	0 to 6 months	8 months	12	Proportion of RTP	■		
						Bout duration	■		
						Proportion of chasing		■	
	Grey-cheeked mangabey, *Lophocebus albigena*	Lucci and Rothman 2020	Infants and juveniles	100 days	-	Frequency of RTP			□
	Black-and-white colobus monkey, *Colobus guereza*	Lucci and Rothman 2020	Infants and juveniles	100 days	-	Frequency of RTP			□
	Red colobus monkey, *Procolobus rufomitratus*	Lucci and Rothman 2020	Infants and juveniles	100 days	-	Frequency of RTP			□
		Worch 2010	Infants, juveniles, subadults	1 year	37	Amount of RTP			■
	Gorilla, *Gorilla gorilla*	Brown 1988	7 to 15 years	91 hours	12	Preference for RTP			○
		Mallavarapu 2002	2 to 4 years	-	5	Time spent in social play			●

		Maple and Zucker 1978	0 to 14 years	-	7	Engagement in RTP			○
		Gomez 1988	15-24 months	16 observation sessions	4	Play	○		
		Palagi et al. 2007	Juvenile	5 months (1103 hours)	10	Gentle social play			●
						Mean hourly frequency of rough social play	●		
		Hoff et al. 1981	0 to 18 months	-	3	Active social play	○		
						Moderate social play			○
	Chimpanzee, *Pan troglodyte*	Bloomsmith et al. 1994	Juveniles and adolescents	154 weeks (792 hours)	21	Social play	○		
		Nadler and Braggio 1974	29 to 56 months	3 months	8	Proportion of RTP	●		
		Moebius et al. 2019	Infants	3567 hours	20	Social play	○		
		Hayaki 1985	Juveniles and adolescents	384 hours	9	Frequency of RTP	☐		
		Markus and Croft 1995	< 7 years	4 months (6 hours per individual)	12	Frequency of RTP	○		
		Montedoro et al. 2017	< 15 years	-	-	Time spent in social play	☐		
		Spijkerman et al. 1994	0 to 10 years	3 years (3120 hours)	90	Amount of play (adolescents)	●		
						Amount of play (younger age classes)			●
		Spijkerman et al. 1996	0 to 10 years	3 years (3120 hours)	90	Duration of wrestling bouts	●		
						Tickling (below 3 years)		●	
		De Lathouwers and Van Elsacker 2006	5 to 56 months	3 years	8	Time spent in social play			●
		Mendoza-Granados and Sommer, 1995	Immature	4 months (154 hours)	11	Chasing	●		
						Frequency of play bouts			○
						Duration of play bouts			○
		Pusey 1990	Juveniles and adolescents	-	13	Rate of play			☐

	Bonobo, *Pan paniscus*	De Lathouwers and Van Elsacker 2006	Infants	3 years	8	Time spent in social play			●
	Orangutan, *Pongo* sp.	Nadler and Braggio 1974	29 to 56 months	3 months	5	Proportion of RTP	●		
						Chasing			●
		Maple and Zucker 1978	0 to 21 years	-	20	RTP			○
	Sumatran orangutan, *Pongo abelii*	Frohlich et al. 2020	Infants	7 years (4297 hours)	4	Social play			■
		Kunz 2015	2 to 14 years	6 months	-	Social play			■
	Bornean orangutan, *Pongo pygmaeus wurmbii*	Frohlich et al. 2020	Infants	7 years (4297 hours)	7	Social play			■
		Kunz 2015	2 to 14 years	6 months	-	Social play			■
Rodentia	Prairie vole, *Microtus ochrogaster*	Chau et al. 2008	20 to 50 days		40	Total play rate			●
	Capybara, *Hydrochoerus hydrochaeris*	Congdon 2007	Juvenile, subadult	15 months (1180 hours)	-	Frequency of play bouts			■
	Alpine marmot, *Marmota marmota*	Perrin et al. 1993	Yearling and juveniles	4 months (415 hours)	-	Play behaviour			□
	Yellow-bellied marmot, *Marmota flaviventris*	Armitage 1974	Yearlings	1714 hours	-	Number of play bouts	□		
	Columbian ground squirrel, *Spermophilus columbianus*	Festa-Bianchet and King 1984	-	299 days (638 hours)	-	Number of playful social interactions	■		
		Waterman 1988	Juveniles and yearlings	520 hours	213	Initiations of play	□		
						Duration of play bouts	■		
		Waterman 1986	Juveniles and yearlings	-	99	Time spent in play			□
	Belding's ground squirrel, *Urocitellus beldingi*	Marks et al. 2017	Juveniles	3 months	67	Rate and duration of social play			■
	Golden hamster, *Mesocricetus auratus*	Goldman and Swanson 1975	0 to 65 days	65 days	54	Amount of playfighting	●		
	Hooded rat, *Rattus norvegicus*	Meaney and Stewart 1981	21 to 55 days	34 days	24	Play initiations	●		

Cetaceans	Bottlenose dolphin, *Tursiops truncatus*	Walker et al. 2017	<1 year to 3 years	One year	5	Level of social play			○
Chiroptera	Common vampire bat, *Desmodus rotundus*	Park 1990	2 to 22 months	-	7	Initiations of social play	○		
Dasyuromorphia	Kowari, *Dasyuroides byrnie*	Meißner and Gansloßer 1985	0 to 220 days	220 days	43	Social play			○
Diprotodontia	Red-necked wallaby, *Macropus rufogriseus banksianus*	Watson and Croft 1993	<20 months	2.5 years	21	Number of playfights	●		
						Median duration of playfighting bouts			●
Perissodactyla	Horse, *Equus caballus*	Rho et al. 2007	-	5 months	53	Play-fighting	■		
		Sigurjonsdottir et al. 2003	Subadults	5 weeks (488 hours)	15	Dyadic play	●		
		Crowell-Davis et al. 1987	0 to 24 weeks	585 hours	15	Number of play bouts	●		
						Duration of play bouts	●		
						Proportion of total play	●		
		Wells and von Goldschmidt-Rothschild 1979	-	5 months	-	Rate of play (yearlings)	■		
						Rate of play (immatures)			■
		Cameron et al. 2008	0 to 110 days	-	98	Fighting play			■
Proboscidea	African elephant, *Loxodonta* sp.	Webber 2017, Webber and Lee 2020	0 to 9 years	-	7 captive, 130 wild	Rate of play			■●
	Asian elephant, *Elephas maximus*	Webber 2017, Webber and Lee 2020	0 to 9 years	-	8 captive, 101 wild	Rate of play			■●

Circles denote captive, square denotes wild, triangle denotes wild but provisioned. Filled indicates a statistical test was carried out, blank that no test was reported

Discussion

This chapter confirms that, across mammals generally, there is higher male engagement in RTP compared to females, including initiations of play and time spent in play. However, I also found an absence of sex differences in RTP across more mammalian species than expected based on prior theory and literature. For species with multiple relevant studies, mixed findings were common, which suggests sex differences in RTP are likely to vary based on context and setting. A small number of species displayed a female bias in RTP, sometimes in specific, less vigorous components of RTP, but it is difficult to conclude whether this was due to methodological factors, and important to consider that they are often not independent data points.

Potential Predictors of Sex Differences in RTP

Sex-differentiated reproductive and life history strategies have consequences for social organisation and behaviour, which may also affect levels of sex differences in engagement in RTP. Our findings provide insight into potential predictors of engagement in RTP and help generate hypotheses to be tested.

The degree to which males are able to monopolise mating varies by species, depending on factors such as sex differences in age at maturity, ecological factors determining female dispersion, synchrony of ovarian cycles, and patterns of female cooperation in response to male mating strategies (Engelhardt et al., 2006). For most mammals, the sex that invests less in offspring care, usually males, competes more intensely for access to the opposite sex, resulting in male-male competition and formation of male dominance hierarchies, although this varies with socio-ecological factors such as the adult sex ratio of a group (Kokko and Jennions, 2008). Ecological factors such as food abundance and predation risk affect components of social organisation such as group size and composition, which leads to variation in mating systems and social structures (Koenig et al., 2013), as females distribute themselves in response to resources, and males adapt to monopolise females (Emery Thompson, 2017). Polygynous males are predicted to invest in body size and weaponry, which is associated with male competition, and higher levels of social play (Clutton-Brock, 1988; Berghänel et al., 2015). Polygyny and promiscuity are the most common mating system of mammals, both of which predict higher levels of male competition (Kappeler et al., 2013), and therefore higher levels of RTP in males than in females in preparation for adult competition.

I found that higher levels of male RTP often coincided with higher levels of adult male aggression compared to adult females, and strict male dominance hierarchies. High dominance status for males is typically associated with greater reproductive success (Clutton-Brock, 1988; Flanders et al., 2013). To the extent that RTP may function to enhance fighting skills (Cenni and Fawcett, 2018), males of species with higher levels of male intrasexual competition should be more likely to engage in RTP as immatures than females. However, this pattern was somewhat disrupted by the Hominidae, for which male bias in RTP was reduced compared to predictions based on male intrasexual competition, but could be at least partly explained by small sample sizes and a reliance on captive populations.

The effects of female intrasexual competition, however, must also be considered. Adult female mammals may engage in competition to secure resources including breeding sites, food sources, shelter, and mates (Stockley and Bro-Jørgensen, 2011). The extent and ways in which females invest in competition is likely to vary by species. For example, the prevalence of female-female contest versus scramble competition for food depends on ecological factors (Stockley and Campbell, 2013). Engagement in RTP for females is likely to change as a result of such variation, where species with high levels of intrasexual female competition which manifests as aggressive behaviour are more likely to engage in juvenile RTP.

This may be reflected in species where both sexes disperse at maturity. Dispersal is associated with increased risks of predation (Bonte et al., 2012) and a requirement of highly developed fighting and social skills (Mitani et al., 2012), which may lead to higher levels of RTP in order to develop these skills. Both the mantled howler monkey and white-lipped peccary showed a female bias in RTP (Zucker and Clarke, 1992; Nogueira et al., 2011), which may be associated with dispersal in males and females for both species. Similarly, saddle-backed tamarins showed a female bias in juvenile RTP (Vogt, 1978), which may have again been associated with similar levels of competition in males and females, as both male and female saddle-backed tamarins engage in infant care, although the link between paternal care and male intrasexual competition is unclear (Koenig et al., 2013). While the evidence from these species is consistent with the idea that similar levels of male and female intrasexual competition leads to reduced or female bias in RTP, the hypothesis would be difficult to test due to the small number of species that display female biased RTP.

Although in some cases a lack of sex differences might be attributed to small sample sizes and lack of statistical power, many studies with larger sample sizes reported no sex differences in either overall RTP or components of RTP. Overall, studies finding no sex differences did not have smaller sample sizes than those reporting male- or female-biased RTP. Therefore, it seems that the variation in sex biases in RTP is not simply a consequence of low statistical power.

The absence of a sex difference in play was common for the Carnivora, particularly the feliformes, suggesting that RTP may be equally important for males and females of predatory species. Carnivores are characterised by specialised diets and predatory behaviour in both males and females (Macdonald, 2014), which may be developed during immature RTP (Caro, 1995). In highly social carnivora, such as wolves, RTP may be used to develop social and fighting skills associated with dominance competition, as well as practice skills used in predation (Lewis, 2003), which are equally necessary for males and females.

Sex differences were highly variable for primates, with many species showing mixed results or a lack of sex differences, which may have been associated with similar levels of male and female adult competition. However, equal rates of male and female play may also be due to limited samples sizes or demographics. For example, Young and Hankins (1979) only analysed the behaviour of infants below three months of age. Lucci and Rothman (2020) reported no significant sex differences in RTP for grey-cheeked mangabeys and red and black-and-white colobus monkeys, although again sample size was limited. They suggest that sex differences may have been observed as expected if groups were larger, as age significantly affected choice of play partner, and often suitable partners were unavailable. Availability of play partners may have influenced the lack of sex differences found in orangutans, which have a solitary dispersed social system (Singleton and van Schaik, 2002), and may have reduced opportunity to engage in RTP. Overall, it seems that a lack of sex differences in some primates seems to be associated with smaller group size and lack of suitable play partners, although low statistical power must also be considered.

Within-species Variation

Webber and Lee (2020) reported higher levels of play and less time spent feeding in captive elephant calves compared to their wild counterparts, suggesting that captivity, with less constraints on energy budgets, could increase levels of RTP. However, caution must be used when comparing behaviour across environments. Differences between studies of wild and captive animals may be caused by a variety of environmental and social factors (e.g. behavioural motivation and adaptation, constraints on energy retrieval and expenditure, and welfare) and/or differences in methodology (e.g. sampling, confounding variables, and variation in ethograms and behavioural definitions) (Howell and Cheyne, 2019).

Furthermore, the effects of captivity could interact with age and sex. Mixed results were found regarding sex differences in the RTP of dogs, where a male bias was more consistent in wild populations (Pal, 2008, 2010) compared to captive populations where differences were only significant at certain ages (Lund and Vestergaard, 1998), in specific dyads (Ward et al., 2008), or no sex difference was found at all (Koscinczuk et al., 2015). However, for Japanese macaques, the male bias in play seems to be consistent for wild and captive populations, and for chimpanzees the extent of sex differences in RTP does not seem to be dependent on whether the group was wild or captive. Therefore, the status of the group and the resulting methodology must be considered carefully for each study, as there seems to be no clear patterns of the effects of captivity with regards to sex differences in RTP.

Energetics and resource availability must also be considered as potential factors in within-species differences with respect to seasonality. Seasonal differences in levels of RTP were reported for bottlenose dolphins (Walker et al., 2017), chimpanzees (Moebius et al., 2019), and Japanese macaques (Eaton et al., 1986; Glick et al., 1986), where higher levels of play were associated with both food and play partner availability as well as hormonal changes. For chimpanzees, the effects of fruit and play partner availability were found to interact, as the effects of partner availability were significantly stronger during seasons with low-fruit availability (Moebius et al., 2019). This suggests that engagement in play can be heavily influenced by interacting factors within the social and ecological environment.

Rates and Duration of RTP

Reported sex differences in RTP differ depending on the way RTP is measured, variously as rates and initiations, total time spent in play, and duration of play bouts. For example, I found that males often showed higher rates of initiation of play bouts compared to females (e.g. Siberian ibex (Byers, 1980), scimitar-horned oryx (Pfeifer, 1985), dogs (Lund and Vestergaard, 1998; Ward et al., 2008; Pal, 2010), vervet monkeys (Fedigan, 1972), Columbian ground squirrels (Waterman, 1988), hooded rats (Meaney and Stewart, 1981) and the common vampire bat (Park, 1990)), which suggests males have a higher motivation to engage in play compared to females. Dogs showed a male bias in juvenile RTP when recording initiations (Lund and Vestergaard, 1998; Ward et al., 2008; Pal, 2010) and frequencies (Pal, 2008), but showed no sex difference in time spent in social play activity (Koscinczuk et al., 2015). Alternatively, in geladas, no sex differences were found for frequencies or initiations of RTP (Mancini and Palagi, 2009), but a male bias was found for overall time spent in RTP (Barale et al., 2015). Therefore, no clear sex-biased pattern emerges, but the way that activity is recorded may influence the conclusions regarding sex differences in a species. Hence, future studies should distinguish between different measures of engagement in RTP and test hypotheses accordingly.

Components of RTP

Specific components of RTP may show different patterns in relation to sex and age. Bramblett (1978) reported that immature female vervet monkeys had a higher mean rate of social play than males, but only between 48 and 61 months old, suggesting the function of RTP may differ by sex and age. This is supported by Förster and Cords (2005), who reported that female blue monkeys engaged in a significantly higher proportion of chasing behaviour compared to males, and Spijkerman et al.

(1996), who reported that females engaged in tickling behaviour significantly more often than males, but only below three years of age.

To understand why specific components of RTP may be valuable to males or females, the typical adult behaviours of each species must be considered. Both adult male and female vervet monkeys display high levels of aggression (Hemelrijk et al., 2020), so it is reasonable to expect that RTP will benefit both sexes in the practice of fighting skills. Immature female blue monkeys only showed higher levels of chasing play (Cheney et al., 1987), which suggests female blue monkeys are engaging in play in order to develop skills other than fighting and dominance, perhaps predator avoidance as blue monkeys are targeted by both aerial and terrestrial predators (Murphy et al., 2013). In the case of chimpanzees, grooming is important for both males and females in maintaining social bonds and establishing dominance hierarchies (Kanngiesser et al., 2011), a behaviour which may be developed in tickling play in infancy and juvenility respectively for females and males, as females mature at a slightly faster rate (Harvey and Clutton-Brock, 1985).

Other Considerations and Future Research

One major factor in the determination of sex differences in RTP which is not considered by this review is the influence of hormones on behaviour. Various endocrine studies have shown that androgenic mechanisms can influence a range of behaviours, including aggression, social dominance, and RTP (Grebe et al., 2019). Both prenatal and postnatal effects of hormones have been shown to affect engagement in RTP. For example, RTP in juvenile male rats is feminised following exposure to an androgen receptor antagonist during prenatal development (Casto et al., 2003) or increased by exposure to testosterone propionate after weaning (Pellis et al., 1992), and exposing female rats to testosterone in the womb or during postnatal development can lead to higher levels of RTP (Hines, 2006). There is also some evidence that prenatal testosterone treatments can increase levels of RTP for male and female rhesus monkeys, although this is dependent on the timing and dosage of the treatment (Wallen, 2005). These effects are mostly outside the scope of this review, which focuses on describing behaviour and excludes studies involving hormonal manipulations. However, the role of androgens in predisposing an animal towards RTP should be considered in further studies, as the consistency of such effects across species is not known.

The presence of a taxonomic bias in published studies towards primates, carnivores, and artiodactyla highlights a need for research into more diverse species from under-represented groups, particularly rodents which were significantly under-represented but are often involved in other types of behavioural research. However, it must be considered that play is more likely to be present in certain orders of mammal. For example, larger brained orders, such as primates, are more likely to contain species that display play consistently (Iwaniuk et al., 2001), and this may explain some of the taxonomic bias in play research.

Despite current methodological limitations in the study of sex differences in RTP, this review helps to form a solid foundation for future comparative analyses, as it highlights potential pitfalls (e.g. taxonomic bias and methodological issues) in addition to collating and exploring the wide range of work regarding RTP and its adaptive significance in both sexes. I also identify various potential factors which may underlie variation in sex differences in RTP across mammalian species, which should be investigated further by comparative studies which take into account phylogenetic relationships between species.

Conclusions

This review summarised the extent to which a male bias in RTP was present across mammalian species, identified patterns within and between taxonomic groups, recognised potential life history-related factors that may underlie sex differences in RTP, and identified contextual and methodological factors which may have contributed to the results of the included studies. As expected, a male bias in RTP was common, particularly for initiations of play, suggesting that in many species of non-human mammal, males are motivated to play more often and for longer durations than females. Males also tended to show a preference for wrestling and more aggressive aspects of RTP, whereas females tended to show a preference for less aggressive aspects of RTP. This suggests that RTP is used as preparation for adult social behaviours, where, in many mammalian species, males engage in higher levels of aggression, and females display higher levels of social bonding. This pattern was also true to some extent where female bias in RTP was shown, with higher levels of female-female competition or lower levels of male-male competition. This pattern was also associated with a lack of sex differences in RTP, particularly for the Carnivora, which also display less divergence by sex in adult social behaviours.

Overall, I conclude that sex differences in RTP were less consistent than expected, with a large number of studies finding no sex differences in RTP. This challenges the idea that male biases in RTP are consistently more likely across juvenile mammals. Sex differences in RTP may be constrained by the environment, sample size, other methodological limitations, and taxonomic bias on reported findings, highlighting potential areas of focus for future play studies in order to support comparative research. This review generally supports the idea that engagement in RTP as an immature aids in preparation for adult roles, although strong conclusions cannot yet be drawn without statistical testing. However, there are trends in sex biases in RTP which suggest that variation in life history-related variables, such as male aggression, dominance hierarchies, and mating system may be associated with such sex differences, which should be investigated further by phylogenetic comparative analyses.

Chapter 4: A Phylogenetic Comparative Analysis of Sex Differences in Rough and Tumble Play in Non-Human Mammals

In Chapter 3, I established that RTP is a widespread behaviour across non-human mammals, which is likely to be associated with the adaptive functions of the behaviour (Grunloh and Mangel, 2015). However, there is a large amount of between-species variation in engagement in RTP (Smaldino et al., 2019), and within-species engagement in RTP can further vary based on individual differences such as age, sex, social relationships, or contextual differences such as changes to the environment (Palagi, Paoli and Tarli, 2006). Life history theory, which is concerned with the timing of life events such as development, growth, and maturity, may help to explain cross-species variation in RTP since it highlights the importance of the optimisation of energy allocation for current versus future reproduction (Hill and Kaplan, 1999; Emery Thompson, 2017). According to life history theory, organisms should invest in RTP at the expense of growth and other activities when it provides sufficient benefits in terms of future reproductive success (Berghänel, Schülke and Ostner, 2015). Juvenile male mammals are often reported to invest in higher levels of RTP than females (Burghardt, 2005), which may be due to the benefits of RTP in developing fighting, dominance, and defence behaviours used in adult physical aggression and intrasexual competition for mates (Paukner and Suomi, 2008). Where competition for mates is more intense in males than females, as is often the case for mammals, sex differences in reproductive strategies likely result in greater investment in RTP by juvenile males than females (Berghänel, Schülke and Ostner, 2015). Although there may be other functions of RTP, as discussed in Chapter 1, I here focus on those which are associated with male competition.

My systematic review of the non-human mammal play literature confirmed that RTP is commonly male-biased, although not as consistently as expected based on typical mammalian life histories (Marley et al., 2022), where males tend to be larger than females (Isaac, 2005), and polygynous mating systems are common and associated with male-biased dispersal (Dobson, 1982). There is some qualitative evidence to suggest that species with strong and consistent male biases in juvenile RTP also tend to display high levels of male competition in adulthood, including higher levels of male aggression and the presence of male dominance hierarchies, and species with no significant sex differences in RTP were often associated with a lack of physical and behavioural sexual dimorphism (Marley et al., 2022). Although cases were rare, some species showed a female bias in RTP, which seemed to co-occur with monogamous mating systems, paternal care, and lower levels of male aggression compared to other species. This suggests that variation in sex-differentiated life history strategies, which are associated with factors such as sexual size dimorphism, mating system, sex-biased dispersal and phylogenetic position, may be associated with varying investment in RTP, which is investigated here using quantitative methods. If sex differences in RTP reflect evolved life history strategies, then we should expect to see a phylogenetic signal, i.e. that closely related species have similar behaviours (Borges et al., 2019). Further, traits related to life history strategies such as sexual size dimorphism, mating system and sex-biased dispersal are also likely to be related to phylogenetic position (Mabry et al., 2013), which suggests that phylogenetically informed models are necessary in order to take into account phylogenetic non-independence when assessing the underlying factors affecting sex differences in RTP.

I aimed to investigate the effects of various traits that are indicative of sex differences in life history strategy on the variation in sex differences in RTP across species, using phylogenetically informed models. I focus on the effects of mating system, sexual size dimorphism (SSD), and sex-biased dispersal, which are likely to be associated with variation in intrasexual competition (Clutton-Brock and McAuliffe, 2009; Weckerly, 1998). Therefore, these factors may be associated with sex differences in RTP, as RTP is associated with the development of fighting skills and navigating dominance hierarchies (Flanders, Herman and Paquette, 2013), as well as the development of cognitive and social skills (Spinka, Newberry and Bekoff, 2001), which may lead to differing engagement in RTP between the sexes, depending on the species' adult social roles.

High levels of male competition in mammals are associated with polygynous mating systems, where males compete with each other to achieve high dominance rank and/or mating success (Clutton-Brock and McAuliffe, 2009). Being dominant within a group allows an individual to secure access to resources and therefore monopolise access to females, maximising their reproductive success (Kappeler et al., 2013). As juvenile RTP is associated with the development of fighting skills, it is suggested that males of polygynous species are more likely to engage in RTP as juveniles in order to prepare for their adult social role which involves navigating a male dominance hierarchy (Flanders, Herman and Paquette, 2013), where rank is typically attained through aggressive, competitive interactions (Wright et al., 2019). Conversely, in species with monogamous mating systems or where females compete, females are also likely to benefit from dominance, engage in high levels of intrasexual competition, and therefore show similar levels of engagement in RTP to males as juveniles in order to prepare for aggressive competition in adulthood (Clutton-Brock et al., 2006). Therefore, I hypothesise that sex differences in RTP should be associated with mating system and other factors influencing intrasexual competition.

Sexual size dimorphism (SSD) also likely reflects sex differences in life history strategies: larger male size and longer male growth periods generally result from intense intrasexual competition among males (Weckerly, 1998). Male-biased SSD is common in primates, such as gorillas and baboons, where males can weigh almost twice as much as females (Plavcan, 2001), and is positively correlated with intensity of male mating competition in primate species with a polygynous mating system (Mitani, Gros-Louis and Richards, 1996). However, Karubian and Swaddle (2001) caution that SSD is unlikely to result from a single selective factor, as variation in SSD is also associated with latitude, seasonal food availability, population density, and female-female competition (Isaac, 2005). Regardless of the selection pressures on SSD, it is associated with differing male and female growth trajectories, where females mature earlier than males in order to prioritise investment in reproduction over growth (Plavcan, 2001). This is likely to affect levels of RTP, where males have longer juvenile periods and therefore invest in RTP at a greater range of ages than females, showing increased levels of RTP over the juvenile period compared to females (Smith, 2005). Therefore, I hypothesise that species with more male-biased SSD in adults will be more likely to show higher levels of male bias in engagement in RTP as juveniles.

Sex differences in dispersal, where upon reaching maturity, an individual leaves the natal group for another in which they can successfully breed (Handley and Perrin, 2007), may also help explain variation in RTP across species. In mammals, it is usually the male that disperses in polygynous and polyandrous species, whereas males and females are likely to disperse at equal rates in monogamous groups (Dobson, 1982). However, the causal link between polygyny and male-biased dispersal is not always clear (Li and Kokko, 2019). There are various costs associated with dispersal, where individuals have to travel across unfamiliar territory and integrate into a new group, which can threaten survival and reproductive success (Wolff, 1994; Bonte et al., 2012). Individuals must be prepared to deal with new, unexpected situations, and have both the social competence and fighting skills necessary for integration into the new group, all of which are skills which may be developed during juvenile RTP (Pellis and Iwaniuk, 2000; Spinka, Newberry and Bekoff, 2001; Flanders, Herman and Paquette, 2013). Therefore, I hypothesise that the sex that disperses within a species is likely to show higher levels of engagement in juvenile RTP.

The aims of this chapter were to:

i) Calculate phylogenetic signal to determine the extent to which phylogeny influences sex differences in juvenile RTP,

ii) Use phylogenetically informed regression models to investigate the factors affecting sex differences in juvenile RTP, including mating system, sexual size dimorphism, and sex-biased dispersal.

Methods

Data Collection

Data were collected by process of systematic review, where sources of information containing sex differences on RTP were collected for non-human mammals (see Chapter 3, as both chapters use the same data). All information sources contained qualitative or quantitative data on intraspecific RTP carried out by non-adult members of a species, which was split by sex, or the authors had carried out a statistical test which identified if sex had a significant effect on level of RTP. Species were deemed to show a male bias, female bias, or no sex bias in RTP if studies showed consistent results; statistically significant differences were not required, but studies for a given species had to consistently show an effect in the same direction, regardless of the size of the effect (which often wasn't reported). Species which showed inconsistent findings across multiple studies or tests within a study were reported as 'mixed'. These values were mapped onto the tips of the phylogenetic tree in Figure 4.1. This phylogenetic tree was sourced from Vertlife, and was constructed using Bayesian inference with a combination of DNA data and birth-death models (Upham, Esselstyn and Jetz, 2019).

Data on predictor variables were retrieved from existing databases and journal articles. Data on male and female body mass were retrieved from a paper by Myhrvold et al. (2015), and data on mating system and dispersal from a paper by Mabry et al. (2013). Where data were missing, additional sources were retrieved by searching for the species name and name of the variable with missing data on Google Scholar, Scopus, and Web of Science. A comprehensive list of data sources can be seen in Appendix A.

Analysis

Phylogenetic signal was calculated to assess the extent to which the variation in sex differences in RTP across species was associated with phylogenetic relatedness. I calculated phylogenetic signal using the delta statistic (see Borges et al., 2019), as the data were categorical, rather than binary, so the more commonly used Fritz's D statistic (Fritz and Purvis, 2010) was not appropriate. The delta statistic (Borges et al., 2019) measures the extent to which the distribution of a categorical trait across species is predictable from phylogenetic relationships, where lower values indicate lower levels of phylogenetic signal. I ran 1 MCMC chain for 10 thousand iterations, discarded 100 as burn-in and sampled every tenth iteration, as recommended by Borges et al. (2019). A p-value was calculated by comparing the observed delta value to a distribution of 100 delta values calculated from randomly shuffled distributions of the data across the phylogeny.

Further analysis was conducted using phylogenetically informed generalised linear mixed models, for which I collapsed the outcome variable, referred to as RTP Bias, into two levels, 'strong male bias in RTP' (N = 23) and 'no strong male bias in RTP' (N = 40) with 'no sex difference', 'mixed evidence', and 'females playing more' labelled under the umbrella of 'no strong male bias'. As I had a limited sample size, I combined the latter groups in order to reduce the number of parameters and improve performance of the model. Therefore, I conducted a further analysis of phylogenetic signal by using Fritz's D statistic, which is appropriate for binary variables (Fritz and Purvis, 2010). In this analysis, D is 0 if the trait is distributed as expected based on phylogenetic relatedness, assuming a Brownian motion model of evolutionary change, where species values at the tips of the tree are distributed entirely according to shared history between species, and D is 1 if the trait is distributed randomly across the tips of the phylogeny. D values can exceed 0 or 1 if the trait is more phylogenetically conserved than under Brownian expectations, or more overdispersed than the random expectaton, repsectively. I conducted the analysis using 1000 permutations.

The phylogenetically informed generalised linear mixed models were conducted in a Bayesian framework, using the MCMCglmm R package (Hadfield, 2010). Included variables are described in Table 4.1. As stated above, there was a binary outcome variable ('strong male bias in RTP' or 'no strong male bias in RTP'); mating system, SSD and sex-biased dispersal were included as fixed effects predictors; and phylogeny was included as a random effect. SSD was a continuous numeric variable, which was calculated as log(male body mass/female body mass). This is an appropriate way of calculating the ratio for SSD, according to Smith (1999) and Fairbairn, Blanckenhorn and Székely (2007), who state that ratios do not lead to biased results when used in regression analyses which control for phylogenetic effects. Mating system was a binary variable, with species classified as monogamous or non-monogamous, and sex-biased dispersal was a categorical variable, with species classfied as showing a male bias, female bias, or no sex bias in dispersal. After removing cases with incomplete data for all variables, the sample size was 40 species. As the models use a Bayesian framework, the ouput provides lower and upper credible intervals (CIs), which indicate that there is a 95% chance that the parameter contributes to the outcome of the dependent variable if these values do not cross 0. I used logit models in MCMCglmm, with a chi-squared prior for the phylogenetic random effect, as this approximated a cumulative uniform distribution, and diffuse normal priors for fixed effects (De Villemereuil, Gimenez and Doligez, 2013). Residual variance was fixed to 1, according to standard procedure for models with a binary response variable where there isn't enough inormation to estimate residual variance. I ran individual models including each fixed predictor variable and controlling for phylogeny, then a model including all predictor variables which also controlled for phylogeny, due to potential low power of the sample. For each model, I ran MCMC chains for 150,000 iterations, discarded the first 3000 as burn in, and sampled every 10 iterations, resulting in an effective sample size (ESS) of over 3000 for all parameters. Heritability (h^2), which is calculated by the phylogenetic variance divided by the total variance plus a constant of $\pi^{2/3}$, was used to assess the importance of the phylogeny within each model. h^2 can range from 0, indicating no phylogenetic signal, to 1, indicating that 100% of the variance is explained by phylogeny (Hadfield, 2010). The sample size is likely to be sufficient as there are more than 10 species per parameter included in the model, and effective sample sizes are large. This, in addition to examination of the diagnostic plots (Appendix B), suggests that the model has sufficient power, and that chains converged, had good mixing, and had low levels of autocorrelation.

To assess the goodness of fit and classification accuracy of the models, I calculated R^2 and AUC values for each model. Calculating R^2 is a method of estimating the goodness-of-fit of the models, and presents a value which shows how much variance each model explains (Nakagawa and Schielzeth, 2013). R^2 can range from 0, in the case that a model does not explain any of the variation in the dependent variable, and 1, in the case that a model explains all the variation in the dependent variable. I calculated both marginal R^2 (which considers only the variance of the fixed effects) and conditional R^2 (which considers both fixed and random effects). Calculating AUC values provides a measure of the predictive accuracy of each model, allowing the quantification of the ability of the models to distinguish the sex difference a species would show in RTP. Results range from 0, where the model is completely inaccurate, to 0.5, where the model performs no better than chance, to 1, where the model is completely accurate (Ling, Huang and Zhang, 2003). AUC values were calculated using the R package cvAUC (LeDell et al., 2022).

Table 4.1. *Variables included in the phylogenetically informed regression models.*

Variable		Levels	Collapsed Levels
Outcome	RTP Bias (N=63)	Males play more (N=23)	Strong male bias in RTP (N=23)
		Mixed evidence (N=12)	No strong male bias in RTP (N=40)
		No sex difference (N=25)	
		Females play more (N=3)	
Predictor	Mating System (N=60)	Monogamous (N=9)	
		Non-monogamous (N=51)	
	SSD (N=47)	NA (Continuous numeric)	
	Sex-Biased Dispersal (N=49)	Predominantly male (N=31)	
		No sex bias (N=10)	
		Predominantly female (N=8)	

RTP Bias levels were collapsed into 'Strong male bias' and 'No strong male bias' to reduce the number of parameters and improve performance of the model.

Results

The phylogenetic distribution of sex differences in RTP across mammalian species is shown in Figure 4.1. Phylogenetic signal for sex biases in RTP was low, with a delta value of 0.652, which suggests that sex biases in RTP are likely to have evolved independently, rather than according to shared history. The p-value was 0.16, which suggests that the observed delta value is not significantly different from what we would expect if sex differences were randomly distributed across the phylogeny. However, although the sample size was appropriate (N = 63), there were only three species which displayed a female bias, which may mean the phylogenetic signal within the data has been poorly estimated.

However, results using RTP as a binary outcome variable and Fritz's D statistic support this conclusion, as phylogenetic signal is again low, with an estimated D statistic of 1.33. A D statistic which is greater than 1 indicates that the trait is over-dispersed relative to random expectation (Fritz and Purvis, 2010). The probability of the trait resulting from random phylogenetic structure was 0.937, and the probability of the distribution of the trait resulting from phylogenetic structure was 0.

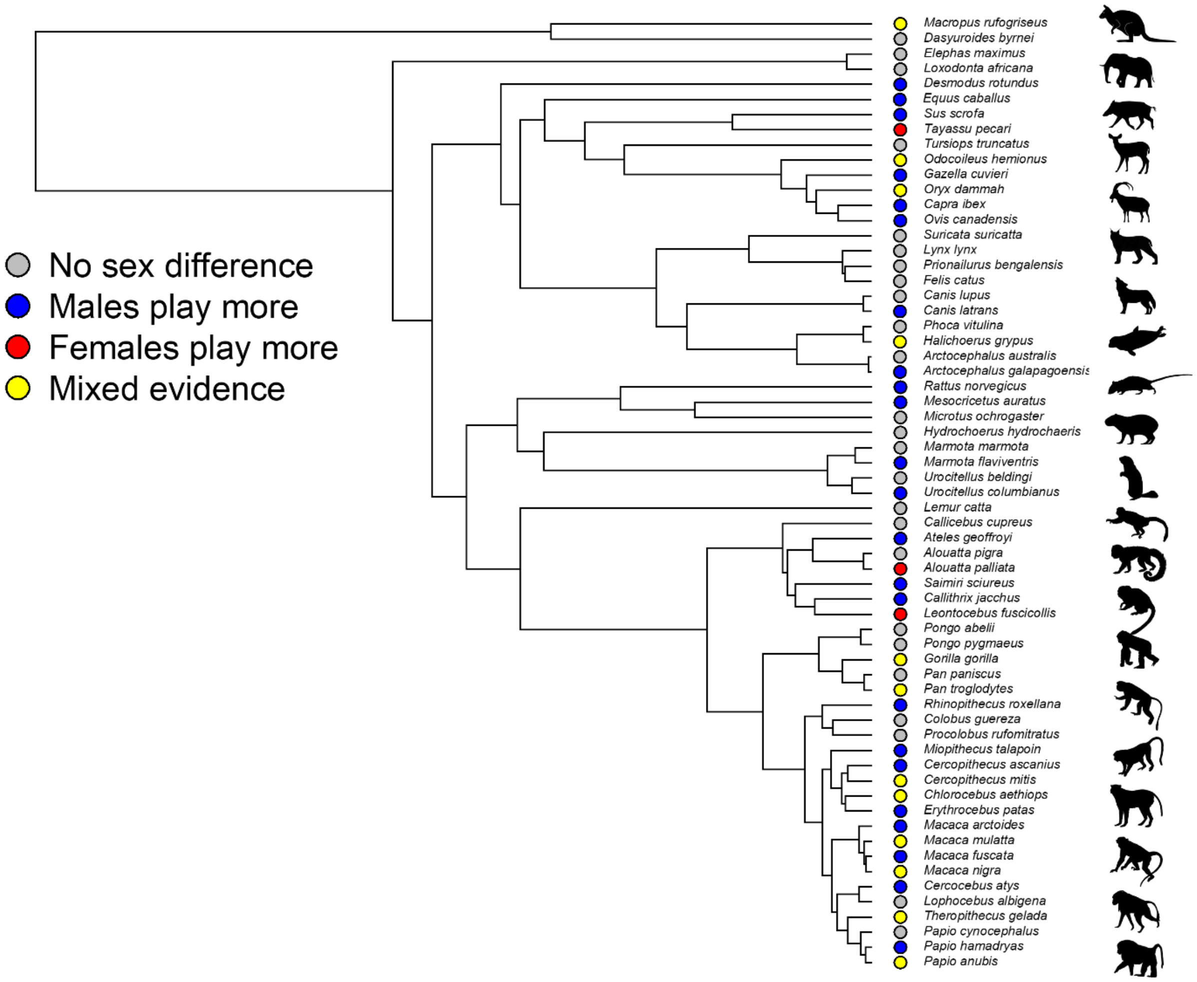

Figure 4.1. *Plot showing phylogenetic distribution of sex differences for RTP in non-human mammals. Images sourced from phylopic.org. Phylogenetic tree sourced from Vertlife, constructed using Bayesian inference with a combination of DNA data and birth-death models.*

The results of the phylogenetically informed regression models are reported in full in Table 4.2. For all models, several indicators suggest the models had converged adequately. Appendix B shows the density plots, which are unimodal for all variables, and the trace plots, which show fairly random scatter around the mean, indicating that chains converged with good mixing and low levels of autocorrelation (Gamerman and Lopes, 2006). Furthermore, effective sample sizes were sufficient, as they were above 3400 for all parameters in all models. There was some correlation between predictor variables, including between mating system and dispersal ($r = 0.31$, $p < .05$), and mating system and SSD ($r = 0.41$, $p < .01$) (Appendix C), which may affect the interpretation of the results of the models. However, correlations were only weak to moderate, indicating that the variables remain suitable for inclusion in the models.

Furthermore, I first ran separate models for each independent variable. None of the independent variables were strongly associated with a male bias in RTP, including mating system (95% CI = [-1.27, 3.30]), SSD (95% CI = [-3.79, 3.10]), or sex-biased dispersal, including male-biased dispersal (95% CI = [-1.22, 3.32]) and female-biased dispersal (95% CI = [-1.56, 4.01]). Again, in the full model which included all three independent variables, none of the fixed effects were strongly associated with a male bias in RTP, including non-monogamous mating system (95% CI = [-1.53, 3.91]), SSD (95% CI = [-5.30, 2.63]), or sex-biased dispersal, either male (95% CI = [-1.65, 3.24]) or female (95% CI = [-1.51, 4.33]). The lack of notable differences in the results between single variable models and the full model suggest that the correlation between variables is not notably affecting the results.

Heritability for RTP was low for all models, including the mating system ($h^2 = 0.12$), SSD ($h^2 = 0.11$), and dispersal ($h^2 = 0.12$) models, and the model including all variables ($h^2 = 0.13$). This indicates that shared evolutionary history is unlikely to contribute much to variation in sex differences in RTP across species. However, the 95% credible intervals are wide, as shown in Table 4.3 and Appendix E, which suggests substantial uncertainty in the heritability estimate. This could be due to limited sample size and/or noise within the data. Alternatively, heritability is calculated on the assumption of gradualistic evolutionary change, which could lead to the underestimation of phylogenetic signal in cases where change is instead episodic or punctuational (Pagel, 1999).

R^2 values were low for all four models, with conditional R^2 values of 0.15, 0.14 and 0.15 for the mating system, SSD, and dispersal models respectively (Table 4.4). The full model had a conditional R^2 value of 0.16. Similarly, AUC values were fairly low, ranging from 0.66 to 0.78, indicating that the model could correctly predict a sex bias in RTP for 66 to 78% of cases. This indicates that the models have limited predictive power.

Table 4.2. *Results of the phylogenetically informed regression models.*

Model	Parameter	Mean	Lower 95% CI	Upper 95% CI	ESS
1	Intercept	-1.4913	-4.0880	0.8432	3990
	Mating System (Non-Monogamous)	0.9137	-1.3798	3.2033	3531
2	Intercept	-0.6636	-2.4056	1.0947	6825
	SSD	-0.3273	-3.8040	3.1028	4666
3	Intercept	-1.6820	-4.1590	0.6642	4266
	Sex-biased Dispersal (Female)	1.3664	-1.2981	4.3028	3790
	Sex-biased Dispersal (Male)	1.0355	-1.1687	3.2770	3531
4	Intercept	-2.0793	-5.0883	0.7077	3514
	Mating System (Non-Monogamous)	1.0675	-1.5275	3.9141	3411
	SSD	-1.2216	-5.3045	2.6253	4044
	Sex-biased Dispersal (Female)	1.3728	-1.5121	4.3320	3549
	Sex-biased Dispersal (Male)	0.8108	-1.6483	3.2436	3481

Models (1: Mating System, 2: SSD, 3: Dispersal, 4: Full Model), Intercept = a mathematical constant; Parameter = explanatory variables included in the model; Mean = mean value of the posterior distribution; 95% CIs = the true value of a parameter with a probability of 0.95, given the data; ESS = effective sample size, the information content of a sample MCMC chain.

Table 4.3. *h^2 values.*

Model	Heritability	Lower 95% CI	Upper 95% CI
1 (Mating system)	0.1182435	0.0001520072	0.4663256498
2 (SSD)	0.1126087	0.0001347538	0.4592128703
3 (Dispersal)	0.1169848	0.0001575187	0.4675722426
4 (Full)	0.1268977	0.0001838112	0.4917625608

Heritability (h^2) = describes how much of the variation in the dependent variables can be attributed to genetic variation; 95% CIs = represents the true value of the parameter with a probability of 0.95, given the data.

Table 4.4. *R^2 values.*

Model	Marginal R^2	Conditional R^2
1 (Mating system)	0.0005037244	0.145048
2 (SSD)	$9.521067e^{-05}$	0.1381508
3 (Dispersal)	0.001054631	0.1451211
4 (Full)	0.001658781	0.1591198

Marginal R^2 = proportion of total variance explained through the fixed effects; Conditional R^2 = the proportion of total variance explained through the fixed and random effects.

Table 4.5. *AUC values.*

Model	AUC
1 (Mating system)	0.7774725
2 (SSD)	0.6565934
3 (Dispersal)	0.7417582
4 (Full)	0.6620879

AUC = the probability that the model can correctly distinguish the outcome of the dependent variable.

Discussion

The results of the regression models suggest that none of the selected potential predictors of sex differences in RTP, including SSD, non-monogamous mating system, sex-biased dispersal, or phylogenetic position, are likely to strongly contribute to variation in sex differences in RTP across mammalian species. This is supported by low R^2 and AUC values, which suggest the models have low predictive power, suggesting that factors I did not investigate, either biological, social, or environmental, are more likely to contribute to variation in sex differences in RTP across mammalian species, or that variation may be affected by noise in the data. I now consider each potential predictor, why it may not contribute to sex differences in RTP to the extent that I expected, and consider other potential factors which may be more likely to contribute to sex differences in RTP.

I found that phylogenetic signal for the distribution of sex differences in RTP was low, suggesting that sex differences in RTP are not likely to be affected by phylogenetic position. Although I acknowledge that phylogenetic signal for sex differences in RTP may have been underestimated due to the low sample size for species which displayed a female bias in RTP, further analysis of phylogenetic signal for sex biases in RTP as a binary variable and low estimates of phylogenetic signal within the regression models suggest this is not the case. Therefore, it is likely that phylogenetic position does not substantially contribute to a species' likelihood of displaying sex biases in RTP and indicates further that sex differences are unlikely to be predicted by biological factors involving life history strategy and male competition, both of which are strongly structured by phylogenetic history. However, I must acknowledge that the heritability (h^2) values had wide 95% credible intervals, which suggests that heritability could vary greatly from the low estimate given here. Estimates of phylogenetic signal within this data set could also be influenced by taxonomic bias, as primates, carnivora, and proboscidea are over-represented in the literature on sex differences in RTP (Marley et al., 2022), and as most are gregarious and diurnal, likely to be phylogenetically clumped. The influence of phylogenetic position could be better estimated with greater amounts of data on a wider range of species, should it become available.

Low phylogenetic signal has multiple potential causes, and does not necessarily imply independent evolution, as it could instead be indicating situations such as trait saturation (Borges et al., 2019). This could be the case for sex differences in RTP, as male biases in RTP are common for mammals, with 23 of 65 species in this study showing a male bias, 12 showing mixed evidence, 25 showing no sex differences and only 3 showing a female bias. Therefore, low phylogenetic signal could be indicating that RTP shows trait saturation and is randomly dispersed. However, inspection of the phylogenetic distribution of sex differences in RTP, where sex differences are scattered throughout the tree, suggests that sex differences in RTP are a result of independent evolution.

The finding that mating system variation is unlikely to be contributing to sex differences in RTP to any notable extent was contrary to my hypothesis, which predicted that males of species with polygynous mating systems would be investing in high levels of male-male competition (Clutton-Brock and McAuliffe, 2009), leading to a male bias in RTP in preparation for intrasexual competition in adulthood. In combination with the results concerning SSD, this suggests that RTP may not contribute to the development of fighting skills to the extent that has been hypothesised, and may not be associated with higher levels of male competition compared to females.

SSD was also expected to contribute to sex differences in RTP, as it is associated with higher levels of male competition (Weckerly, 1998), and therefore likely greater male investment in RTP as a means of gaining dominance and status within the group, and learning the skills necessary for aggression in adult with other males (Cenni and Fawcett, 2018). In species where males are much larger than females, females are likely to invest relatively more energy into reproduction, rather than size and competition, compared to males (Isaac, 2005). However, I found that male-biased SSD did not strongly contribute to sex differences in juvenile RTP, contrary to my hypothesis. Karubian and Swaddle (2001) suggest that SSD is unlikely to result from a single selective factor, and can instead be a result of natural or sexual selection acting on females, resulting in decreased female size, rather than just sexual selection acting on males. Therefore, SSD could be capturing a range of selective forces on both males and females, resulting in a lack of clarity in hypothesis testing, as perhaps SSD captures a type of competition which is not as relevant to RTP.

I also examined the effects of sex-biased dispersal on sex differences in RTP, as dispersal requires skills including cognition and the ability to deal with unexpected situations (Spinka, Newberry and Bekoff, 2001), social skills which call for the individual to create affiliative bonds (Smith, 2005), and/or skills associated with fighting, aggression, and dominance behaviours. Therefore, I predicted that the sex which predominantly disperses within a species would be more likely to engage in juvenile RTP, in order to develop the skills necessary for integration into unfamiliar territory and a new social group (Wolff, 1994). However, contrary to this prediction, sex-biased dispersal was another predictor that was unlikely to contribute to sex differences in RTP according to the regression models. Nevertheless, the costs associated with dispersal do vary by species, including exposure to predators, risks of encountering aggression, energy costs, and/or loss of social rank (Bonte et al., 2012), all of which may require different skills from the individual dispersing. Therefore, although juvenile RTP may be associated with all of the above skills, this may not be captured by sex-biased dispersal, and therefore there may not be a direct link between sex differences in juvenile RTP and sex-biased dispersal. Male-biased dispersal is often associated with polygynous mating systems (Dobson, 1982). Therefore, the lack of correlation between male-biased dispersal and male biases in RTP further suggests that there may not be as strong a link between male competition and male biases in RTP as expected.

Therefore, as male biases in juvenile RTP in the mammalian order are prevalent, though not universal (Lonsdorf, 2017; Marley et al., 2022), I must consider other factors that were not included in the regression models which may underlie the distribution of male biases in RTP. There are various issues which could have introduced noise to the data, including the lack of consideration of variations in the environment across the juvenile lifespan of the individual, which are likely to change rapidly and are not necessarily associated with species differences. All behaviours create ways in which individuals can respond flexibly to environmental conditions (Barsbai, Lukas and Pondorfer, 2021), and ecological changes are likely to impose constraints on behaviours such as RTP. For example, in both captive and wild settings, environmental factors including temperature, weather, food availability, and changes to predator pressure have all been shown to affect levels of play (Smith, 2005). Changes to the social environment have also been shown to affect rates of play, as changes in the age and sex of available play partners has been shown to change the intensity of RTP for captive squirrel monkeys (Biben, 1989), infant male rhesus macaques show higher levels of RTP when raised in mixed-sex rather than all-male peer groups (Brown and Dixson, 2000), and partner availability for immature chimpanzees significantly contributed to rates of play, particularly during periods of low food availability (Moebius et al., 2019). I therefore suggest that rates of RTP are more likely to be affected by contextual circumstances, including changes in the physical environment (which can affect energy demands and allocation of energy to RTP) and the social environment (where individual differences and changes to the social group can affect engagement in RTP), which can change over the lifespan of an individual and affect engagement in RTP, potentially to different extents for males and females. This creates a lack of phylogenetic signal in the data, as it results in a species' classification being potentially unstable and affected by variation on timescales that phylogenetic comparative methods cannot capture.

Another potential methodological issue with the data is the small sample size, which could be leading us to miss potentially significant results in the factors I examine in this chapter. Although our sample size is sufficient based on a number of indicators (including convergence of the models and inspection of diagnostic plots), there are high levels of taxonomic bias in animal research (Clark and May, 2002), and this is reflected in our data set, in which primates, carnivora, and proboscidea were over-represented to a statistically significant degree (Marley et al., 2022). As a result of this, classifications of sex differences in RTP are based on varying numbers of studies, and may be more unreliable for species in which there is only a small body of evidence. Therefore, I suggest that although these models are somewhat reliable, future studies could be improved by an increased sample size which includes a wider range of less-studied mammals, when such data become available.

A further methodological issue with the data was the range of definitions and measures of RTP (Marley et al., 2022). Measurement error, where the value for each species is measured with some degree of unbiased error, can result in low phylogenetic signal as a result of noise in the data (Freckleton, Harvey and Pagel, 2002). This may have been the case for RTP, as there were a wide range of measurement approaches, including rates, durations, and frequencies, and definitions of RTP, including RTP being split into separate components e.g. wrestling or chasing, or categorised differently e.g. aggressive play, social play, or general play. Although care was taken to exclude studies which did include behaviours I do not define as RTP, such as real aggression or solitary play, there was variation within the definition I applied, which could have caused noise in the data, and must be considered as a factor in determining levels of phylogenetic signal within this data set. Future studies could benefit from using a more standardised definition of RTP that would increase the strength of subsequent comparative studies.

However, another suggestion for future research would be to explore other predictors, which focus on proximate rather than ultimate causes of sex differences in RTP, such as changes in energy constraints. Phylogeny, mating system, SSD, and sex-biased dispersal are all factors which contribute to the evolutionary history of the behaviour, but according to the results of this analysis are unlikely to contribute to sex differences in RTP. Therefore, I suggest exploring other potential factors which could affect rates of RTP and how the behaviour develops across the lifetime, such as variation in the physical and social environment, as well as methodological factors.

Conclusions

Overall, the results of this chapter indicate that sex differences in juvenile RTP appear unlikely to be driven by phylogenetic position, SSD, mating system, or sex-biased dispersal, suggesting limited support for adaptive hypotheses for the origin and distribution of male-biased RTP in mammals. However, caution must be taken with these results, particularly regarding phylogenetic signal, as low phylogenetic signal could indicate either that RTP is an evolutionarily labile trait, or that the null findings are a consequence of methodological issues, particularly sample size, taxonomic bias and measurement error. I suggest that future studies should consider alternative potential predictors, particularly those that focus on changing environmental considerations such as food availability or predator pressure, as well as improving the consistency of measures and definitions of RTP across species and widening the number of species on which we have studies on RTP and sex.

Chapter 5: A Cross-Cultural Phylogenetic Analysis of Gender Differences in Rough and Tumble Play

RTP is a widespread form of play in both humans and non-human social mammals (Flanders, Herman and Paquette, 2013; Marley et al., 2022). As in non-human mammals, rough and tumble play (RTP) in humans refers to physically active behaviours, in which aggressive actions are simulated in a playful context (Pellegrini and Smith, 1998a). Similarly to that of other social mammals, human RTP incorporates behaviours such as running, chasing, wrestling, and open hand hitting, and involves the alternation of roles alongside self-handicapping behaviour (Pellegrini, 2002). RTP is distinguished from real aggression by differences in facial expression (RTP is generally accompanied by 'play face' or laughter), actions (aggression involves more closed hand hitting, shoves, pushes, and kicks) and lack of alternating roles (aggression involving a clear aggressor and aggressee). As addressed in previous chapters, in non-human mammals, RTP has been proposed to have an adaptive function in helping juveniles to learn skills essential for survival and reproductions as adults (Smith, 2005). Similarly, in humans it is possible that RTP is a key part of children's socialisation processes into adult roles considered appropriate in particular cultural contexts (Bosacki, Woods and Coplan, 2015).

In non-human mammals, many species show sex differences in RTP whereby juvenile males invest more time and effort in RTP than females (Marley et al., 2022). This pattern supports the idea that RTP has an adaptive function as male mammals are often more likely to engage in aggressive competition for dominance and mating success as adults (Berghänel, Schülke and Ostner, 2015). Similarly, many studies of human children report higher rates of RTP in boys than girls (Smith, 2005), and similar adaptive functions have been proposed for RTP in humans, given that in many societies adult men are more likely to perform more physically active, aggressive roles than women, such as hunting (Pellegrini, 2002) and warfare (Ember, Ember and Low, 2007). It is therefore possible that for humans, boys have a greater predisposition towards RTP than girls due in part to biological sex differences which have deep roots from our mammalian evolutionary history. If so, we should expect that male biases in RTP are common or even universal across human cultures. However, sex differences are in fact highly variable across mammalian species (Marley et al., 2022) meaning that expectations for humans are unclear. Humans are far from a typical mammalian species given our low sexual size dimorphism (Plavcan, 2001) and tendency to pair bond (Quinlan, 2008). This, combined with our enormous cultural diversity and behavioural flexibility, means that any inherited predisposition for gender differences in RTP will be manifested in highly variable ways across different cultural contexts.

In high income Western countries, RTP is reported to show consistent patterns of gender differences, where boys engage in significantly more RTP than girls (including in the UK, Boulton, 1996; Spain, Braza et al., 1997; the US, DiPietro, 1981; and Canada, Moller et al., 1992)). Such differences in RTP in Western populations have been suggested to be due to cultural influences; for example, boys may be expected to engage in RTP to assert dominance, whereas girls are assumed to engage in other less physically aggressive dominance behaviour such as the exclusion of others from the playgroup, due to traditional gender roles and expectations of caregivers (Bosacki et al., 2015). Parents in the UK are more likely to reinforce rough play for sons, but discourage rough play for daughters (Boulton, 1996). Although early childhood educators vary in the extent to which they allow RTP (Humphreys and Smith, 1984), in the US gender biases are found in the application of rules against RTP between boys and girls (Logue and Harvey, 2009), and the extent to which boys ignore rules prohibiting RTP (Fagot, 1985). Therefore, it is likely that gender differences in RTP are at least partially influenced by, or mediated by, social values and wider cultural influences, as boys and girls may engage in RTP to develop gender role-specific skills.

However, gender differences in RTP may not be so consistent when considering a more diverse range of human societies beyond Western industrialised contexts. Although Fry (2005) examined the eHRAF database and found that for 30 societies where wrestling behaviours were recorded, 21 descriptions were linked only to boys, 6 were linked to both girls and boys, 3 did not contain gender-differentiating information, and none were linked solely to girls, other studies show weaker or less consistent gender biases. Through naturalistic observation of Hadza and BaYaka youth, Lew-Levy et al. (2019) found that adolescent boys engaged in significantly higher levels of RTP than adolescent girls, but younger boys engaged in a similar level of RTP compared to younger girls. For the Aka and Ngandu forager groups, there were no significant gender differences in RTP, with Ngandu girls displaying similar levels of RTP compared to boys (6.4% vs. 4.2% of total play behaviour spent in RTP for girls and boys respectively) (Boyette, 2016a). A similar lack of gender differences in RTP is found for Parakana Indians (Gosso et al., 2005) and Zapotec farming communities (Fry, 2005). This suggests that gender differences in RTP may vary across subsistence societies, which may be a result of cultural and environmental factors which differ between groups. Subsistence societies show variation in factors such as marriage system (Ember et al., 2007), sexual division of labour (Edwards et al., 2004), and time spent in productive activities versus play (Lew-Levy et al., 2021), which may have effects on engagement in RTP for boys and girls.

It is important to investigate gender differences in RTP across societies, to identify cultural factors which may underlie engagement in RTP. Culture defines the settings in which play can take place, and the types of behaviour which are acceptable during play (Boyette, 2016a). Cultural norms are reinforced during play, which children use to practice cultural scripts and specific skills (Lew-Levy et al., 2018), which can lead to gendered socialisation where children play in patterns specific to their gender (Edwards et al., 2004). In the Hadza and BaYaka hunter-gatherer groups, boys between the age of 3 and 18 were more likely than girls to engage in hunting play, whereas girls were more likely to engage in pretend play (playing 'house' and with dolls) and foraging play, reflecting typical adult roles within that society (Lew-Levy et al., 2019). The study of how cultural norms and values affect gender differences in RTP can shed light on potential cultural drivers of the behaviour, as children may only engage in high levels of RTP when it is deemed culturally acceptable for their gender and important for the skills required in adulthood. Therefore, I consider cultural factors such as gender roles, marriage and descent system, and age at marriage, all of which may influence norms regarding gender differences in RTP.

Gender differences in adult social roles may be associated with gender-role scripts, which are socially constructed schemas in which a child groups acceptable behaviours according to gender (Levy and Fivush, 1993). Eagly and Wood (1999) suggest that gender-differentiated social roles may be related to sex-specific differences, such as physical size and childbearing, which lead to different social roles, and potentially psychological differences between men and women, where individuals will produce behaviour which confirms their gender role (Eagly and Wood, 2012). Warfare is almost exclusively conducted by men, potentially due to the sex and gender-specific nature of competition, and for societies where warfare is common, it is likely that male social roles are associated with toughness and aggression (Goldstein, 2003). Therefore, I predict that for societies which idealise male toughness, engagement in RTP will be more common for boys, as children imitate and learn adult social roles through play.

Another potential predictor of gender differences in RTP is the marriage system of the culture in which RTP is taking place. Polygynous marriage systems (where men are able to enter marital relationships with multiple wives) are common for cultures in the eHRAF database, and are associated with high male mortality (either due to war or high levels of pathogen stress), which increases competition among women for healthy men (Ember et al., 2007). I predict that polygyny will be associated with male RTP, as polygynous societies are associated with high levels of warfare, male mortality, the importance of male status, and competition for status and resources within groups, thereby increasing the need for young boys and men to practice skills associated with warfare and other physical skills. Furthermore, polygyny is associated with ritual fights such as wrestling (Llaurens et al., 2009) and a tendency for men to seek high status positions (Von Rueden et al., 2011), and as high status and physical formidability are associated with reproductive success (Murray, 2014), it is likely that boys will be expected to engage in RTP to improve their skill and therefore status.

I also predict that gender differences in RTP will be less common in societies with exclusively monogamous marriage system. Monogamous systems are associated with higher levels of male parental investment, particularly in harsh environments where resources are limited, and there is reduced male competition over wives (Sanderson, 2001). It is likely that monogamy in humans is associated with a lack of male RTP as males are less likely to require the skills associated with RTP, such as dominance and fighting behaviours. However, this could lead to female juvenile RTP, as monogamy is associated with increased female competition, where females compete for mates and paternal care (Iwasa and Harada, 1998).

Another potential predictor of RTP for boys and girls may be the descent system of the society in which they live. In patrilineal kinship systems, descent is traced through the male line, which can decide the allocation of resources, obligations, and leadership succession (Ensor, 2017). Alternatively, in matrilineal kinship systems, which are less common, inheritance is traced through the female line. This can result in women having greater access to assets such as land and possessions, resulting in decreased reliance on husbands and continuous kin support, which has important implications for the role of women and girls within a society (Giuliano, 2017). The elevated status of women within matrilineal societies may be reflected in differences in competition, as competition between girls is less likely to be discouraged. For example, in a throwing task, women within a matrilineal society (the Khasi in India) were more likely to choose to compete compared to men within that society (Gneezy et al*.,* 2009). This is also likely to affect childhood behaviours, as girls within patriarchal societies were shown to become less competitive at the onset of puberty, compared to girls within matrilineal societies where levels of competitiveness remained consistent throughout childhood (in a comparison of Indian villages, Andersen et al., 2013). As RTP is likely to display elements of competition, and aid in preparation for adulthood, I hypothesise that patrilineal societies will be associated with boys' RTP, and matrilineal societies with girls' RTP.

Another factor to consider with regards to gender differences within societies is the age at which boys and girls are first expected to marry, which tends to be younger for women across cultures (Allendorf et al., 2017). Boys and girls typically mature at different rates, with boys reaching puberty at a later age, and continuing to grow into their 20s, whereas girls are fully physically mature by approximately 16 years of age. This may be reflected in the social process of marriage; on average, women enter their first marriage 3 years before men, although this does vary by culture (Ortega, 2014). Weisfeld and Weisfeld (2002) suggest that men marry later as they require more time to gain resources and become economically and socially suitable for marriage, whereas women marry earlier as their fertility declines more sharply at an earlier age. Therefore, I predict that in societies where girls are expected to marry at younger ages, RTP will be less common for girls as they are instead expected to devote their time to domestic duties and childcare, to which the skills gained through RTP are less important. I would also predict that for societies where boys are expected to marry at younger ages, that they would be less likely to engage in RTP.

The final variable considered in this chapter is the extent to which a population suffers from food stress or hunger, which is a contextual, environmental factor, rather than one related directly to cultural norms. From a behavioural ecology perspective, behavioural strategies dictate an individual's ability to acquire energy and convert this into reproductive effort and therefore offspring (Pontzer, 2015), so for RTP to occur and be maintained over time it must have reproductive benefits for the individual within a specific environment. Levels of play have been shown to reduce in unsafe environments, such as in dangerous urban environment in the US (Molnar et al., 2004). In animal studies, behaviours which are accompanied by high energetic demands, such as RTP, are reduced or abandoned in response to challenging environmental conditions, such as limited resources (Altmann et al., 1993). Therefore, I suggest that the effects of food stress and hunger within a culture may lead to the absence or reduction of RTP for boys and girls, as the presence of food stress may discourage RTP for individuals that would otherwise engage in such behaviour. This effect may be more pronounced for girls, where RTP is likely to have less of a benefit for adult social roles, and therefore would not persist under constraints of resource shortages, where it may persist for boys.

To examine these potential predictors of RTP, I analysed ethnographies from the eHRAF database, which is a collection of ethnographies containing social and cultural information on a range of past and present societies ('eHRAF : HRAF collection of ethnography', 1996). Ethnographic descriptions of play are useful for understanding the nature, patterning and variability in RTP across societies, as they contain rich description of play activities in a number of societies. Furthermore, play within subsistence societies is less constrained by formal educational settings compared to industrialised societies (Boyette, 2016a), so the use of ethnography in subsistence societies is useful for investigating unstructured and spontaneous RTP. Searches were limited to the Standard Cross Cultural Sample, which contains 186 cultures and was designed to facilitate cross-cultural research with a representative and unbiased sample (Murdock and White, 2006).

In general, cultures are more likely to share traits if they are descended from a recent common ancestor, warranting the use of phylogenetically-informed methods to take this non-independence of cultures into account (Mace et al., 1994). Gender differences in RTP have been found to differ across cultures (Boulton, 1996), but the extent to which this is patterned by the relationships between cultures in as yet undetermined. There are various potential methods of transmission for gender norms with regards to engagement in RTP to be transmitted within and between cultures, including vertical and horizontal cultural transmission. Vertical transmission refers to socialisation that takes place within families, where children learn from adults including parents and grandparents, and horizontal transmission refers to socialisation that takes place between peers, through processes such as imitation and social learning (Bisin and Verdier, 2011). It has been argued that peers influence children's cultural learning to a greater extent than adults, which would suggest that RTP may be more affected by horizontal than vertical transmission (Boyette, 2016b). Alternatively, it has been suggested that vertical transmission is more prevalent until around five years of age, where the influence of peers and horizontal transmission becomes more influential (Hewlett et al., 2011). If RTP is affected to a large extent by vertical transmission, cultures which have a shared genetic and linguistic history should show similar patterns of engagement for boys and girls. If RTP is affected to a greater extent by horizontal transmission, similar patterns of engagement for boys and girls should occur in cultures which are spatially close to each other, as norms of behaviour would be transmitted between cultures where they are more likely to interact. If no patterns are found between closely related cultures, either with regards to shared history or spatial distance, it could also be the case that RTP is affected by recent, rapidly changing circumstances, such as environmental constraints (e.g., resource availability) or social constraints (e.g., availability of suitable play partners). Therefore, I consider both phylogenetic signal and spatial autocorrelation, to investigate the extent to which the presence or absence of RTP behaviours for boys and girls is distributed according to the cultural history and/or spatial location of a society.

The distribution of RTP by gender was further investigated by splitting RTP into its component behaviours, namely chasing and wrestling, which have been described as the two most fundamental types of RTP in humans (Fry, 2005). Previous evidence suggests that there may be gender differences in participation in each activity. Greek kindergarten teachers reported that only boys participate in games that include physical contact (such as fighting, wrestling, punching, hitting, and open hand slapping), and reported that play fighting games are considered appropriate for boys only, whereas chasing games are considered appropriate for boys and girls (Koustourakis et al., 2015). Maccoby (1988) claims that boys' play is more likely to involve rough body-contacts than the play of girls, which further suggests there may be differences between wrestling and chasing between the genders. For that reason, gender differences are expected in the presence of wrestling and chasing across cultures, with boys engaging in both components of RTP, and girls more likely to engage in only chasing behaviours. However, it could be the case that these findings from industrialised Western societies do not generalise to subsistence societies.

To summarise, this chapter aims to:

i) Quantify cross-cultural variation in the presence of wrestling, chasing, and overall RTP in boys and girls,

ii) Analyse the phylogenetic distribution of RTP for boys and girls, comparing societies based on shared cultural history and geographical distance, to determine the extent to which vertical and horizontal cultural transmission affects the presence of RTP for boys and girls, and

iii) Identify the extent to which phylogeny and cultural and contextual factors including marriage and descent system, female age at marriage, ideologies of male toughness, and food stress influence the presence of RTP for boys and girls across cultures.

I predicted that juvenile male RTP would be more common for societies which are polygynous, have patrilineal descent systems, and idealise male toughness, due to higher levels of male competition. This also leads to predictions that juvenile female RTP would be less common in polygynous and patrilineal societies, and where girls are expected to marry at earlier ages. I expected that the presence of food uncertainty would reduce RTP for both genders, although potentially to a larger extent for girls.

Methods

Data Collection

Data on RTP were collected from the eHRAF database ('eHRAF : HRAF collection of ethnography', 1996), for cultures included in the Standard Cross Cultural Sample (Murdock and White, 2006). The SCCS was designed to provide a large and varied sample of cultures which are appropriate for cross-cultural analysis, avoiding Galton's problem (where closely related cultures are not statistically independent). RTP was operationalised as the presence or absence of wrestling and/or chasing as part of play behaviour for boys and girls within each society, and was classified using a pre-defined coding scheme (Appendix F). Wrestling RTP was defined as contact behaviour (e.g. wrestling, grappling, kicking, tumbling, pushing) and chasing RTP was defined as running, chasing, or fleeing, both of which must occur in a playful context and with alternation of roles. These behaviours were not coded as RTP if they appeared in the context of a ceremony or ritual, as this behaviour may not have been freely chosen by the children involved. Each behaviour was recorded as absent (ethnographer states that the behaviour is rare or was never witnessed), inferred absent (coder could infer from the information provided that the behaviour is absent or rare, as play was described in great detail but RTP was not mentioned), or present (behaviour described in sufficient detail), unless there was not enough information to make a judgement e.g. ethnographer did not describe the gender of the children involved, or did not provide sufficient detail on the type of play to know if wrestling or chasing was present. For an example, see Table 5.1. For statistical analysis, the absent and inferred absent categories were combined, and the cultures for which ethnographies did not provide enough information were omitted.

Table 5.1 *Example of coding scheme for boys wrestling.*

Code		Definition
0	Absent	No wrestling RTP. Ethnographer states that boys do not, or rarely, engage in wrestling RTP behaviours
0.5	Inferred Absent	Inferred absence. Ethnographer describes the typical play activities of boys in sufficient detail to be able to infer that if wrestling RTP is not mentioned it probably is absent or rare
1	Present	Boys participate in wrestling RTP. Ethnographer describes boys engaging in wrestling RTP behaviours
9	Not Enough Information	Ethnographer does not mention wrestling RTP of boys, or does not provide enough information to make a judgement

Potentially relevant paragraphs of ethnographic descriptions were flagged for societies within the SCCS (Murdock and White, 2006) and were marked as including information on the OCM identifiers 'childhood activities [857]', 'games [524]' or 'athletic sports [526]'. OCM (Outline of Cultural Materials) identifiers are part of the indexing system of the eHRAF database and are used to find relevant information across the collection of ethnographies. Coding took place for each society within the SCCS which included information under these OCM Identifiers, which was a total of 184 out of 186 societies. As coding took place, data were recorded in a spreadsheet, in which the judgement and relevant quotes were recorded, alongside the name of the culture. Further information on each culture was also recorded, including its location, alternative society names, and name on the SCCS supertree, which maps the shared cultural history between societies. Relevant quotes were included alongside their ethnographic source, and the timeframe in which data was collected for each ethnography.

To account for the effect of shared history, I used a phylogenetic supertree, which was constructed using genetic and linguistic data (Minocher et al., 2019). This tree included all 186 populations within the Standard Cross Cultural Sample, and was chosen as it is believed to currently be the most comprehensive human phylogeny. To account for the effects of spatial location, spatial information was sourced from D-PLACE (Kirby et al., 2016), which lists the midpoint of the historical range of each society, using longitude and latitude co-ordinates. This was converted into a spatial distance matrix using the R packages 'geosphere' (Hijmans et al., 2017) and 'phangorn' (Schliep, 2011).

Data on marriage system, ideology of male toughness, presence of food stress/hunger, age of girls at marriage, and descent system were also collected from D-PLACE (Kirby et al., 2016). See Table 5.2 for identifier codes and factor levels. For the categorical variables, factor levels which were deemed similar were combined for analysis where it was deemed theoretically appropriate, in order to improve the performance of the model through reducing the number of parameters. Marital composition was collapsed into monogamous and polygynous (combining various categories of polygyny), and food stress was collapsed into food constant and food uncertainty (combining levels from occasional hunger to starvation). Descent system was collapsed into patrilineal, matrilineal, and other (combining duolateral, quasi-lineages, ambilineal, bilateral, and mixed societies).

Table 5.2. *Sources for predictor variable data, alongside levels for analysis.*

Predictor Variable	**Identifier Code**	**Original Levels**	**Levels for Analysis**
Marital Composition	SCCS211/ EA009	Monogamous	Monogamous
		Limited polygyny	Polygynous
		Polygyny, sororal cohabit	
		Polygyny, sororal separate	
		Polygyny, non-sororal cohabit	
		Polygyny, non-sororal separate	
		Polyandrous	NA
		Female Exclusively	NA
Food Stress or Hunger	SCCS678	Food constant	Food constant
		Occasional hunger or famine	Food uncertainty
		Periodic of chronic hunger	
		Starvation or evidence of protein deficiency	
Descent System	SCCS247	Patrilineal	Patrilineal
		Duolateral	Other
		Quasi-lineages	
		Ambilineal	
		Bilateral	
		Mixed	
		Matrilineal	Matrilineal
Ideology of Male Toughness	SCCS664	Absent	Absent
		Present	Present
Female Age at Marriage	SCCS2000 and B021	Continuous data	

Identifier Code = code assigned to variable on D-PLACE. Original levels = levels assigned to each society in the original data. Levels for analysis = original levels were collapsed to reduce the number of parameters and improve the performance of models.

Phylogenetic Signal and Spatial Autocorrelation

Effects of phylogenetic signal and spatial autocorrelation on the distribution of RTP for boys and girls were analysed using functions from the R packages caper (Orme et al., 2012), ape (Paradis and Schliep, 2019), and phytools (Revell, 2012). Phylogenetic signal and spatial autocorrelation were calculated using the D statistic (Fritz and Purvis, 2010), which is appropriate for binary traits. Each calculation was made with 1000 permutations. Cultures were removed from the analyses if they were not included in the supertree or lacked spatial data. One analysis was carried out using the genetic and linguistic tree, and another carried out using the spatial data tree. The spatial data tree was created from a matrix of distances between cultures, using the upgma function in the R package phangorn (Schliep, 2011).

Regression Models

Bayesian regression models were used to identify which variables contribute to the presence of RTP for girls and boys, using the MCMCglmm R package (Hadfield, 2010). Variation in girls and boys RTP was considered in separate models. Two models each were then used for the boys and girls data, one with the phylogeny based on genetic and linguistic data, and the other with the tree based on spatial data, both fitted as random effects. Regression models for girls' RTP were additionally fitted with marriage system, presence of food stress/hunger, age of girls at marriage, and descent system as fixed effects, while models for boys' RTP were fitted with marriage system, presence of toughness ideals, presence of food stress/hunger and descent system as fixed effects. Age of boys at marriage could not be included due to high levels of missing data. The level of correlation between each variable was calculated to ensure that all variables were suited for inclusion in regression models. The formula for both girls RTP models were Girls RTP ~ (Phylogeny) + Marriage System + Hunger + Age at Marriage + Descent, and the formula for both boys RTP models were Boys RTP ~ (Phylogeny) + Marriage System + Hunger + Ideology of Male Toughness + Descent.

All regression models used uninformative priors for the fixed effects variables and a chi-squared prior for the phylogeny (Hadfield, 2010; De Villemereuil, Gimenez and Doligez, 2013). For all analyses, I ran MCMC chains for 1,500,00 iterations, discarded the first 3,000 as burn in, and samples every 100 iterations. This resulted in effective sample sizes (ESS) of over 1000 for all models, suggesting adequate model convergence. The importance of phylogeny in each model was assessed using heritability (h^2), which ranges from 0, indicating no phylogenetic signal, to 1, indicating maximum phylogenetic signal (Hadfield, 2010). Credible intervals (CIs) are given for each parameter, which indicate that the parameter is likely to contribute to the outcome of the dependent variable if these values do not cross 0.

For the regression models, several indicators of model convergence were present, which provides evidence that the models have high reliability. This can be seen in Appendix G by the density plots, which are unimodal for all variables and the intercept, and by the trace plots, which show random scatter around a mean value for all variables, indicating that chains have mixed well. Effective sample sizes are also sufficient, as all are over 4000.

To assess the accuracy and fit of the models I calculated R^2 and AUC values. Calculating R^2 is a method of estimating the goodness-of-fit of the models, and presents a value which shows how much variance each model explains (Nakagawa and Schielzeth, 2013). R^2 can range from 0, in the case that a model does not explain any of the variation in the dependent variable, to 1, in the case that a model explains all the variation in the dependent variable. Calculating AUC values provides a measure of the predictive accuracy of each model, with results typically ranging from 0.5, where the model does not perform any better than it would due to chance, to 1, where the model is completely accurate (Ling et al., 2003). AUC values were calculated using the R package cvAUC (LeDell et al., 2022).

Results

Frequencies

Across cultures, wrestling and chasing were much more likely to be present for boys than girls, in the 73 cultures which could be confidently classified (See Figure 5.1). Wrestling was present for boys in 59 of 73 cultures (80.8%), whereas it was present for girls in only 23 of 61 cultures (37.7%). Chasing was present for boys in 53 of 65 cultures (81.5%), yet only present for girls in 33 of 55 cultures (60.0%). When the two variables were combined to analyse the presence of any kind of RTP across cultures, RTP was present for boys within 76 of 86 cultures (88.4%), but only present in 39 of 61 cultures for girls (63.9%).

For most cultures, there was not enough relevant ethnographic information to make a judgement on the presence of wrestling or chasing, which suggests that the clear reporting of RTP is uncommon within ethnography. This is particularly true for girls, for which the ‘not enough information’ judgement was made more common for boys, for both wrestling and chasing. For example, 120 societies did not contain enough ethnographic information to make a judgement on the presence of RTP for girls, compared to 93 for boys.

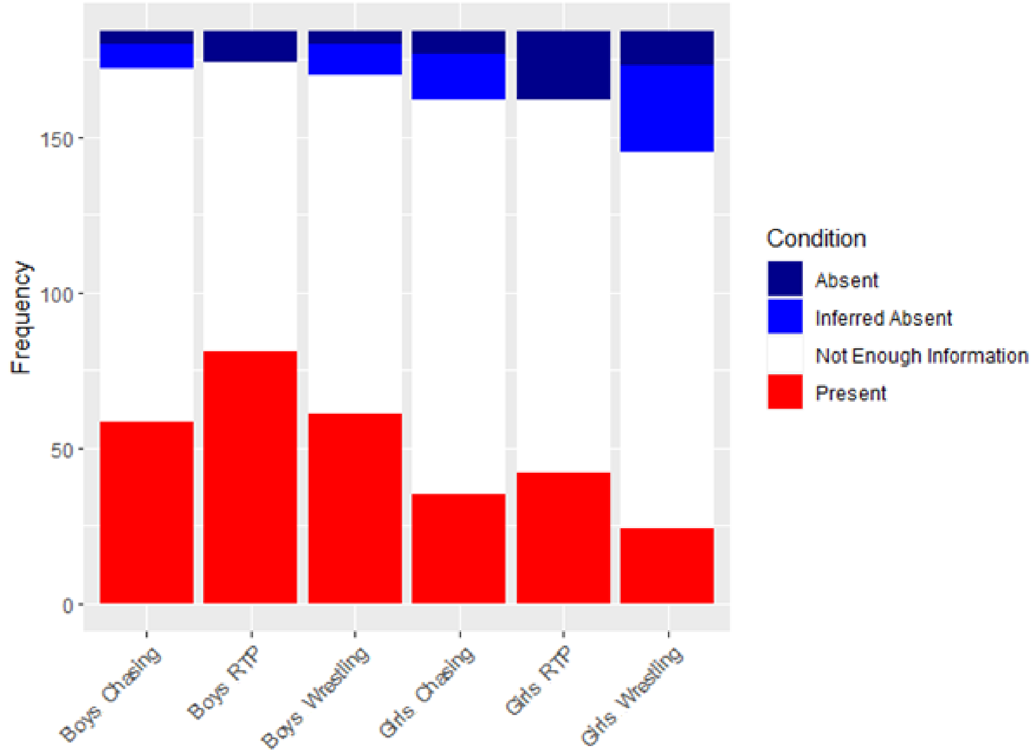

Figure 5.1. *Bar plot showing frequency of wrestling, chasing, and RTP for boys and girls across cultures.*

Distribution of RTP

Figure 5.2 shows the distribution of RTP mapped on to the genetic and linguistic phylogeny for boys and girls. Figure 5.3 shows the distribution of RTP mapped onto a network which represents geographical distances between cultures. The presence of RTP does not seem to be clustered in any way, suggesting very limited influence of shared cultural history.

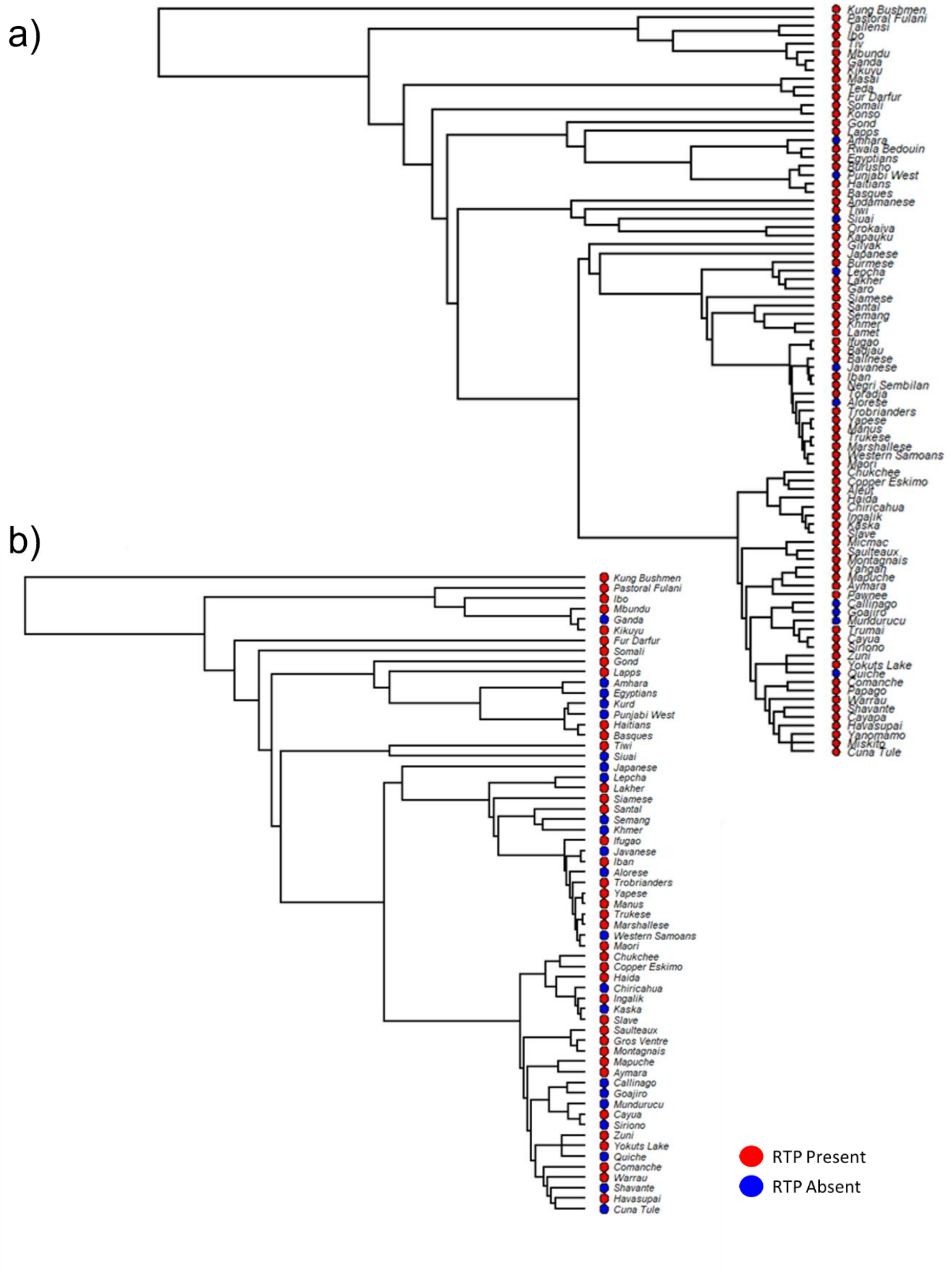

Figure 5.2. *Distribution of boys' (a) and girls' (b) RTP using genetic and linguistic phylogenetic trees.*

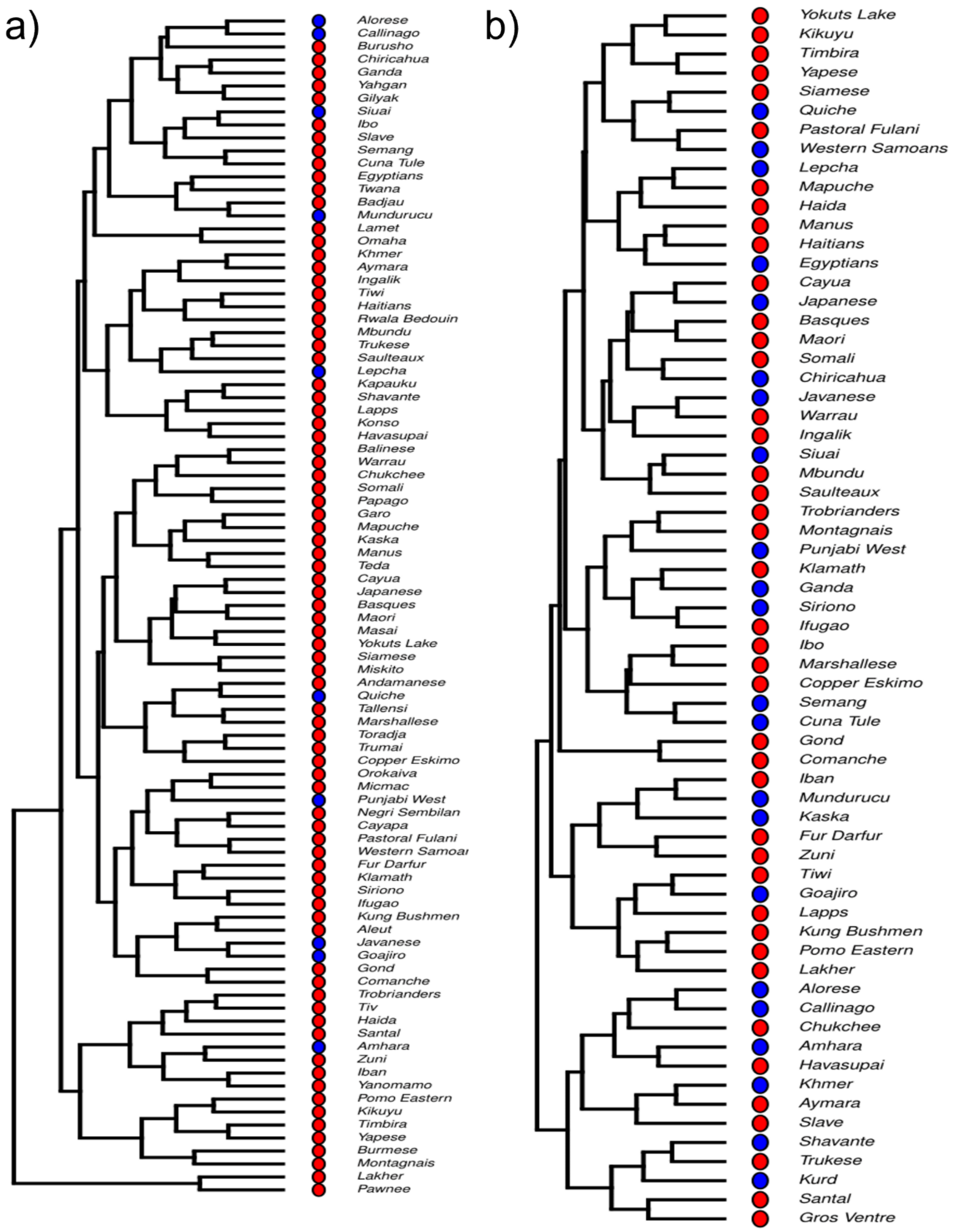

Figure 5.3. *Distribution of boys' (a) and girls' (b) RTP using spatial data. Branch lengths represent geographical distances between cultures.*

Phylogenetic Signal of Genetic and Linguistic Data

Table 5.3 shows the estimated D statistic, representing the amount of phylogenetic signal for boys and girls RTP using genetic and linguistic data. Results show that D was significantly different from the Brownian expectation (D = 0), but not significantly different from a random distribution (D = 1), for RTP for both genders. Therefore, the distribution of each trait is unlikely to be affected by the structure of the phylogeny. For the RTP of girls, the estimated D statistics was greater than 1, which tells us that the distribution of the trait is overdispersed to a greater degree than if the trait was distributed randomly. This means that shared cultural history is unlikely to contribute to variation in the presence or absence of RTP for both boys and girls.

Table 5.3. *Phylogenetic signal results for boys' and girls' RTP.*

Data	Variable	Frequency		Estimated D	Probability of E(D) resulting from no (random) phylogenetic structure	Probability of E(D) resulting from Brownian phylogenetic structure
		Absent	Present			
Genetic and linguistic	Boys RTP	10	76	0.810848	0.139	0.007*
	Girls RTP	22	39	1.05293	0.614	0*
Spatial	Boys RTP	10	81	0.4347214	0.061	0.24
	Girls RTP	22	42	1.282493	0.915	0*

Estimated D = phylogenetic D statistic, which measures phylogenetic signal in a binary trait. * indicates significance, p<.05.

Spatial Autocorrelation

Table 5.3 also shows the estimated D statistic, representing the amount of phylogenetic signal for boys and girls RTP using spatial data. Again, D was significantly different from the Brownian expectation (D = 0), but not significantly different from a random distribution (D = 1), for RTP for both genders. Therefore, the spatial position of the society is unlikely to contribute to variation in the presence or absence of RTP for both boys and girls.

Regression Models

Correlation Between Variables

As seen in Appendix H, most of the predictor variables were not correlated (p>.05), except for the ideology of male toughness and presence of food uncertainty, which were significantly positively correlated (r = 0.27, p = 0.0066). However, this is only a weak correlation, so both variables were still included in the boys RTP model. The presence of RTP for boys and girls was also significantly correlated (r = 0.61, p<.001).

The results of the models for girls show that none of the included predictor variables are likely to contribute to the presence or absence of girls RTP across societies (Table 5.4, models 1 and 2), as all of the 95% credible intervals crossed zero. This included marriage system, food uncertainty, age of girls at marriage, and descent system. The results of the models for boys also show that none of the included predictor variables are likely to contribute to the presence or absence of boys RTP across societies, as all of the 95% credible intervals crossed zero. As shown in Table 5.4 (models 3 and 4), this included marriage system, the presence of an ideology of male toughness, the presence of food uncertainty, and descent system.

Table 5.4. *Results of the phylogenetically informed regression models.*

Model	Parameter	Mean β	l-95% CI	u-95% CI	ESS
1 (Girls genetic and linguistic)	Phylogeny	0.9249	$8.126e^{-09}$	3.529	10095
	Intercept	4.0431	-3.4643	12.0128	4695
	Polygyny – Monogamous	0.1824	-3.8471	4.4660	4887
	Hunger – Food uncertainty	0.1568	-2.2643	2.6879	6165
	Age of girls at marriage	-0.1387	-0.6222	0.3277	5775
	Descent system – Other	-0.5188	-4.4306	3.0148	4277
	Descent system – Patrilineal	-1.6693	-5.7690	2.3605	4319
2 (Girls spatial)	Phylogeny	1.006	$1.444e^{-09}$	3.865	14970
	Intercept	4.39421	-3.64439	12.58667	13922
	Polygyny – Monogamous	0.01878	-4.00421	4.20638	13905
	Hunger – Food uncertainty	-0.05993	-2.63838	2.42491	14532
	Age of girls at marriage	-0.15974	-0.65845	0.32159	14074
	Descent system – Other	-0.63642	-4.37384	3.12443	13649
	Descent system – Patrilineal	-1.80409	-6.19758	2.15558	13722
3 (Boys genetic and linguistic)	Phylogeny	0.8093	$2.346e^{-09}$	3.153	4451
	Intercept	3.1422	-0.4500	7.0027	2087
	Polygyny – Monogamous	-0.5717	-2.9867	1.9681	3112
	Ideology of Male Toughness - Present	0.3995	-2.0611	2.8328	3194
	Hunger – Food uncertainty	-2.2368	-5.4749	0.7150	1368
	Descent system – Other	2.1519	-0.7140	5.1461	2931
	Descent system – Patrilineal	0.7648	-1.7585	3.3762	4620
4 (Boys spatial)	Phylogeny	0.8128	$1.138e^{-09}$	3.161	12195
	Intercept	3.2012	-0.2444	7.1395	8984
	Polygyny – Monogamous	-0.6756	-3.0312	1.7954	12186
	Ideology of Male Toughness - Present	0.4303	-2.1427	3.0217	12271
	Hunger – Food uncertainty	-2.3715	-5.6743	0.7430	6494
	Descent system – Other	2.1263	-0.7559	5.2233	11053
	Descent system – Patrilineal	0.7736	-1.7996	3.5023	13790

Intercept = a mathematical constant; Parameter = explanatory variables included in the model; Mean = mean value of the posterior distribution; 95% CIs = the true value of a parameter with a probability of 0.95, given the data; ESS = effective sample size, the information content of a sample MCMC chain.

Table 5.5 shows the heritability scores, which were low for all analyses. h^2 was 0.14 and 0.15 for girls (CI = [0.0002, 0.5228] and [0.0002, 0.5400]), and 0.13 for both boys' models (CI = [0.0002, 0.4904] and [0.0002, 0.4970]), although the wide credible intervals and plots (Appendix I) suggest that this estimate may be inaccurate. However, these low heritability values are in line with estimates of phylogenetic signal in the previous analyses.

R^2 values were low for all four models, with conditional R^2 values of 0.18, 0.19, 0.16 and 0.16 for the girls genetic and linguistic model, girls spatial model, boys genetic and linguistic model, and girls spatial model respectively. Similarly, AUC values were fairly low, ranging from 0.67 to 0.77, which indicates that the models have low predictive power. Results of the R^2 and AUC analyses can be found in Table 5.6 and 5.7.

Table 5.5. *h^2 values.*

Model	Estimate	2.5%ile	97.5%ile
Girls (genetic and linguistic)	0.1407087	0.0001922845	0.5228481203
Girls (spatial)	0.1507854	0.0002082527	0.5399554463
Boys (genetic and linguistic)	0.1288681	0.0001885849	0.4903648570
Boys (spatial)	0.1278137	0.0001666965	0.4969770996

Heritability (*h^2)* = describes how much of the variation in the dependent variables can be attributed to genetic variation; 95% CIs = represents the true value of the parameter with a probability of 0.95, given the data.

Table 5.6. *R^2 values.*

Model	Marginal R^2	Conditional R^2
Girls (genetic and linguistic)	0.001603108	0.1786797
Girls (spatial)	0.001711925	0.1913924
Boys (genetic and linguistic)	0.001669921	0.160109
Boys (spatial)	0.00167142	0.1607022

Marginal R^2 = proportion of total variance explained through the fixed effects; Conditional R^2 = the proportion of total variance explained through the fixed and random effects.

Table 5.7. *AUC values.*

Model	AUC
Girls (genetic and linguistic)	0.6691
Girls (spatial)	0.7353
Boys (genetic and linguistic)	0.7575
Boys (spatial)	0.7675

AUC = the probability that the model can correctly distinguish the outcome of the dependent variable.

Discussion

RTP is considered to be a near-universal behaviour across human societies, with a robust gender bias across Western societies, where boys engage in significantly more RTP compared to girls (Boulton, 1996). However, previous studies have suggested that this gender difference is not as consistent in subsistence societies around the world (Fry, 2005). Although large amounts of data on frequency or duration of play is not available for subsistence societies, I used ethnographies from the eHRAF database to code whether wrestling and/or chasing was present or absent for girls and boys across societies in the Standard Cross Cultural Sample. I found that boys in 76 of 86 (88.4%) cultures engaged consistently in RTP, compared to girls in only 39 of 61 cultures (63.9%). This suggests that engagement in RTP is more likely to persist in boys, even under different cultural circumstances, than it is for girls.

However, the gender differences in RTP across cultures where not as consistent as expected. When examining the components of RTP, this pattern becomes less consistent for chasing behaviour. Wrestling was present in 59 of 73 cultures (80.8%) for boys compared to 23 of 61 cultures (37.7%) for girls. This is in line with findings from industrialised societies, where boys are more likely to engage in wrestling than girls (Boulton, 1996). However, when focusing on the chasing component of RTP, there is evidence that boys and girls are equally likely to engage in chasing, with boys in 53 of 65 (81.5%) of cultures engaging in chasing and girls in 33 of 55 (60.0%) of cultures engaging in chasing. This was in line with the findings of Koustourakis et al. (2015), where Greek kindergarten teachers reported that although play which involves intense physical contact is exclusive to boys, girls and boys often engage in chasing games, and Maccoby (1988), who states that boys' RTP is more likely to involve rough body contact. However, Boulton (1996) reports that boys in UK schools engaged in significantly more chase initiation than girls, which suggests that boys may be more likely to initiate RTP, but girls are more likely to accept chase initiations than wrestling initiations.

Cultures across the world divide labour between the sexes in different ways, with some emphasising different, strict gender roles and others engaging in the same or similar work (Edwards et al., 2004). This is often reflected in the socialisation of boys and girls, who are likely to be assigned gender-specific tasks and occupy gender-specific spaces as a result of the gender division within their culture. This is an example of vertical cultural transmission, where parents make choices in the socialisation of children that will affect their behaviour (Hiller and Baudin, 2016). For example, children begin to identify with and imitate the behaviours of same-sex adults from the age of six (Draper, 1975), and girls may often be assigned chores at an earlier age than boys, resulting in less time for play (Boyette, 2016a). Therefore, gender differences in RTP are expected where societies have greater gender differences in adult roles, which are associated with cultural factors such as marriage and descent system and attitudes towards the opposite gender. However, analysis of the phylogenetic signal of RTP using genetic and linguistic data suggests that the shared history of cultures has very little effect on the distribution of gender differences in wrestling or chasing behaviours, or overall RTP. This finding is supported by the regression model analyses, where cultural factors such as marriage and descent system did not contribute to the presence or absence of RTP for boys or girls. Ideologies of male toughness did not contribute to RTP for boys, and the age at which girls get married did not contribute to the absence of RTP for girls.

Alternatively, I consider that RTP may be more affected by horizontal rather than vertical cultural transmission (Nunn et al., 2010), where juvenile RTP is under stronger influence from current neighbouring societies and the transfer of ideas from peer-to-peer (Lycett et al., 2013). Children may learn to engage in specific types of play according to the gendered adult role they are expected to fulfil (Lew-Levy et al., 2019), but this is likely to be reinforced by peers, as children have been shown to learn tasks, skills, and games from siblings and peers during play (Zarger, 2002). Children are more likely to imitate peers during play activities (Boyette, 2016b), and are more likely to imitate individuals who are similar to themselves, such as those of the same gender (Lew-Levy et al., 2018). Phylogenetic signal was also low when comparing societies with spatial distance data, which suggests the prevalence of horizontal transmission for RTP gendered norms is also unlikely. One explanation for this is that engagement in RTP may vary rapidly as a result of changes in the social environment, such as changing demographics within the play group and availability of play partners. For example, RTP can only occur when a sufficient number of suitable play partners are available, which may differ by age, gender, and the number of children available, as children are more likely to play in gender-segregated play groups when groups are larger (Lew-Levy et al., 2019). Depending on the age and sex of the children within a group or society, play may be altered, to contain more or less RTP for boys and/or girls. Changes to the social environment such as this may result in rapid changes in gender differences in RTP, which mask the effects of vertical and horizontal transmission in these analyses.

Similarly, it could be the case that an individual's given physical environment is more likely to affect changes in engagement in RTP, such as resource availability or suitable play spaces. Engagement in RTP is much more likely to occur when an individual feels secure and content (Flanders et al., 2013), so those societies which have plenty of resources may be more likely to feature RTP, for both boys and girls. However, according to the regression models, the presence of food uncertainty was unlikely to contribute to the absence of RTP for boys or girls. Therefore, I consider other environmental factors which may affect levels of RTP. Physical environmental factors involved in engagement in RTP may include conditions such as the terrain, built environment, and access to suitable play spaces (Berg and Medrich, 1980), particularly rough play which requires sufficient space in which to move around without restriction (Carlson, 2011). This may be particularly relevant to the gender differences found for wrestling and chasing, as boys are reported to play in a more active manner when more space is available (Fry, 2005), and tend to have more freedom of movement away from the home, in which they discover large enough spaces to interact freely and may pressure one another into what they consider masculine behaviour i.e. wrestling play due to the sex-segregated nature of play (Edwards et al., 2004). The physical environment is reported to dictate which types of play are possible, and requirements of the environment for play may differ by gender; boys tend to play outdoors in large groups where they have more opportunities for physically active play, whereas girls are more likely to play indoors in smaller groups, with less opportunity for active play (Fry, 2005).

However, the models presented in this chapter do have some limitations. Low phylogenetic signal may reflect the relationships between cultures having little effect on the presence of RTP for boys and girls, but it could also reflect the process of character displacement. This is a pattern of trait evolution where closely related societies diverge from one another in order to lessen resource competition by enhancing distinctiveness and increasing diversification (Pfennig and Pfennig, 2009). However, this was not reflected in the D statistic results for either the boys and girls models, as the results did not indicate less clustering than expected even by chance. Other limitations are due to the limited sample size as a result of missing data. For many societies, RTP was not mentioned within the ethnographies included in the eHRAF database ('eHRAF : HRAF collection of ethnography', 1996), particularly for girls, which resulted in only a limited number of societies being available for analysis. I suggest that ethnographies may be biased in favour of recording the RTP of boys, which could be investigated further by qualitative analysis. Furthermore, data on all predictor variables were not comprehensive, which further reduced the sample size in some cases, and resulted in the exclusion of some potentially predictive variables from the model, such as boys' age at marriage. Alternative predictive factors should be identified by further cross-cultural and qualitative analysis of RTP.

Conclusions

In summary, I found that RTP is typically more common for boys across cultures in the Standard Cross Cultural Sample, and that this gender difference is more pronounced for wrestling compared to chasing behaviours. Low phylogenetic signal when using both genetic and linguistic data and spatial data for the distribution of RTP for both boys and girls suggests that patterns of RTP are not associated with relationships between cultures, and therefore may be more contextual than culturally determined. For example, environmental changes or group demographics may be more relevant in determining levels of RTP for both boys and girls. Phylogenetically informed regression analyses of the effects of various cultural and contextual factors suggest that polygyny, descent system, and the presence of food uncertainty were not associated with the presence of RTP for boys and girls. Cultural ideology of male toughness was also unlikely to be associated with boys RTP, and age at marriage for girls was also unlikely to be associated with girls RTP. This suggests that either the effects of these variables are less than assumed, or that the data may have been biased or limited by sample size. I suggest that the data should be further analysed qualitatively to clarify the involvement of the chosen predictor variables on RTP for boys and girls, and/or identify and investigate further cultural and environmental factors which may influence the presence of RTP in childhood.

Chapter 6: A Cross-Cultural Analysis of Ethnographic Data on Gender Differences in Play Across Subsistence Societies

In Chapter 5, I found that although boys are more likely to engage in RTP, particularly wrestling, gender differences in RTP do vary across cultures. However, the exact patterns and underlying factors behind the variation in gender differences in RTP across cultures are not known, so it is important to examine the details of gender differences in play in detail. Here, rich description is helpful to contextualise previous quantitative analyses, as well as to ground hypothesis formulation and subsequent quantitative analyses. Therefore, I propose that a qualitative analysis of ethnographies describing the play of boys and girls could further identify the gendered patterns of play within subsistence societies, identify potential cultural and individual factors associated with gender differences in engagement in play, and assess potential functions of RTP within the context of culture and gender. Qualitative analyses are particularly suited to cross-cultural research, as they allow the researcher to preserve the context of the original research and take into account the complexity of the original data (Thomas and Harden, 2008). In the context of cross-cultural research, qualitative analyses are particularly useful as they allow the researcher to identify commonalities and differences across cultures throughout the process of identifying wider themes and patterns (Lew-Levy et al., 2018). The qualitative approach has the potential to identify potential factors and considerations that may not have been obvious from the previous literature or quantitative studies. The approach will also allow me to identify whether or how sociocultural influences either reinforce or constrain the gendered expression of possibly innate predispositions to engage in RTP. This can help us explore the ultimate and proximate causes of engagement in RTP, and consider why gender differences arise.

Furthermore, the qualitative approach to investigating gender differences in RTP may also allow for potential biases of the ethnographer to be taken into account. Ethnographic accounts are affected by a researcher's implicit political and social biases, which may be unavoidable throughout the process of fieldwork as an unsystematised process (Harrell, 2006). Ethnography is not a fixed qualitative method, but varies in length of contact with the population, methodology (including a mix of participant observation, open ended interviews, and study of documents), level of immersion within the culture, and treatment of informants (Hammersley, 2006). Furthermore, the theoretical, political, and professional interests of the ethnographer are likely to influence practice in the field and the subsequent analysis of collected data (Scheper-Hughes, 1983). In particular, androcentrism in anthropology has resulted in inaccuracies, omissions, and distortions of women's behaviour within ethnography, but the resulting feminist literature has also been criticised as containing false expectations about the commonalities of the female experience (Scheper-Hughes, 1983). Therefore, in the discussion I consider the potential biases of the ethnographers, and how this could affect the texts and our analysis.

To summarise, in this chapter I use qualitative analysis to examine ethnographies with regards to play in the context of gender and wider societal and cultural norms. I aim to establish the ways in which boys and girls play in each society, and whether gender differences are consistent within and between societies, or change based on culture or changes to the environment. The analysis will focus on examining the potential functions of play, particularly RTP, and how norms in the expression of RTP for boys and girls are transmitted between individuals and cultures. I also consider how the behaviour is balanced with other activities such as subsistence or domestic responsibilities, or other avenues of learning or development. Contextual factors which affect play will be examined with regards to how they may promote or constrain RTP for boys and girls. Qualitative analysis of ethnographies will allow for inferences to be made not only about the distribution of and functions of play, but also the potential biases of those recording the behaviours.

Overall, this chapter aims to:

i) Identify gendered patterns of play within subsistence societies, such as differing behaviours for boys and girls,
ii) Explore potential functions of RTP, and how they relate to gender differences in childhood play and gendered adult social roles,
iii) Identify cultural factors associated with gender differences in engagement in play for boys and girls, and how gendered norms around play are transmitted,
iv) Explore contextual factors that may affect rates of play throughout childhood, including changes in the physical and social environment, and
v) Examine biases of ethnographers and time periods in order to further understand reported gender differences in play within context of the selected texts.

Methods

Data

A subset of ethnographies from the eHRAF database which contain sections relevant to juvenile play were chosen for qualitative analysis. These cultures were selected for further analysis as they were identified as containing substantial amounts of relevant information on play for boys and girls. The geographical location of each culture can be seen in Figure 6.1. The Hopi, O’odham, and Chiricahua cultures are relatively close geographically, which may affect comparisons between these cultures. Relevant documents were identified by using the browse subjects function on the eHRAF database, selecting documents which were tagged as containing information on ‘play of children’, within ‘childhood activities [857]’. This results in a list of 79 documents, which were screened to select documents with the most relevant information, and exclude those without enough detail. A final list of ethnographies and the relevant section which will be included can be seen in Table 6.1.

Table 6.1. *List of ethnographies and relevant sections which are included in the narrative synthesis.*

Culture	**Location**	**Ethnography**	**Section(s)**	**Author**	**Year of Publication**	**Time Frame**
Fellahin	Egypt	Growing up in an Egyptian village: Silwa, Province of Aswan	Chapter Seven: Description and Analysis of Children’s Play and Games	Ammār, Ḥāmid	1954	1900-1954
Central Thai	Thailand	Children's play and games in rural Thailand: a study in enculturation and socialization	Part II	Anderson, Wanni Wibulswasdi	1973	1969-1970
Hopi	US	The Hopi Child	Chapter III: Hotavila Child Care Chapter VI: Behaviour of Young Children	Dennis, Wayne	1940	1937-1938
San	Namibia, Botswana	Kalahari hunter-gatherers : studies of the !Kung San and their neighbors	Social and economic constraints on child life among the !Kung	Draper, Patricia	1976	1969-1971
San	Botswana	Technological change and child behavior among the !Kung	Technological Change And Child Behavior Among The !kung	Draper, Patricia Cashdan, Elizabeth	1988	1968-1969
Gros Ventre	US, Canada	The Gros Ventres of Montana: Part 1, Social Life	Chapter VIII Childhood: Play	Flannery, Regina	1953	1835-1885
O’odham	US	The desert people: a study of the Papago Indians	Chapter IX: The Child From Five to Ten, Play Activities	Joseph, Alice	1949	1942-1943
Manus	Papua New Guinea	Growing up in New Guinea: a comparative study of primitive education	VII: The Child’s World	Mead, Margaret	1930	1928-1929
Eastern Apache	US, Mexico	An Apache life-way: the economic, social, and religious institutions of the Chiricahua Indians	Play	Opler, Morris Edward	1941	1840-1886

Figure 6.1. *World map showing location of cultures included in the cross-cultural qualitative analysis.*

Qualitative Analysis

I undertook qualitative analysis of the data, seeking common themes within and between the texts. As ethnographies vary in context, setting, and time period, as well as in researcher and methodology, I was mindful of the varying study characteristics, context, and quality of findings, aiming to discuss such factors in a clear and systematic manner. Qualitative analysis is particularly useful for studies of play, where researchers are likely to record different levels of detail in a wide range of settings, as it allows for the consideration of multiple potential biases within the data.

The relevant ethnography chapters were read in detail, and sections of text labelled and assessed based on the content and context of play, or factors which prevent play from occurring. The focus was on identifying common topics and factors which were associated with play, such as which activities children chose to engage in, how play related to gendered adult roles, how other responsibilities and expectations prevented engagement in play or RTP, how play groups were constructed and organised, and the settings in which play was common or permitted. Attention was also given to changes in play over time, according to time period or season. The process was iterative, where topics that were identified throughout the process were then assessed in all ethnographies. The aim was to summarise gender differences in play for each culture, and then to identify from the above themes where similarities and differences were apparent, and the underlying reasons for this variation. Finally, I assessed the methodology and potential sources of bias within each ethnography, focusing on factors such as gender bias and time period of the ethnography.

Results

Summary of Cultures: Descriptions of Play and Gender Differences

Fellahin:

Growing up in an Egyptian Village: Silwa, Province of Aswan (Chapter Seven: Description and Analysis of Children's Play and Games)

This ethnography focused on the village of Silwa in Egypt, between the years 1900 and 1953. The author, Ḥāmid Ammār, pointed out that childhood was very much associated with play in Silwa, with children spending up to an hour in play each day, peaking at eight to nine years of age. However, time spent in play was reduced by the introduction of irrigation, as children, especially boys, have more responsibilities which takes time away from play. Play groups were described as mixed gender, particularly where older children, usually girls rather than boys, are expected to supervise and care for their younger siblings. However, the most common form of play took place within organised games, which are often segregated by gender. The author did note that children would, on rare occasion, engage in gendered constructive or imaginative play (e.g. boys imitating animals, and girls constructing pots and jars).

Ammār described a list of organised games in great detail, most of which were exclusive to boys. Many of those games included some form of RTP, including wrestling and chasing. He described the boys' games as aggressive in nature, requiring 'exertion and brute strength', and attributes this to boys attempting to imitate their fathers. He went on to note that adults within this culture considered boys' rough play as a test for hardihood and endurance, and further stated that boys were clearly developing motor skills, balance and co-ordination through participation in their games. However, Ammār also suggested that the rough play of boys may have been a method of 'letting off steam' in their resentment of having to move into the adult world.

In contrast, the girls' games were described as mostly sedentary. Ammār suggested that this was due to girls focusing on the imitation of adult women's tasks through play, such as the imitation of spinning cotton or wool, or the use of straw figures to act out ceremonies such as marriage or other social meetings. However, girls were also described as playing games similar to marbles, or imitation or guessing games, which were also played by boys and did have some physical components (e.g. squeezing fingers to register guesses). Ammār did note that the marble games played by girls did require skill and co-ordination, which I suggest could fulfil a similar purpose of skill development to the RTP of the boys' games, such as in the development of fine motor control for activities such as crafting or spinning in adulthood. He described girls' play as compatible with the 'female ethos' of the community, and reflected that these social pressures are apparent much earlier for girls rather than boys.

Central Thai:

Children's play and games in rural Thailand: a study in enculturation and socialization (Part II)

This ethnography focused on children's play and games in the rural village of Ban Klang in Thailand, between the years 1969 and 1970. Anderson described play as a prominent feature of the lives of children from around the age of one year old, with children spending most of their waking hours in play until they had to attend school. The ethnography described children engaging in a wide repertoire of play activities, engagement in which depended on factors such as the setting, season, tides, time available to play, consideration of adult needs, availability of play equipment, and the number of children available to play. Many of the play activities children engaged in were traditional games which had been played by their parents and grandparents, but had sometimes been modified to suit current cultural norms and environmental conditions. Children also played some new games which have been introduced through contact with other cultures. Children below the age of six tended to play alone or in groups of two or three, but began to be accepted into larger games in mixed age and gender groups once they were around five years old. Play groups at home consisted of siblings, cousins, and relatives of both genders, ranging in age from around six to fifteen years. However, at school, which starts at around age seven, children were more likely to play in same-gender groups. Girls were more likely to stick to playmates within their age group when at school, whereas boys tended to play more active games such as policemen and robbers, which require more playmates and therefore incorporate wider age gaps. When at school, play was restricted to before school and during recess, whereas on vacations and weekend, children were free to play almost all day. Children continued to play both at home and at school until around the age of 16, although the withdrawal from play was often gradual and a result of the increase of adult responsibilities.

Anderson described the games of the Central Thai children as involving motor-sensory skill, strategy, chance, mimicry, and/or ‘vertigo’. There was a large focus on strategy, and the author suggested that the game category of ‘physical skill’ does not seem appropriate for Ban Klang games. The focus instead seemed to be on developing nimbleness and agility. Elements of RTP are apparent in the games described, such as tug of war (see games such as ‘long is the rice grain’), chasing (e.g. ‘store the pork oil’), and wrestling (e.g. ‘robbers’), particularly during spatially unrestricted games, and the author described certain games as requiring physical skills such as alertness, quick reactions, and speed in running. Some games even included imitation of warfare, such as in ‘riders and horses’ or ‘riders and elephants’. However, the RTP elements seem to be secondary to the role-playing elements of games (see games such as ‘daughter abduction’), and children seemed to prefer working together in strategy, rather than using individual strength or skill to win games. Furthermore, boys and girls over the age of 11 were forbidden from touching each other, which often lead to the exclusion of players after a certain age, or modifications to games to avoid touching and therefore RTP.

Some of the rougher games were specific to boys only, such as combat on ‘horseback’ or ‘elephantback’, where boys would ride piggyback on older players and imitate warriors. This game was described by Anderson as a release of aggressive impulses, and Anderson stated that the game did not appeal to girls because it was too rough, and girls would not ride on the back of another child. However, it was not only the rougher games which were restricted to boys. Games such as ‘stone balls’, ‘rolling coins’ or ‘shoot the pile’, where players must hit targets with marbles, coins, or rubber bands, were also played by only boys, although the reasons for gender segregation in these games are not clear.

Other games were exclusive to girls, such as ‘jump rope’ and ‘step in front’ (a chasing game played in pairs). Most of the spatially restricted games were played mostly or exclusively by girls, which was attributed to their quiet and inactive nature being more appropriate. Some games were considered girls' games but would occasionally also be played by boys. 'Playing house' started as appropriate for boys and girls, but boys tended to stop playing in this manner once they started school. Most of the games that were exclusive to girls seemed to focus on small movements, particularly for younger children, which I suggest may be associated with the development of fine motor control. The spatially restricted games that were for both sexes seemed to involve larger movement, such as jumping and running, or were more competitive and strategic, such as games of dice or cards.

Children also played unorganised games, which ranged from subdued to the more boisterous. The most physically vigorous games involved joining hands and spinning in circles to induce dizziness, joining hands to create arches which other children run under, or joining legs and hopping about. Other play activities included racquets and kites, or other homemade play equipment involving objects such as discarded ropes or coconut shells. Girls were described as more inclined to play quietly and engage in more artistic pursuits such as paper folding. Toddlers and young children would imitate fishing activities, either through using make-shift nets or pretending to be boats. Imitation extended to playing at being students, or at being adults through shooting at targets with home-made toy guns, and the imitation of adult rituals and ceremonies. Pre-school children would imitate their mothers, pretending to cook, which extended into playing at running a restaurant when there are more available playmates. In this scenario, the girls were cooks and boys or smaller children were customers.

Hopi:

The Hopi Child (Chapter III: Hotavila Child Care and Chapter VI: Behaviour of Young Children)

This ethnography focused on Hopi life in the village of Hotavila in the United States, in the years 1937 and 1938. For the Hopi, children were expected to play only once work is done, which began as light duties in childhood and increased with age. Boys usually had less responsibilities, and therefore had more time to play, with younger boys spending almost the full day playing. Girls were expected to stop playing completely at around ten to twelve years of age, whereas boys were able to continue playing together throughout adolescence. Girls and boys seldom played together, with the exception of young boys who were in the care of their elder sisters.

Boys' playgroups were often split by age, as older boys' play was restricted to late afternoons and evenings after their responsibilities had been fulfilled. This also served the purpose of grouping boys by skill and strength, ensuring that games remained fair. Organised games for boys included shinny (a team game where balls are shot into goals), spinning tops, stick throwing, the snake game (children line up and imitate the movement of a snake), archery, dart throwing, dice, hidden object games, and 'playing witch' (a boy beating a drum must run and hide, chased by pursuers). The unorganised play of boys often consisted of imitation, either of men’s work (e.g. building miniature corrals and using peach seeds to represent sheep, or imitating rabbit hunts by throwing sticks at tin cans), or the imitation of horses, where one boy would use ropes and tin cans to pretend to be a horse, and another boy would follow him around or straddle him, whipping him with a weed or twig. Boys would also imitate American tourists or missionaries, but would never imitate women’s activities such as grinding corn. Newer games which were appropriate for boys included rolling tires or hoops. In the past, boys played war games, where boys would throw rocks at each other and wrestle. However, at the time of the ethnography, war games were no longer played as they were deemed to be too dangerous.

Girls also participated in organised games, including shinny, spinning tops, grinding parties, the snake game, hidden object games, alalatami (which involves singing, tug of war, and imitation of rabbits), breaking the piki stone (sand painting and guessing games), and the pursuit game (where girls chase each other to a centre point, sticking to a twisting path). Although there was some overlap here with the boys’ games, girls and boys would never play these games together, but instead in separate groups. Other games that girls played included imitating adult life and household duties, such as pottery making, grinding grain, or powdering pigments. Girls did have dolls, but did not play with them much and would easily discard them.

San:

Kalahari hunter-gatherers: studies of the !Kung San and their neighbors (Social and economic constraints on child life among the !Kung)

This ethnography focused on the children of the !Kung San between the years 1969 to 1971. The San were located in Namibia and Botswana, and had the predominant subsistence style of hunting and gathering. San children were described as having large amount of free time in which to play, due to a lack of involvement in both subsistence activities and childcare duties. Because of this, children were free to play as much as they liked, until around the age of 14 for girls and 16 for boys. Play groups were described as typically of mixed age and gender, as villages were small, and therefore peers of matched age and gender were usually unavailable. Draper commented that the limited number of playmates and the subsequent restriction to mixed gender and age play groups placed constraints on the games that children could play, and resulted in a lack of competitiveness due to the unlikely probability of a child being evenly matched with an opponent. The only game that was described in detail is ‘zeni’, which was a game of skill where a pebble or nut is attached to a feather and thrown around without being allowed to touch the ground. It seems that children played quite actively, but this rarely manifested in RTP.

Technological change and child behavior among the !Kung

The second ethnography regarding the !Kung San regards the years 1968 and 1969, and focused on the changes that new subsistence styles had on children's lives and behaviours. Draper compared two groups of !Kung San people; one which remained nomadic, and another which had become sedentary. In the sedentary camp, children were expected to engage in economic and subsistence activities to a greater degree, which involved herding for boys and smaller errands for girls, such as fetching water or processing food.

With regards to RTP, Draper reported figures for both the nomadic and sedentary groups. In the nomadic group, boys and girls engaged in RTP at equal rates, engaging in roughly 0.4 minutes of RTP per 10 minute observation period. Although not a statistically significant difference, boys in the sedentary group engaged in more RTP than girls, with boys spending 0.58 minutes per 10 minute observation period in RTP, compared to the girls' 0.18 minutes. Draper suggested that RTP was supressed for girls in the sedentary camp, as adults would discourage RTP due to closer proximity with younger children and adults, compared to boys who spent less time within the camp's boundaries. Boys were also more likely to work with other boys who were closer in age to themselves, which suggests RTP would be more likely to take place as boys were more evenly matched. Draper predicted that gender differences in RTP would increase in the sedentary camp as child work became more regular and institutionalised, as girls would become increasingly expected to care for younger children compared to boys.

Gros Ventre:

The Gros Ventres of Montana: Part 1, Social Life (Chapter VIII Childhood: Play)

The Gros Ventre culture is based in the US and Canada, and was studied in this ethnography between the years 1835 and 1885. The children of the Gros Ventre engaged in many forms of play, although the extent to which they played is largely attributed by the author to individual differences such as the strictness of their caretaker and the amount of formal training the child was engaged in, rather than group differences. Boys were given much more freedom than girls, which often resulted in more time spent in play. Girls were expected to stop playing at the onset of adolescence, whereas boys were allowed to play until adulthood.

Boys and girls sometimes played together, particularly during imaginary play such as playing 'house' or 'married folk'. Here, boys and girls imitated the daily routine of gendered adult life, including cooking for the girls and hunting for the boys. They also enacted mock battles, followed by mock funeral ceremonies. Boys and girls would often play in parallel, where they played in separate gender-segregated groups while engaging in the same activities, such as swimming or racing. Boys would sometimes interrupt and attempt to break up girls' play, but girls would never interfere with boys' play.

Games exclusive to boys mostly involved shooting arrows, which was considered training for adulthood, where men were expected to hunt and engage in warfare. Boys were also reported to play hoop and pole games, which seem to require skill and co-ordination, and were not common games for girls. Girls engaged in a range of play, including imitative play (with dolls to imitate childcare, sticks to imitate camp life, and recreation rituals observed in adult life) and games which contained a significant component of active or rough play. These games were described as including walking on stilts, swinging from ropes, and pinching, jumping on each other, wrestling, carrying each other, and vigorous tickling. They also played ball games, which involved hitting each other and chasing.

O'odham:

The desert people: a study of the Papago Indians (Part II: Growing Up On the Desert)

The O'odham are based in the US and were studied by Alice Joseph in 1942 and 1943. The time spent in play rapidly decreased for the children of the O'odham from around the age of five to ten years, where children were expected to help with subsistence activities. Girls tended to start work earlier and to a greater degree than boys. Within the household, sibling and cousins of opposite genders were allowed to play together, but this rarely happened outside, where playgroups were always segregated by gender, except for young girls' who were supervising younger siblings. Siblings of the opposite gender could play freely together, but this was rare. Girls had to play within the settlement under supervision of adults, whereas boys were free to roam the village and fields.

Children would often engage in object or imitative play, although this was often themed by gender. In the past, boys would play at racing and kickball, but traditional games had gone out of favour at the time the ethnography was written. At the time of writing, boys would play jackstones, or engage in imitative play, imitating fiesta dances or cowboys. At school, younger boys would play marbles, chase and wrestle with each other, and play on swings and slides. In adolescence, boys who had not yet dropped out of school (which usually happens at around 13 to 15 years of age) would occasionally throw around a basketball or have a game of marbles, but would no longer wrestle together as they did when young. Girls would also play games such as jacks or marbles, and would engage to some extent with playground equipment, such as the swings. Imitative play for girls involved playing with ragdolls or playing house. However, girls often preferred walking around the playground, talking, listening to records, reading magazines, or observing adults.

Manus:

Growing up in New Guinea: a comparative study of primitive education (Part One: Growing up in Manus Society)

Margaret Mead studied the Manus in Papua New Guinea, with this ethnography focusing on the years 1928 and 1929. In the Manus culture, children were almost entirely free of household tasks or other work, and were free to spend most of their time playing. Children were expected to gain as much physical proficiency as possible, as until they were skilled in navigating the waters they were not safe anywhere within the village. Play was viewed by adults as essential for developing the physical skills necessary for life in Manus, and was therefore never interrupted or stopped unless the child was directly in danger. Therefore, childhood was exceptionally playful, with children described as spending over half their waking hours in play. The playgroup, which was never to any degree segregated by age or gender, consisted of girls from the age of 4 to 14, and boys from the age of around 5 to 20 years of age. Playgroups were likely to consist of children who were similar in personality and social standing; for example, one group would be full of more aggressive, noisier children, whereas another would consist of quieter children. Younger children tended to play in smaller groups, in pairs or trios, but playgroups would often get larger and more varied with age.

Children in Manus were not expected to engage in specific types of play based on either age or gender. The play was described as ‘the most matter of fact, rough and tumble, non-imaginative activity imaginable’. The eldest boys in the playgroup, usually around 14-15 years of age, would organise play, usually consisting of swimming and boating, racing in canoes, pelting each other with seaweed, wrestling, tug of war, sailing toy boats, creating and distorting figures and shadows, and playing football. Imitative and pretend play was extremely rare, only observed on a handful of occasions, and attributed to the fact that children have much contempt for adult life; the only play activity that imitates adult life was spear fishing, which was predominantly a boys’ activity. The only type of play that was exclusive to boys was playing at war, where boys would playfully imitate spear throwing and dodging.

Eastern Apache:

An Apache life-way: the economic, social, and religious institutions of the Chiricahua Indians

The oldest ethnography reviewed is based on the years 1840 to 1886, and focused on the Eastern Apache of the US and New Mexico. Children were instructed in the gendered division of labour early, and were taught specific rules during play such as not to steal, to be kind to others, and not to laugh at others. Fighting was discouraged among children, an expectation that was particularly placed on girls as they were regarded as weaker than boys. Both boys and girls were expected to be strong and vigorous, although this was an expectation particularly placed on boys, who began hard physical training in order to be warriors at around 10 years of age, whereas girls began to be trained in household tasks. Time spent in play was reported as diminishing as children were given these responsibilities, which increased throughout adolescence until the child had fully assumed their adult duties.

Eastern Apache children played in both mixed and single gender playgroups, although children were instructed to be reserved with their siblings of the opposite gender. From the age of approximately 14 years, boys were forbidden from playing with their sisters. Much of the play of the Eastern Apache focused on exploiting resources within the environment. Children would gather delicacies such as cherries or cacti fruit, eating them or making beads to play with, or would chase birds and butterflies. Children also enjoyed swimming, imitating ceremonial practices or adult occupations, or playing house. Children were described as playing games of chance and ball games, but it is unclear if this took place in mixed or same-gender groups.

Certain play activities were also exclusive to boys or girls. Only girls would fashion dolls from grass and cherries, playing at mothering the doll and re-enacting scenes from village life. They would also braid wild plants and play at carrying water jars or other objects which were given to them by parents. Play that was exclusive to boys focused on mock hunts and battles, in preparation for hunting as adult men. This involved playing with bows and arrows, or using branches to whip pellets of mud, where boys would aim at birds. From around six years of age, boys stopped playing games that were considered appropriate for girls, and instead joined older boys and men in hunts for small birds and mammals. Boys also played arrow games in order to build skill with bows and arrows, and participated in mock battles. These were seen as masculine pursuits and were encouraged by adults in the village for boys to develop physical strength and display their bravery.

Rough and Tumble Play

Although RTP is present in all the cultures examined here, it seems to be more prevalent in some cultures compared to others. RTP is described in great detail for the Manus and Gros Ventre children, where both boys and girls routinely engage in RTP. Mead described the play of Manus children as rough and tumble without incorporating imaginative play at all, including swimming, racing, wrestling, and tug of war for both boys and girls. There is much emphasis on physical development during play for boys and girls, in order to learn the skills necessary to navigate the village. Similarly, for the Gros Ventre, RTP is a large component of play for both boys and girls, consisting of elements such as jumping on and carrying each other, wrestling, and tickling. However, both cultures do have forms of RTP that are exclusive to boys, mostly in the form of mock battles, where Manus boys learn to throw spears and Gros Ventre boys learn to shoot bows and arrows. This suggests that RTP can also be used as training for warfare, which tends to be male-exclusive, in addition to its general physical and cognitive development functions which are beneficial to both boys and girls. It is possible that gender differences in RTP, where girls engage in RTP but not to the same extent as boys, are driven by this essential preparation for warfare in cultures where war and aggressive competition is common for men.

On the other hand, children in some cultures were described as engaging in very little RTP. For the San, RTP was described as rare, with children described as spending around 0.4 minutes in RTP per 10 minute observation period, and there were no statistically significant gender differences in time spent in RTP. However, when comparing the nomadic and sedentary groups, boys were more likely to engage in RTP in the sedentary group compared to sedentary girls, which was attributed to boys spending less time in the presence of adults and girls spending more time in the camp, where RTP is discouraged by adults. For the Hopi and Eastern Apache, RTP is not described as a significant component of play. Hopi boys are described as having engaged in mock warfare in the past, which incorporated wrestling as well as throwing stones, but was later forbidden as it was too dangerous. This suggests that norms surrounding RTP can change over time within a culture, sometimes very rapidly.

Play and Adult Roles

The role of play and training often seems to be centred around abilities that are needed in adulthood. For the Gros Ventre, Flannery stated that adults saw play as training for adult life, preparing girls for marriage and boys for hunting duties. Similarly, the play of the Eastern Apache children was described as preparation for adult life, especially for boys. Before beginning physical training to be warriors at around 10 years of age, boys were encouraged by adults to play at mock hunts and mock battles, which were described as ‘masculine’ pursuits by the community. Boys were given bows and arrows to play with, to shoot at birds and small mammals, or play arrow games, and the skills learned during such games would be used during hunting as adults. This suggests that play contributes to preparing children for their adult duties, which may be gendered, and therefore affects the play activities which boys and girls are encouraged to engage in.

Another example of this is apparent in the Central Thai culture, where play has changed as adult roles changed over time. When adult gender roles and the sexual division of labour were stricter, this was reflected in children’s games, where boys played more competitive and physical games, or gambling games with stakes, and girls played games of manual skill and precision. Where girls did play physical games, they were less active than boys’ games. However, as time passed, girls became more likely to play active games that used to be exclusively played by boys. Anderson attributes this to the change from fish-sauce production to tugboat transport businesses, where the women's role changed from domestic duties to becoming her husband's work assistant. Women began to play a more active part in economic life, and some men began to contribute to childcare. At the time of the ethnography, boys and girls were more likely to play in mixed groups, and define fewer games as exclusive to one gender. This provides evidence that play will reflect adult roles, and norms surrounding play and gender can change over time.

Work Responsibilities According to Gender and Age

The duties that girls and boys were given tended to be divided by gender, and often reflected gendered adult responsibilities. Often, girls' responsibilities centred around household tasks, and boys' responsibilities centred around hunting, trapping, or farming. In the Eastern Apache and Central Thai cultures, the sexual division of labour is explained to children early in life, and they are instructed to observe and imitate older relatives of the same gender. Boys would watch men make bows and arrows (Eastern Apache) or crab traps (Central Thai), and girls would watch women gather food and cook. O'odham girls were expected to become proficient in household tasks to become suitable marriage candidates, which included duties such as sweeping, washing dishes, setting the table, cooking, and laundry. As girls got older, they were often expected to help with harvesting. Gros Ventre girls were taught to gather roots and berries, slice meat for drying, and tan hides, whereas boys were trained to trap and hunt, often playfully through the use of bows and arrows. Hopi girls were given household and childcare duties, and boys were expected to hunt and care for animals. Therefore, it is apparent that a gendered division of labour is often prevalent at young ages, and this can affect factors such as the location of play and the constraints placed on children's time.

Furthermore, in most of the cultures examined, girls were expected to engage in domestic tasks at an earlier age than boys. O'odham girls were expected to provide childcare, run small errands, collect wood and water, and carry out small household chores from around 5 to 10 years, at which time, boys have almost complete freedom, other than small errands. At around 10 years, some boys start to engage in a small share of farm work with their older male relatives, a responsibility which increases with age. In the Manus culture, although children are almost completely free of responsibilities, girls are expected to engage in some household tasks from around 11 years, whereas boys do almost no work until they are married at around 20 years. This shift in responsibilities tends to follow a girl getting engaged, after which she was expected to be at home and available to carry out household tasks such as gathering firewood, fetching water, or stringing beads. Even for the

Central Thai, whose children were rarely expected to engage in domestic or subsistence responsibilities, when tasks were given, they were most often assigned to girls rather than boys.

However, in other cultures children were expected to engage in responsibilities from the same age. For the Hopi, boys and girls were both given duties from around 4 or 5 years, although these are gender-specific, and boys' duties are much lighter. Similarly, the Gros Ventre expected both boys and girls to engage in some responsibilities from around 7 years, although girls' training for adult responsibilities is much more formal and rigorous. Therefore, the intensity of tasks given may also affect rates of RTP, as higher intensity tasks are more likely to prevent engagement in RTP than lighter duties.

The subsistence style of a culture may affect the level of responsibility that children are given. For the !Kung San, children were not expected to engage in economic and subsistence activities until around the age of 14 for girls, and 16 for boys. However, in the sedentary group, children were beginning to receive more requests from adults to engage in tasks, although they were often disobeyed. Draper suggested that children were increasingly expected to engage in tasks over time, as the group increasingly became sedentary and child work became institutionalised. She predicted that the effects would be greater for girls, who spend more time in the camp and around adults, and are therefore more available to be requested to work. This had direct effects on RTP, as girls' RTP was shown to be reduced in the sedentary camp, whereas boys' RTP increased as they spent more time away from adults due to herding responsibilities.

There were some mentions of children engaging in tasks which were usually associated with the opposite gender, although they were rare. At younger ages, boys may be more willing to engage in tasks that are typically given to girls or women. Eastern Apache boys were expected to collect wood and water when they were young, but they quickly become aware this is women's work and are then reluctant to help due to teasing from other boys. Similarly, O'odham boys were expected to help with small errand at young ages, but this soon transitioned into participating in men's work. Gros Ventre girls were taught how to skin and butcher animals, even though this is mainly considered a man's task. This shows that gendered expectations are often prevalent and do have large effects on behaviour, but are not always strict, especially for younger children.

Childcare Responsibilities

The most common gender-specific task was childcare, or babysitting, which fell almost entirely on girls, particularly for the Eastern Apache where childcare was one of the earliest responsibilities given to girls. The age at which children can be left in the care of elder siblings varied by culture, ranging from 6 months for the Hopi, up to 3 to 5 years for the Fellahin. Usually, the responsibility fell on older sisters, although for the Hopi and O’odham, boys would be required to look after younger children if there were no girls in the family. The effects this had on play differed by culture. For the O’odham, childcare duties were described as restricting the play that girls could engage in, as it kept them in closer proximity to the household and adults. For the Fellahin and Central Thai, children were given responsibility for younger siblings, but younger children were fairly independent, and would play together nearby, often imitating the play of the older children. For the Hopi, girls were expected not to play if they were caring for an infant, but were allowed to play if the younger child was old enough to be part of their playgroup.

However, in some of the cultures examined, no childcare responsibilities were given to children of either gender. The San and Manus cultures did not expect children to care for their younger siblings. In the Manus culture, they reasoned that if older children had to take care of younger children, this would disrupt their play, which was seen as unacceptable, as intrusions on children’s leisure must be avoided. Childcare was instead dependent mostly on the father, so that younger children were not interrupting the play of their elder siblings. The contrast between the Manus society and others demonstrates that childcare responsibilities may be used to restrict play, and that development as a result of play may be different in cultures where elder siblings, particularly sisters, are expected to provide childcare.

Composition of Play Groups

The extent to which play was segregated by gender differed by culture. Mixed gender play was common for the San, Manus, and Central Thai societies. For the San and Manus cultures, mixed gender play was necessary due to the smaller groups, and lack of same-gender playmates. For both of these cultures, play could become segregated by gender; for the San, this was associated with boys being given herding tasks that take them away from the village, where there are no girls to play with, and for the Manus, this was associated with girls ceasing to play at younger ages, so there were no girls of a suitable age to play with older boys. For the Central Thai culture, play at home was always mixed age and gender, although this was not seen as acceptable when playing at school. For the Eastern Apache, mixed gender play was common and acceptable for younger children, but boys began to stop playing with girls at around 6 to 7 years, and mixed gender play is completely forbidden once boys reach 14 to 15. This provides evidence that parental control over reproduction acts as a constraint on engagement in RTP.

In contrast, the play of Hopi and O’odham children was nearly exclusively segregated by gender. Exceptions to this included older Hopi girls having to care for very young children, or siblings playing together for the O’odham, although this was rare and only occurred when play took place within the household. This did not seem to be driven by engagement in different play activities according to gender, as Hopi children would play the same games in gender segregated groups. Therefore, gender segregation did not necessarily lead to greater gender differences in RTP.

Gros Ventre children did not seem to fit either pattern, as they seem to equally engage in both mixed and single-gender play. Mixed play groups were necessary for children to play house, with boys and girls acting out their assigned adult social roles. Both genders would also play in parallel for activities such as swimming, with only little interaction between the two groups. Boys would often interfere with girls' play, but girls would not attempt to interfere with boys. Sometimes boys would engage in girls' games, such as imitating horses for girls to ride (by following behind them). Overall, it seems that the expectations of adults drive gender segregation in play, as gender segregation seems to occur according to adult sanctions, rather than the activities in which children engage.

One of the proposed reasons for gender segregation in play is due to the different play styles of boys and girls, where boys are expected to play in a more vigorous and rough manner, resulting in boys and girls playing with same-gender peers in different, suitable spaces (Pellegrini, 2002). This may be a result of underlying or innate preferences of each gender leading to self-selection of appropriate play spaces (Pellegrini, 2009), or may be a result of impositions placed on each gender where adults limit the spaces and activities which are appropriate for boys and girl, although there is little evidence for this in Western societies (Maccoby and Jacklin, 1987). However, in the ethnographies I examined, gender-segregated play often seemed to be driven by adult expectations, and the expectation that girls should stop playing earlier than boys. The extent to which gender segregation in play appears has been shown to differ by culture, and same-gender play partner preferences may be stronger for boys (Fouts, Hallam and Purandare, 2013). Lew-Levy et al. (2019) found that children in larger groups are more likely to play in gender-segregated groups, which is likely to be due to a greater availability of same-gender play partners, which seems to be supported by the ethnographies examined here.

Context and Setting of Play

Suitable settings for play seemed to differ by culture, and may also differ within cultures depending on the type of play. One of the most common restrictions placed on play was that it should take place outdoors. For the Fellahin, indoor play will be met with scolding and punishment. This was particularly true for active types of play, such as RTP, which seemed to be a result of children needing to be considerate of adults. For example, Thai children were free to play wherever they wished, as long as they considered the needs of adults who were often working or sleeping nearby.

Other contextual factors that affected play included environmental changes, such as season, tide, or weather. Hopi children played outdoors unless it was a particularly cold day, where play was more likely to be permitted indoors. For Thai children, play could be restricted by floods and high tides, which resulted in play being restricted to indoors, such as in classrooms and houses. Furthermore, some games were seasonal, as they depended on specific weather conditions, or fruits and buds for object play, which could only be acquired during specific seasons.

For the cultures where proficiency in navigating water was important, play often seemed to centre around being in the water, presumably to develop this proficiency. Manus children would spend over half their waking hours playing in the water, including paddling, punting, racing, and playing with canoes. The importance of this skill seemed to be reflected in the fact that where swimming was a form of play, both genders would participate, even if there was gender segregation. The Gros Ventre would play at swimming, but girls would use breaststroke and boys overhand stroke, and would play separately, even if in close proximity. This reinforces the idea that where a skill is important, play will reflect development of that skill.

Gender and context seemed to interact with one another in determining appropriate play activities. One of the important components regarding context and setting of play was proximity to adults. San children were limited in their movements, as they were not allowed to stray far from the village and were nearly always under adult supervision. This resulted in interruptions to play where it became aggressive, which may have resulted in lower rates of RTP. San boys' play was more likely to be interrupted by adults, which suggests that they more often began to engage in RTP than girls. For Central Thai children, when their games were restricted to be near houses by weather or tides, children would engage in less vigorous and quieter play, so as not to disturb nearby adults. Proximity to adults may have been influenced by gender, as girls in some cultures were expected to be closer to home, which limited the ways in which they could play, as demonstrated by the sedentary San group, where girls spent more time in the camp and less time in play. Being in close proximity to adults also lead to girls being more likely to be asked to help with household tasks, which further reduced the time they had to play.

Another setting that influenced the play of children according to gender is whether they were at school or at home. O'odham boys were more likely to chase and wrestle with each other in the school setting compared to when they were playing at home, and Central Thai boys and girls showed greater gender differences in their activity preferences at school compared to their preferences for activities at home. Boys were more likely to engage in more active games at school, whereas girls were more likely to engage in sedentary activities, compared to the activities they played at home. This demonstrates that play changes in response to differences in the environment, and changes in play activities based on setting could be due to a range of factors including differences in adult supervision or the amount of available space.

Imitation

Most of the cultures I investigated involved some form of imitation of adults in play, with the exception of the San where imitation was not described at all. Many of the forms of imitations were gendered, with children imitating their same-gender adult counterparts, mostly parents. This was particularly true for girls; Fellahin, Hopi, and Central Thai girls were described as engaging in play which imitated domestic tasks such as cooking and cleaning. Other imitative play that girls engaged in included playing house, playing with dolls, or using objects such as sticks to imitate camp life. Playing house was often a pastime of boys and girls, although boys were reported to stop playing this at an earlier age than girls. When playing house, boys were more likely to play the role of men, and girls that of women; when Gros Ventre children played house, boys would re-enact hunting and bringing home meat, or mock battles, and girls would play at preparing food and mock funeral ceremonies. For the Hopi, children would imitate ceremonial patterns, but only those appropriate for their gender. This provides further evidence that play is used in preparation for gendered adult social roles and the specific skills and knowledge required to fulfil them.

However, another significant component of imitation within certain cultures was the imitation of animals, although this was more often a feature of boys' play. Fellahin boys imitated animals such as mice, donkeys, and buffalo within organised games, and Hopi boys played at imitating horses, reflecting the roles of those animals within their culture. Animal imitation also seemed to be a method of incorporating RTP into games, as it often involved physical contact and chasing. Central Thai boys and girls played many organised games which were named after animals, such as 'mother crow', where a child would play at being a crow defending her nest from egg thieves, or 'crocodile', where a child would play at being a crocodile in a river and other children must attempt to pass the river without being caught. These games seemed to incorporate RTP, but also seemed to be a method of learning how to safely navigate the environment and provide subsistence, either through hunting or gathering.

Fairness

The maintenance of fairness in children's games was particularly noteworthy, particularly during organised games and rougher play. For the Fellahin, fairness was valued highly and seemed to be moderated almost entirely by children themselves, as they played mostly away from adult supervision. The emphasis on fairness ensured the continuation of participation in play, as children were in with a fair chance of being on the victorious team, and knew that their participation in play would be reciprocated on subsequent play occasions. For the Central Thai, game rules were modified to allow for the participation of younger and less skilled players, and the emphasis seemed to be on playing the game as a cooperative group, rather than competition. The cultural values of the Central Thai emphasised tolerance, and this was reflected in children's group games where younger participants were given advantages to keep games fair. Central Thai children had many techniques for dividing themselves into teams, which seem to have the purpose of keeping teams balanced and fair in strength or numbers, or making sure children had the same number of turns at each role.

Adult Restrictions on Play

Across societies, the extent to which adults were involved in restricting play varied. For cultures where play was seen as necessary for development of essential skills, less restrictions were placed on play. Gros Ventre and Manus adults saw play as training for later life, and therefore placed few restrictions on play, leaving children to develop skills in their own way. The only restriction placed on Manus children was that they should be home at night. This may be associated with the lack of gender differences in play, where boys and girls played in mixed groups with the exception of war games, as a result of the lack of adult intervention, potentially demonstrating the expression of inherent predispositions which are expressed when not constrained by adult control. San adults were nearly always present when children were playing, but they had little involvement in directing when or where children could play. Similar to the O'odham, they only intervened in play when aggression occurred, which was rare. The Eastern Apache encouraged children to be kind, and not fight, but other than this there were few restrictions on play. Girls were expected to be more obedient than boys, but they did not seem to have more restrictions placed on their play.

In other cultures, play was restricted so that it did not disturb adults or disrupt adult life. Fellahin adults acknowledged that play is necessary for the development of skills and learning of social roles, but they discouraged play within their own sight, especially within indoor settings. Hopi adults believed that children should be industrious, rather than lazy, so play was often restricted until the child had finished their chores. When play was in proximity to adults, children were restricted to less boisterous and noisy games, and certain types of imitative play were taboo, such as playing at being sick, or playing with prayer sticks, due to superstition. Central Thai children were free to choose their own play activities, but were trained to play quietly and keep movements restricted when an adult was working or resting nearby.

Discussion

In this chapter, I aimed to assess how different types of play are distributed according to culture and gender, and to examine the constraints on and promoters of play, particularly RTP, in different cultures. As expected, play differed by gender to varying degrees across cultures. This supports previous research which acknowledges that although there are common characteristics of play across cultures, there are also differences which are tied to cultural factors which may dictate who children spend time with, where children are allowed to play, how long a child can spend in play, and the activities in which they are allowed or want to engage in (Edwards, Knoche and Kumru, 2004). However, it is likely that RTP has evolved under the constraints of both biological and cultural factors, so the potential functions of RTP must be considered with regards to sex and gender differences, as well as the cultural factors that either reinforce or lessen gender differences.

There were various components of play that seemed to be consistent across cultures. Although children often played in mixed-gender groups, play was often gender-specific, particularly for certain play activities. Boys and girls often both engaged in rough play, but this was often more likely to involve chasing for girls, and wrestling for boys, providing further evidence for the findings in Chapter 5. In some societies, such as the San, RTP was described as an uncommon behaviour for boys and girls, although this was changing as the subsistence style of the culture moved towards agriculture and a sedentary lifestyle. In other societies, such as Manus, both boys and girls participated in play which contained large amounts of RTP, such as chasing, wrestling, and other active behaviours. However, within cultures where RTP was frequent, gender differences still varied, as in some cultures there were play activities which contained RTP which were exclusive to boys, such as the imitation of hunting or warfare. Other play activities were sometimes exclusive to girls, such as the imitations of women's domestic tasks or imitations of women's roles in religious ceremonies. Gender exclusive play activities often reflected the adult's gendered division of labour. Across cultures, girls were often expected to be closer to home and stop playing at earlier ages, so that they could engage with adult work and higher proportions of domestic chores compared to boys. This was often linked to earlier age of marriages and the expectation of maturity at earlier ages for girls compared to boys.

Below, I explore cultural variation in gender differences in play, with a focus on RTP, through the lens of biological and cultural evolution. I focus on the proposed functions of play, and how RTP may functionally be more beneficial to boys, resulting in gender differences. I then consider aspects of cultural evolution, such as gender roles and biased social learning, and cultural factors such as gender segregation, which may have further reinforced or weakened gender differences in play and RTP. Finally, I consider contextual factors that may further influence gender differences in RTP.

Biological Functions of Play

According to life history theory, an individual will differentially invest resources into growth or energy demanding activities that may benefit that individual in later life, leading to optimal reproductive success (Stearns, 2000). Where play is performed at the expense of growth, it must be of ontogenetic importance and provide fitness benefits to the individual in adulthood (Berghänel, Schülke and Ostner, 2015). RTP has been implicated in the development of social skills and building social relationships (Smith, 2005), cognitive development (Palagi, 2018), the development of fighting and aggressive behaviours and the establishment of dominance hierarchies (Fry, 2005), physical development including the motor and sensory systems, cardiovascular fitness and muscle strength (Trawick-Smith, 2014), and constructing knowledge of the social and/or physical environment (Gray, 2009). I assess the importance of RTP and the domains of development it is linked with across cultures to assess which functions are likely to be associated with juvenile RTP. It is likely that RTP persists for boys or girls where it contributes to the adult skills necessary for that gender within a specific culture.

The importance of play for physical development was highlighted by multiple authors. RTP which was specific to boys was described as having the function of developing motor skills, endurance, and co-ordination for Fellahin boys, and dexterity and co-ordination for Gros Ventre boys. Physical development in these areas was necessary for boys to achieve success in their adult roles, which involved masculine displays of hardihood and endurance for the Fellahin, and the development of physical skills for hunting for Gros Ventre boys. In other cultures, physical development was seen as important for both boys and girls, as described in the Central Thai and Manus cultures. In these cultures, physical development was important for both genders as all Central Thai children were expected to develop physical strength and agility, and in Manus, all children must develop strength and balance to be able to navigate the waters in the village. The only play which was exclusive to boys in Manus was spear fishing and playing at war, both of which were skills necessary exclusively for men. This suggests that play varies to allow children to develop the physical skills necessary for childhood and adult life, which may or may not vary by gender according to culture.

This also suggests that children use play as a method of learning about their environment, which differ with regard to gender, particularly concerning the social environment. Ammār observed that play was encouraged for Fellahin boys and girls, although girls used play as a method for learning the ‘female ethos’ of the community, practicing domestic duties necessary for their adult roles. Fellahin boys, on the other hand, used play to learn physical skills such as using bows and arrows for hunting and warfare. In other hunter-gatherer groups, imitation has been found to be a major component in learning gender roles and their associated skills (Lew-Levy et al., 2018). In Andersen’s ethnography regarding the Central Thai, mimicry was alleged to be one of the major functions of play. It is likely that children use imitation of same-gender adults and older children to dictate their own behaviour, including which play activities are appropriate, which results in the knowledge and skills the child learns during play being gendered (Smith, 2005). This seems to be reflected in the gender differences in play described in the chosen ethnographies.

Play also seemed to be associated with learning about the physical environment, as in cultures where there are specific dangers, such as water or animals, children’s games incorporate learning about and overcoming these dangers. One of the major hypotheses concerning the development of play is the ‘training for the unexpected hypothesis’, which suggests that play enables the development of flexible physical and emotional responses to stressful situations and unexpected events in the individual’s environment (Spinka, Newberry and Bekoff, 2001). Early childhood games for the Central Thai focused on developing the physical skills necessary to navigate water, either in jumping across platforms or learning how to successfully use a canoe. Games for older children focused on plants or animals which may pose danger (e.g. playing games which involve avoiding ‘crocodiles’) or provide sources of food (e.g. playing games involving the narrative of retrieving eggs from a nest). This suggests that children use play to learn about and reinforce lessons about the physical environment, so that they can avoid dangers and exploit natural resources. This hypothesis is supported by Katz (1986), who suggests that play is a method of acquiring skills for exploiting the environment, including knowledge of planting, harvesting, trapping, and gathering, and Gray (2009) who gathers evidence that hunter-gatherer children are often left to independently explore their environments, encountering and learning to deal with hazardous situations and objects with minimal adult interference. Pellegrini, Dupuis and Smith (2007) also suggest that children in industrialised societies use play to develop new strategies and behaviours with which to navigate their environment.

There is also some evidence that play contributes to cognitive and social development. Anderson suggested that in addition to the development of physical skills, the games of the Central Thai allowed children to develop their strategic thinking and learn how to evaluate chance and probability, facilitating co-operation among children as they work together to win at games. Unfortunately, the role of social skills is mostly ignored by authors when speculating as to the function of play in these ethnographies. However play, especially RTP, has been associated with the development of social skills such as affiliation, social signalling, bargaining, manipulating, and the ability to redefine social situations, in both competitive and cooperative interactions (Siklander, Ernst and Storli, 2020). I believe there is evidence of cognitive and social development via play in the chosen ethnographies, as children seemed to emphasise fairness and tolerance during play, regardless of adult input. This requires children to assess their own and others skills, intentions, and needs during play, which shows the presence of cognitive and social skills such as theory of mind (Newton and Jenvey, 2011). However, the direction of causality cannot be confirmed; it is possible that children learn cognitive skills outside of play, and those who are more competent already are more successful at play.

Within the chosen texts, there was also evidence that play leads to the development of fighting and dominance behaviours. There is evidence for Western children that RTP is linked to both the development of fighting skills and the establishment of dominance behaviours (Boulton, 1996), with some stronger evidence for dominance functions (Pellegrini and Smith, 1998b). Ammār noted that boys' play was characterised by roughness, which he suggested helped them learn to deal with competitive situations. Although girls' play was not rough, it was also often competitive. The competitive nature of play for the Fellahin was linked to competition in adults, where there were strong rivalries between families and clans, and Ammār suggested play may be preparing boys and girls for these rivalries. In some cultures, such as the Hopi, boys' play groups were split by age, which may indicate that there is some grading based on competence and physical development. Although the emphasis on these groupings seemed to be on ensuring fairness in play, it is possible that boys were learning their place in the dominance hierarchy through being matched with other boys of similar levels of skill and physical development. Evidence from these ethnographies suggests that play had the function of preparing children for future competition and was instrumental in the creation of dominance hierarchies

Finally, Ammār suggested play may be a safe method of venting frustrations and aggression, specifically for boys. He stated that play is characterised by mimicry and ridicule of others, which may allow for the release of aggressive impulses as boys enter adulthood and become frustrated with having to enter into the adult world. RTP has been linked with the development of social competence, including tolerance for frustration (Eig, 2017), although this is linked to the development of the frontal cortex rather than RTP being a release for aggression. RTP is also considered an activity which is distinct from aggression, which instead involves negative affect rather than positive affect (Pellegrini, 1994). This suggests that Ammār's assertion that play is a method of venting frustration is outdated and refuted by more recent evidence.

Overall, there seems to be strong evidence that RTP is associated with various functions, including physical development, learning about the physical and social environment, and the development of skills required for adult life, such as hunting or warfare. Although the chosen ethnographies do not focus on the development of social and cognitive skills, there is evidence of children using such skills during play. Therefore, it is likely that the processes of biological and cultural evolution have maintained RTP in cultures where these aspects of development are most important, for the gender where these skills are appropriate.

Cultural Variation in Play

I also aimed to assess cultural variation in gender differences in play with respect to cultural evolution and the transmission of gendered social norms relating to play and RTP. Children in hunter-gatherer societies have been shown to learn through play, as it allows them to practice cultural scripts and specific skills, which often involves processes including observation, imitation, and teaching (Lew-Levy et al., 2018). Social learning is a key component of play (Terashima and Hewlett, 2016), and children's play reflects both vertical cultural transmission, where children imitate parents, and horizontal cultural transmission, where children imitate and learn from peers (Hewlett et al., 2011). In Chapter 5, I considered the effects of vertical and horizontal transmission on gender norms regarding children's RTP, but found low levels of phylogenetic signal and spatial autocorrelation. This may have been due to a lack of effects of social transmission, or due to the effects being masked by more rapid changes to the environment. Therefore, I used qualitative analysis of the ethnographic data regarding gendered variation in play to further explore the explanations for cultural variation, through the lens of social learning and cultural transmission.

In most cultures I examined, girls and boys were expected to engage in different play activities according to their gender. Although there are often gendered divisions of labour in forager societies, this may be tempered by common values of gender egalitarianism (Boyette, 2016a). Often in subsistence societies, the lines between work and play are blurred, with children's activities providing gender role socialisation and training for gender-specific adult work tasks (Lew-Levy et al., 2021). Children in the ethnographies I examined often imitated adult roles within their play, and although many play activities were common for boys and girls, some activities were strictly for one gender, particularly as children got older. Eastern Apache children's gender-exclusive play activities included fashioning dolls and braiding wild plants for girls, and playing with bows and arrows for boys. Imaginative play was often strictly themed by gender; for the O'odham, only girls would play with dolls, and only boys would play cowboys. Even in cultures where children played in mixed gender groups, activities such as playing house were often themed by gender, with girls imitating domestic tasks and boys imitating hunting, as observed in the Gros Ventre. Boys and girls that adhere to typical gender roles tend to be praised, and penalised for deviating from gender roles (Eagly and Wood, 2012). For example, the play of Fellahin girls and boys was described as being compatible with the 'ethos' of their gendered adult counterparts, which suggested that play was affected by social pressures which designated the behaviours which were appropriate for each gender. This likely shapes play behaviour, and may make RTP more common for boys where it links to men's social roles. Therefore, the gendered divisions in play that I discuss may be a result of gendered divisions of labour and adult roles, which dictate the activities that children engage in according to the skills they must develop for adult life.

A common feature of gendered divisions of labour is that women are expected to provide childcare. For hunter-gather societies, this is usually linked to conflicting mating and parenting goals (Panter-Brick, 2002), and the biological and social demands of lactation (Gurven and Hill, 2009), but is also seen in the expectations of childcare by older siblings, where in both subsistence and industrialised societies female children are more likely to be given the responsibility of caring for younger siblings compared to male children (Larson and Verma, 1999). This was true for most of the ethnographies I analysed, as one of the major responsibilities which kept children from playing was childcare, which when given to children fell predominantly to elder sisters. This created gender differences in the time girls could spend playing compared to boys who were less likely to be given childcare responsibilities. For societies where boys and girls were not expected to engage in childcare, such as the San and Manus cultures, boys and girls had greater amounts of time to spend in play. In both of these societies, children engaged in similar types of play, including RTP. However, in these societies, girls were still expected to stop playing earlier than boys so they could assume adult responsibilities, so gender differences were still perpetuated to some extent.

One of the central mechanisms of cultural evolution is social learning, which is when knowledge passes between individuals and the behaviour of one individual influences another (Jones and Rendell, 2018). Social learning can be biased in a number of ways, where an individual might have a predisposition to imitate certain behaviours over others, may adopt the most common behaviours, or may adopt behaviours that are demonstrated by those most similar to themselves (Laland, Brown and Brown, 2011). Children learn through play, and previous research has also found that they often imitate adults of the same gender during play activities (Lew-Levy et al., 2018), which could lead to the reinforcement of gender roles and gendered social norms. This may explain boys' preference for imitating men's adult roles, and girls' preferences for imitating women's adult roles, such as engaging in the specific subsistence tasks that men and women engage in. It is further demonstrated in children's re-enactments of village life, such as boys and girls imitating men and women's roles respectively in religious ceremonies or while playing house. As play is therefore likely to be susceptible to biased social learning with regard to gender, it is likely that gender differences in play activities, including RTP, are often reinforced where adult gender roles are different for men and women.

Another common cultural theme was that girls were expected to stop playing earlier than boys. A notable example of this was the Hopi, where girls were expected to stop playing at ten to twelve years of age, whereas boys continued to play until adulthood. Other societies followed similar patterns, such as the Manus, where girls played until they were around 14 years of age, yet boys continued to play until they were around 20 years. Manus girls and boys played together in mixed gender groups, until girls were expected to stop playing due to increased responsibilities in domestic and household chores at around age 14. These responsibilities were not placed on boys, who continued to play until they were married at around 20 years. The San showed a similar pattern, although with a reduced age gap, where girls were expected to stop playing at around 14, but boys continued to play until they are around 16 years. For boys and girls of the San, play ceased due to the expectation of carrying out adult duties, which were domestic tasks for girls and caring for animals for boys. Across many cultures, girls are found to spend more time doing chores and less time in play, and play is reduced when chores and labour are introduced (Whiting and Edwards, 1973; Larson and Verma, 1999), which suggests gender differences in time spent playing are driven to some extent by chore allocation according to gender and gendered social norms with regards to behaviour. This is supported by comparing the nomadic and sedentary San groups; in the sedentary groups, girls were being given more duties than boys, which reduced their time spent playing.

Finally, I consider the role of gender segregation in adherence to gendered social norms of play. In cultures with strong gender segregation during play, boys' and girls' play more rigidly adhered to gender roles. This supports the idea that gender-segregated play can lead to gender-specific peer cultures and socialisation processes, which Maccoby (1998) suggests can lead to the development of different skills and activity preferences. However, the direction of causality is unknown; gender-specific preferences for certain play activities may lead to the segregation, and/or segregation may lead to gender-specific preferences as the groups develop their own distinct culture. However, in most of the societies described, children played regularly in mixed-gender groups, often as a result of older children providing care for younger siblings. In these groups, play did not become overly rough, and children engaged in the same games, although sometimes the roles they engaged in during these games were dictated by their gender. When playing 'house', boys would take on the role of men and imitate hunting, whereas girls will take on the role of women and imitate household tasks. When imitating ceremonies, boys and girls would imitate roles specific to their gender. Engagement in gender stereotyped activities is usually associated with gender segregation during play (Fabes, Martin and Hanish, 2003), so it is interesting that mixed gender play presented an opportunity for children to engage in gender-specific roles within the same play activities. This suggests that gender segregation during play was not solely driven by children or adults creating opportunities to practice gender-specific roles.

Overall, it is apparent that gender differences in play are linked to cultural factors such as gender roles within a given society. Biological evolutionary factors may result in predispositions towards certain activities, such as RTP for boys, and these often seem to be reinforced by cultural factors such as gender segregation and adherence to gendered social norms. There is evidence that social transmission is often biased by gender, where children are likely to imitate same-sex adults and peers within gender segregated play groups. However, there is also evidence of cultures where gender norms in play are less strict, such as cultures where physical activity is equally important for girls, which shows that cultural variation can also lead to children engaging in less gender-specific play activities. This suggests that play and RTP are affected by interactions between biological and cultural evolution.

Contextual Factors affecting Play

I also aimed to assess how contextual factors affect rates of play throughout childhood, i.e., more rapid changes in the physical or social environment. Individuals will respond to changes in the environment in order to exploit resources or avoid risks (Barsbai, Lukas and Pondorfer, 2021), and rates of RTP in non-human mammals have been shown to respond to changes in the environment such as temperature and weather (Y Li et al., 2011), food availability (Moebius et al., 2019) or risk of predation (Smith, 2005). For children in industrialised societies, various factors have been shown to influence rates of physical activity and play, including available space for play and level of supervision from teachers (Cardon et al., 2008), weather, and fear of older children (Brockman, Jago and Fox, 2011). Barriers to play can be part of the physical or social environment (Stanley, Boshoff and Dollman, 2012), and it is likely that similar environmental barriers can also affect engagement in play across childhood for children in subsistence societies. Although Lew-Levy et al. (2022) found in a cross-cultural study that engagement in play was unlikely to be affected by environmental factors such as mean annual temperature, rainfall, or level of ecological risk, it is potentially true that smaller scale changes across time rather than culture, or more social environmental factors, can affect rates of play, if it limits time available for RTP.

In the ethnographies I examined, rates of play and RTP did seem to be affected by the physical environment and setting. For cultures in which children attended school, play was described as changing according to the context. Boys' play became more active, as demonstrated by O'odham and Central Thai boys, who were reported to engage in higher levels of wrestling and chasing when playing at school, whereas Central Thai girls engaged in more sedentary play activities. Play was restricted to windows of activity before school and in breaks between lessons, and in industrialised societies the intensity of physically active play has been reported to increase when children are restricted in time spent playing (e.g. Kobel et al., 2015). Play was also restricted by environmental conditions such as bad weather or flooding, where play was subsequently restricted to indoor or safer settings, resulting in less vigorous play in response to these changes. This suggests that the physical environment can affect rates of RTP, and that the effects of the environment can differ for boys and girls. This would result in the specific time period and context of data collection influencing the types of play that are recorded within any given ethnography.

Changes in play were also apparent as a result of changes to the social as well as physical environment. Proximity to adults during play varied according to culture, but also interacted with gender and seasonal factors. For example, girls are often expected to be closer to home, which results in a greater proportion of time spent in household tasks and limits their freedom in choice of play activities, which often resulted in less active or rough play compared to boys who are less restricted in their movements. Proximity to adults often occurred as a result of restricted locations for play, as a result of changes to weather or temperature, which restricted RTP of both boys and girls. Finally, for cultures where children attended school, the qualities of play changed based on setting. Gendered preferences for play activities tended to be more apparent at school, and children were more likely to play in gender-segregated groups at school, both of which were attributed to differences in adult supervision or the amount of available space. Therefore, it is clear that changes in the social and physical context of play interact with each other and with individual characteristics such as gender to affect rates of play across childhood.

Potential Issues in the Use of Ethnography as Data

Gender

In modern literature, the terms ‘sex’ and ‘gender’ are defined and used differently, with sex usually referring to biological, anatomical, and physiological differences between boys and girls, and gender referring to individual identities and the surrounding psychological, cultural, and social constructions surrounding that identity (Muehlenhard and Peterson, 2011). It is now acknowledged that the distinction between male and female sex characteristics are medically constructed, and that the concept of gender changes based on cultural and historical context (Johnson, Greaves and Repta, 2009). Modern, feminist understandings of gender also take into account intersectionality, understanding gender in relation to social identities and the personal relationships and power relations embedded within them (Shields, 2008). Although modern ethnographies which focus on hunter-gatherers may take these contexts into account, such as incorporating gender into behavioural models (Lee, 2018), gender was not historically incorporated into anthropological research, as the default approach was a male-oriented perspective, with women seen as requiring special attention (Shapiro, 1981). This may be particularly true for those written in the 19th century (*An Apache Life-way* and *The Gros Ventres of Montana*).

However, as ethnography developed, anthropologists such as Margaret Mead began to consider the role of women and sex roles within the cultures they were studying, and the interplay of culture and biology in determining individual identity and behaviour (Coffman, 2021). This exploration of sex and gender through ethnography was apparent in Mead's first work *Coming of Age in Samoa*, but was not formalised fully until the mid-1930s in Mead's work *Sex and Temperament in Three Societies*. I consider Mead's work *Growing up in New Guinea: a comparative study of primitive education*, which was published in 1930 and focuses on child development in relation to education, family life, and how the child relates to and enters into the adolescent and then adult world. However, in regard to play, Mead mostly focuses on descriptions of play and childhood life, without in-depth analysis of how this related to adulthood gender roles or individual differences in the rejection of gender-specific activities.

Consideration of gender and gender roles is also apparent within other ethnographies considered in this chapter. This could focus on the gendered expectations placed on children (e.g., the different expectations for boys and girls regarding participation in chores for O'odham children) or the gendered social roles of adults (e.g., the role of the father in childcare is mentioned with regards to the Fellahin). Draper in particular focuses on the role of gender in expectations placed on children, discussing how the impacts of the move towards subsistence farming are different for San boys and girls. However, discussion of gender mostly sticks to description of the behaviour of boys and girls, or men and women, and the theoretical background of gender roles remains largely ignored. Within descriptions of play, gender is mostly discussed with regards to acceptable behaviour, such as appropriate gender of play-partners, or appropriate play behaviours for boys and girls.

Therefore, although there is some consideration of the roles of sex and gender within the included ethnographies, the time period in which they were written must be taken into account, including sex and gender being used as interchangeable terms and the views and theoretical positions of the ethnographers. I have endeavoured to separate the terms sex and gender where appropriate, using gender to refer to culturally constructed differences in self-identity and behaviour, although I cannot always be certain that this was as intended by the participants or ethnographers. I also acknowledge that ethnographer biases regarding gender may have influenced the reporting of behaviours of boys and girls, particularly behaviours which would be seen as heavily gendered, such as RTP. For example, girls' RTP may have been under-reported, as ethnographers may not have focused on behaviours they did not expect to see.

Influence of Colonialism

It is also important to note that the method of ethnography was developed in colonial contexts (Van Bremen and Shimizu, 2013), which could influence both the findings of the ethnographers and our own findings and conclusions. This is particularly relevant for the ethnographies I have chosen, as they were all conducted in the 19th or 20th century, which was when anthropology became a university discipline and a modern science, but was also the period in which Western nations were pushing to bring the non-industrialised non-Western world under their political and economic control (Huizer and Mannheim, 2011). Colonial influences upon the studied cultures are evident within the ethnographies, particularly where children were sent to schools, which were often run by white Americans, as was the case for Hopi and O'odham children.

For the O'odham, it was noted that interest in old Papago games has waned, with children having to ask older relatives for the rules. In some areas, the older games had been replaced with American sports such as baseball, football, and basketball, but Joseph noted that this was not the case for the group studied here. Papago children often went to school, although it was not compulsory, but attendance was often encouraged by parents and peers. At school, Papago children were usually taught by white American women, and Joseph notes that young girls tended to spend more time with teachers than boys did. Children were introduced to American games at school, but it is noted that children still mostly preferred to engage in unorganised play. However, there was some engagement in English verbal guessing games, which were introduced by schoolteachers with the intention of children practicing their English language skills.

Colonial influences were also discussed for Hopi children, where parents would often send children to American schools at six years of age, to learn English and various trades. However, not all the norms introduced by the American schools were accepted by the Hopi; practices such as school dances were regarded as sinful as social dancing and embracing are not acceptable between boys and girls. Hopi girls were often keen to engage in the customs they learn at school, as they viewed American girls as having greater freedoms. However, their knowledge of non-Hopi roles was limited, and although they would often play at being nurses who were employed by the government, they would rarely imitate schoolteachers.

One of Mead's primary interests was on the impact of Western contact and colonialisation, and the subsequent changes to the cultures she studied (Mcdowell, 1980). Mead went on to study the culture in Manus for over 50 years, documenting the impacts of Western colonialisation (see Mead, 1956), but the ethnography I use here was published in 1930 and focuses on describing the culture as it was found by Westerners in 1929 (Mcdowell, 1980). Therefore, although the work of Mead often centred on colonial influences, that is not the case for the ethnography studied here. Furthermore, ethnography is tightly linked with colonialism, even unintentionally on behalf of the ethnographer (Huizer and Mannheim, 2011), so I must acknowledge the potential impacts of the presence of the ethnographer and any contact with Western cultures, which is relevant to all ethnographies. For example, the ethnographers' expectations of gender roles may have influenced the behaviours of children included in the ethnographic accounts.

Conclusions

Overall, I provide further evidence that gender differences in play vary widely across cultures, and that there are common themes within play that support and explain previous findings. Accounts of girls' and boys' play in these ethnographies suggest that play is used to develop skills necessary for both childhood and adulthood, which may differ by gender according to biological and cultural factors. Gender differences in play first seem to vary according to function. For example, where high levels of physical proficiency are required for both genders, I found that both boys and girls are usually more likely to engage in play with physical and rough aspects, such as RTP. Play also seems to be an avenue for learning about the environment, whether as a means to learn the social role and gender-specific tasks expected of the child in adulthood, or as a means to explore how to navigate and exploit the physical environment. To a smaller extent, it is suggested that play is a method of establishing social skills such as cooperation, particularly reflected in team games, where children expect each other to establish fair teams and play within the rules. These proposed functions are reflected in the play activities engaged in by each gender, with boys and girls seeming to engage in the play activities which most benefits their adult gender-specific social role.

These expected gender differences are then suggested to be reinforced or lessened according to cultural variation in gender roles, due to mechanisms such as social learning and the processes of vertical and horizontal transmission of gender norms in play. In the ethnographies I examined, social transmission was often gender-biased, which led to the imitation of same-sex adults and peers, and play within gender-segregated groups, leading to the reinforcement of strict gender-specific play activities. However, other cultures displayed less strict gender norms, where children were often likely to play in mixed-gender playgroups and play activities were less segregated by gender.

Finally, I examined the role of contextual factors in determining gendered play. Factors in the physical and social environment were found to affect engagement in play, particularly RTP, such as proximity to adults, environmental conditions, and social setting. I also consider potential biases of the ethnographers, including outdated notions of sex, gender, and gender roles, and the impacts of colonialism. Overall, I provide evidence that gender differences in play are likely to be a result of interactions between biological and cultural evolution, and that expected gender differences may be altered by contextual factors that change engagement in play over childhood.

Chapter 7: Discussion and Conclusions

Overall, the aim of this thesis was to explore variation in sex and gender differences in RTP in mammals, including humans, and identify potential biological, cultural, and contextual factors which may underlie these differences. Chapters 3 and 4 focus on behavioural ecology and sex-differentiated life history strategies in order to understand the potential functions of RTP, which may influence engagement in juvenile RTP for males and females across non-human mammalian species. Chapter 5 focuses on gender norms which may influence engagement in RTP for boys and girls in diverse subsistence societies, considering cultural evolution and the mechanisms of social transmission with regard to vertical and horizontal transmission of gender norms regarding RTP across cultures. In Chapter 6, through qualitative analysis of the ethnographic data, I consider biological, cultural, and contextual factors with regards to RTP within the context of variation in cultural norms and children's other activities and responsibilities. In this chapter, I summarise the findings of each empirical chapter, reviewing the sex and gender differences that were found across species and across cultures, and the potential biological and cultural factors which may contribute to sex and gender differences in RTP, primarily through the lenses of behavioural ecology and cultural evolution. I also consider contextual and environmental factors which may lead to rapid changes in engagement in RTP, and methodological factors in the study of RTP which may have affected the results of the studies and ethnographies I reviewed. I finally consider the significance of the findings, and suggest avenues for future research, which should incorporate biocultural approaches to sex and gender differences in RTP and more consistent methodological approaches.

Sex Differences in RTP in Non-Human Mammals

With regards to cross-species data, the systematic review (Chapter 3) found that although a male bias in RTP was common among diverse mammal species, sex differences were smaller and less consistent that expected. Many studies found mixed results, many studies found no significant differences between the sexes with regards to RTP, and a small number of studies found a female bias in RTP. Through inspection of the phylogenetic relationships between species and the associated sex differences, it was clear that variation was not strongly phylogenetically patterned, which was confirmed by statistical analyses of phylogenetic signal (Chapters 3 and 4).

After establishing that sex differences in RTP showed variation across species, I examined the texts of all studies included in the systematic review to identify potential factors associated with sex biases in RTP (see Chapter 3). Potential factors were examined with regards to life history theory i.e. how RTP functions as part of sex-differentiated life history strategies. Male biases in RTP are often attributed to high levels of male competition in polygynous species, where male juveniles will invest in RTP to acquire motor skills and fighting skills in preparation for adulthood intrasexual competition and male dominance hierarchies (Clutton-Brock, 1988; Berghänel, Schülke and Ostner, 2015). In the studies that were included in the systematic review, species which showed higher levels of male RTP did often also show high levels of male competition, and strict male dominance hierarchies. According to sexual selection and life history theory, high dominance status within male hierarchies is associated with greater reproductive fitness (Flanders, Herman and Paquette, 2013), so this provides support for the fighting skills hypothesis. However, according to this hypothesis, strong male biases would be expected for the Hominidae, which mostly show high levels of male intrasexual competition, excluding bonobos (Harcourt, 1981). This was not supported by the findings of the systematic review, where a lack of sex differences, or mixed findings, were common findings for studies of the great apes. However, methodological factors must be considered in this case, due to a strong reliance on small sample sizes, often from captive populations, in this family.

Sex-biased dispersal was another factor that appeared to be associated with sex differences in juvenile RTP. Dispersal, in which an individual disperses from the natal group (Handley and Perrin, 2007), can be either male-biased, female-biased, or equal between sexes, and requires highly developed fighting and social skills to deal with the demands of integration into a new social group (Mitani et al., 2012), and motor and cognitive skills with which to deal with increased risks of predation (Bonte et al., 2012). Two of the three species which showed a female bias in juvenile RTP also showed evidence of equal male and female dispersal at maturity (the mantled howler monkey and white-lipped peccary), and male biases were also common for species in which males disperse (e.g., spider monkeys).

I also considered factors which might have led to the high prevalence of species which showed a lack of sex differences in RTP, or mixed results. Reduced sex biases in RTP were particularly common in the Carnivora, which I suggest may be due to the importance of predatory behaviour for both males and females, which may be developed in juvenile RTP (Caro, 1995). However, an absence of a sex difference could be attributed to small sample sizes, either due to a lack of statistical power or lack of suitable play partners. This was particularly notable for primates, where for many species which showed a lack of sex differences, the relevant studies were associated with low sample sizes and captive groups, although the differences were not statistically significant with regard to sample size. Therefore, future studies may consider the role of setting and/or sample size in determining rates of RTP, whether as a result of low statistical power, or a lack of suitable play partners.

In Chapter 4, I further explored potential biological factors which are associated with sex differences in RTP using quantitative phylogenetic comparative analyses. As high levels of male competition and dispersal appeared to be associated with male biases in RTP, both in the literature and by the findings of this systematic review, I assessed the effects of mating system, sexual size dimorphism (SSD), and sex-biased dispersal on sex differences in RTP for the species identified within the systematic review. According to phylogenetically informed regression models, phylogenetic position, mating system, SSD, and sex-biased dispersal were all unlikely to contribute to sex differences in juvenile RTP. This suggests that the effects of male intrasexual competition in adulthood may be overstated, and that RTP may have other adaptive functions which are more important with regards to the distribution of the trait across mammalian species. However, other hypotheses must be considered which could explain the lack of phylogenetic signal and contribution of male-competition-related traits, such as contextual and methodological factors, and the possibility that RTP is a rapidly changing trait that is difficult to link to other, slowly evolving traits such as body size.

As mating system, SSD, and sex-biased dispersal were shown to be unlikely to contribute to sex differences in RTP, according to the phylogenetically informed regression models, the potential of other factors to contribute to sex differences in RTP must be considered. This could include variation in the environment across the juvenile lifespan, which could not be captured by such a model due to the difficulty of measuring various contextual factors which could change rapidly over the lifespan. Changes to the physical and social environment have been implicated in affecting rates of play in previous research, including changes in temperature, weather, food availability, and predator pressure (Smith, 2005), and changes to the demographics of available play partners (e.g. Biben, 1989), which can affect males and females to different extents. Changes to the environment over small timescales are likely to affect rates of play, due to changes in energy demands and availability, or social demands, but these are hard to capture with regards to species differences due to differences in methodology across studies.

There are also a number of methodological factors which are important to consider with regard to Chapters 3 and 4. Although I endeavoured to include as many mammal species as possible, there were limitations with sample size and in the range of species included. A significant issue in research regarding mammals is taxonomic bias, which describes the phenomenon in which certain species attract more research than others, often due to factors such as ease of observation and presence of more ‘interesting’ traits (Clark and May, 2002; Ducatez and Lefebvre, 2014). In Chapter 3, I carried out a permutation test to investigate taxonomic bias within the sample used in this thesis, finding that there were strong biases which were likely to affect the results. Primates were the most over-represented order within the sample, alongside the carnivora and proboscidea, which were also over-represented. This is in line with expectations, as play is associated with larger brained mammals (Iwaniuk, Nelson and Pellis, 2001), and previous studies of taxonomic bias show a research preference for species with greater body mass and larger brains (Santos et al., 2020). In this thesis, many orders were under-represented, particularly small and nocturnal species such as the rodentia and chiroptera, and many orders were not represented at all. This suggests that taxonomic bias could affect the results of this thesis, as it is possible that variation in sex differences in RTP could differ in orders and species which were not included in this research. Phylogenetic signal may have been underestimated due to the low sample size, and under-representation of variation in species across the taxonomic order. Heritability estimates had wide credible intervals, which suggests that phylogenetic signal could be higher than initially suspected. Therefore, future research could focus on expanding the number of species for which RTP, and sex differences in RTP, are commonly studied.

Other methodological factors affecting the collection of data on sex differences in RTP includes the variation in how data on RTP is collected. Within the studies collected by the systematic review, RTP is measured variously as rates, frequencies, total time spent in RTP, or duration of bouts, all of which change the context of data collection. No clear sex-biased patterns emerged with regards to variation in how RTP was measured, but reported sex differences did often differ between studies of the same species using different measures of RTP. This suggests that biases may have been introduced by using more than one measure of RTP, or that different measure capture different aspects of a complex behaviour. However, it was important to include as many studies as possible to maximise the sample size, and often methodological differences were small (e.g. initiations and frequencies are similar measures). As in this thesis, it is important for future studies to be clear about methodology in studies of play, and ensure that the method of measurement is considered when discussing sex differences in RTP.

Gender Differences in RTP in Humans

I also considered gender differences in RTP for humans, using cross-cultural data to explore how gender differences vary between societies. Although a solely biological framework can be used to generate predictions for sex differences in human behaviour, it is likely that cultural factors will also lead to variation in gender differences, due to wide cultural variation across humans. Humans, unlike other mammals, are able to self-identify as men, women, or other non-binary genders (Wood and Eagly, 2015), which introduces factors such as gendered social roles which can further influence behaviour (Eagly and Wood, 2012). Therefore, I looked at cross-cultural variation in gender differences in RTP through the lens of cultural evolution, focusing on how gender norms regarding RTP may be socially transmitted, and which social factors may interact with biology and determine rates of RTP for boys and girls across cultures.

Using ethnographic data from the eHRAF database (‘eHRAF : HRAF collection of ethnography’, 1996), I explored how gender differences in RTP varied across cultures. I examined ethnographies for cultures across the Standard Cross Cultural Sample, coding RTP (split into wrestling and chasing) as present or absent for boys or girls. Wrestling was much more likely to be present for boys compared to girls across cultures, which contributed to male biases in RTP across cultures, and suggests that boys may be more likely to engage in the vigorous or more dangerous aspects of RTP. However, the distribution of RTP for boys and girls did not appear to be patterned according to the relationships between cultures, either based on cultural history or spatial proximity. This was supported by analyses of phylogenetic signal, which were low across all analyses, suggesting that variations in gender differences in RTP may be affected to a greater extent by rapidly changing cultural or social factors, rather than vertical or horizontal transmission. However, the fact that RTP was more common for boys than girls may have multiple explanations, which I further explored using both quantitative and qualitative methods.

Using phylogenetically informed regression models, I explored a number of factors that were potentially linked with gender differences in RTP. For boys, marriage system, descent system, food uncertainty, and strong ideologies of male toughness were all unlikely to contribute to the presence of RTP for boys. Similarly, marriage system, descent system, food uncertainty, and the average age of marriage for girls were all unlikely to contribute to the presence of RTP for girls. This was surprising, as these factors have been linked with strong gender norms for men and women. For example, factors such as polygynous marriage systems and ideologies of male toughness are often linked with high levels of competition between men (Goldstein, 2003; Ember, Ember and Low, 2007). Low phylogenetic signal and the lack of contribution to gender differences by the factors investigated in these models suggests that gender norms concerning RTP do not seem to be stably transmitted via vertical or horizontal transmission.

However, other factors must be considered which could be leading to low phylogenetic signal and a lack of evidence for the contribution of the considered factors. Changes to the environment across a child’s lifespan may be more likely to affect their rate of engagement in RTP to a greater extent than cultural factors such as marriage or descent system, or gendered social norms. Due to the nature of ethnographic research, it is unlikely that our data was fine-grained enough to pick up on rapid changes across childhood. For example, even when considering food uncertainty within an environment, an ethnographer may be studying a culture within a time period where food is more available, leading to higher rates of play for boys and/or girls, or less available, leading to lower rates of play. This may also be true for other physical environmental factors, such as changes to the built environment, or social environmental factors, such as changes to the demographic populations of the group, which could lead to differences in engagement in play for boys and girls. Rapid changes such as these could result in the obfuscation of phylogenetic signal, as phylogenetic comparative methods are suited for changes on larger timescales. Therefore, future research should focus on factors which vary on a smaller timescale than those focused on in this thesis and consider how engagement in RTP can change across time.

Although the models in Chapter 5 suggest that the factors I investigated are unlikely to contribute to gender differences in RTP, this may be a result of limitations of the data. Although coding was conducted for all cultures within the SCCS, many ethnographies did not contain enough information for a judgement to be made, particularly regarding RTP for girls. This resulted in a limited sample size, which was reduced even further due to missing data in the independent variables introduced in the regression analyses. R^2 values were low for the regression models, although this could be a result of either low sample size or alternative factors being more relevant to determining gender differences in RTP. Therefore, I further explored a subset of ethnographic data in order to uncover more details of gender differences in RTP within the wider context of play, cultural factors, and context, which could not be captured by the quantitative analysis in Chapter 5.

In Chapter 6, qualitative analysis of ethnographic data on play further supported some of the findings of Chapter 5, as gender differences varied across cultures, with most showing some male bias in RTP. Some ethnographies focused on the purported functions of RTP, which included the development of physical proficiency, developing social skills, learning about the environment, and learning about social roles. These functions were often gendered, as these skills could be more important for boys or girls. For example, in societies where children required physical proficiency for moving around the environment, such as in settlements which were near large bodies of water or flooding, RTP was often valued for both boys and girls. On the other hand, in cultures where physical proficiency was more valued for boys, focusing on their role in hunting and food provisioning, there tended to be greater male biases in RTP. Play which focused on imitation of adults was also often gendered, with boys imitating men in hunting behaviour, and girls imitating women in household tasks, for societies in which a strict gendered division of labour was upheld. This suggests that there may be vertical cultural transmission that was not picked up by the quantitative models in Chapter 5, as the roles of adults and the expectation that children should imitate and learn gendered social roles seemed to be a major factor in determining play activities, including RTP.

However, I also examined contextual factors that were affecting play in the ethnographic data. Environmental conditions, particularly changes to the weather, were found to affect RTP, perhaps more so for boys. Factors such as these often resulted in changing the setting of RTP, which was reduced when in proximity to adults or in inappropriate social or physical settings. This was particularly relevant to boys, who were more often allowed further from their villages and from the sight of adults, which was associated with elevated rates of RTP compared to girls who were often more restricted in their movement and freedom to choose their activity. Outside factors such as the influence of colonialism, often introduced by attendance at school, were also shown to influence rates of play, as boys would often play more actively in the playground, compared to girls whose play often became more sedentary or ceased in favour of activities such as reading magazines or talking. This suggests that contextual factors which were not picked up by the quantitative analyses are likely to contribute to gender differences in RTP, and that future analyses should consider rapidly changing factors when assessing play, particularly over time.

Common Findings for Non-Human and Human RTP

Previous research demonstrates that there are many similarities between non-human animal and human RTP, including the motor patterns (Scott and Panksepp, 2003), indications of positive affect (Pellis and Pellis, 1996), restraint (Lutz and Judge, 2017), and role-reversals (Power, 1999) which are involved in RTP. In the course of reviewing cross-species and cross-cultural patterns of play, a number of other common properties of RTP were identified, which could lead to insights into the biological and/or social functions of RTP. One of these properties were the components of RTP that males and females engage in. For the non-human mammal literature, specific components of RTP were associated with sex differences, with chasing and less aggressive aspects of RTP being associated with females, most notably in blue monkeys and chimpanzees. Similar patterns were picked up in the human literature, as when RTP was coded into wrestling and chasing behaviours, girls were more likely to engage in chasing rather than wrestling, and boys were more likely to engage in wrestling than chasing. This was further explored in the qualitative analysis of the ethnographic data, where I considered wider contexts of play. Across cultures, girls and boys were often expected to engage in different play activities according to their gender, often along the lines of traditional gender roles where girls would engage in play involving household tasks and boys would often imitate hunting or warfare. This often resulted in more physically active and aggressive play for boys compared to girls, which may be reflect sex-differentiated life history patterns, such as preparation for higher levels of competition for males, or cultural factors, such as gender roles and the preparation for male activities in adulthood such as hunting.

Another common conclusion across the animal and human analyses was that changes to the environment over small time scales may be affecting engagement in play, and therefore sex and gender differences in RTP due to factors having different effects for males and females, although this could not be appropriately assessed by the models I used. Variation in rates of RTP were reported for animals as a result of seasonal changes, both due to differences in energy availability and differences to the availability of suitable play partners. This was supported by evidence in humans, where children engaged in higher rates of play when weather was good and when they could play in groups which were of the appropriate age and sex. This may have affected the data in similar ways, as variation within a species or group introduces noise into the data. Future research into sex and gender differences in RTP could focus on smaller-scale changes which affect engagement in RTP, with a specific focus on how these changes could differentially affect males and females, or boys and girls. This could be achieved by being aware of changes which happen over timescales, such as changes in weather, and incorporating such factors into the coding process.

Interactions between Biological and Cultural Factors

In Chapter 1, I considered that individual predispositions may interact with environmental factors to determine rates and patterns of RTP for individuals, affecting sex and gender differences in RTP. The results of this thesis could suggest that RTP may be a rapidly changing trait due to changes in the environment throughout ontogeny, and therefore sex and gender differences vary over time, and are not necessarily picked up by the quantitative comparative analyses in this thesis, which cannot take changes over such short timescales into account. Although it was important to first establish the variation in sex and gender differences in RTP across species, and then across cultures, in turn considering the biological and social factors affecting rates of RTP, future studies may turn to considering the interactions between biological and cultural factors which influence sex and gender differences in RTP. As a result of factors such as genetics, development, and changes to the environment interact, rates of RTP may change for males and females, resulting in changes to sex and gender differences over time.

In the discussion of Chapter 6, I first consider the potential functions of RTP and other play activities, as most of the ethnographies I examined highlighted the importance of RTP in various domains of physical, social, and cognitive development. However, the importance of each domain varied based on factors such as the environment and the subsistence style of each culture. This further interacted with factors such as gender and the gender norms which were tied to play. For example, boys were more likely to play at hunting and warfare, where these skills were important for adult men, whereas girls were more likely to play at house or domestic chores, where these skills were important for adult women. This suggests that potential biological tendencies for girls and boys to engage in different levels of RTP may interact with cultural factors, as cultures where developing physical skills were equally important for boys and girls tended to display less gender differences in RTP. Therefore, future studies should consider the potential interactions between biological and cultural factors, where cultural norms could reinforce or lessen gender differences in RTP.

Future studies could consider RTP from a biocultural approach, emphasising the role of interactions between biological and cultural factors in the development of behaviour (Khongsdier, 2007). Bioculturalism emphasises the relationships between biological and sociocultural aspects which underlie human behaviour, explicitly emphasising the intertwined nature and dynamic interactions between physical, social and cultural environments (Zuckerman and Martin, 2016), particularly during the growth and development period where behavioural plasticity is high (Thomas, 2016). A biocultural approach could centre evolutionary concepts such as adaptation, but could also take into account the interactions between biology and the role of culture and social dynamics in determining behaviour (Hoke and Schell, 2020).

An example of a theoretical basis on which to model this variation could be based on Waddington's epigenetic landscape model, which is designed to explain the relationships between genotype and phenotype, through the image of a surface which is underpinned by genetic variation as a result of natural selection, and a rolling ball that travels through the landscape in way determined by developmental processes and interactions with the environment (Jamniczky et al., 2010). The model can be applied to social behaviours, such as RTP, through thinking about how interactions between conspecifics are influenced by epigenetically mediated changes which affect factors such as physiological phenotype, resulting in changes to behaviour (Seebacher and Krause, 2019). For example, neuroendocrine factors such as the hypothalamus-pituitary-adrenal (HPA) axis respond to environmental changes and social interactions, modifying social behaviour. In the case of RTP, changes to the environment, whether physical or social, could interact with hormonal mechanisms, resulting in rapid changes to RTP behaviour. These effects could be moderated by sex, where male mammals tend to have higher levels of testosterone than females (Hines, 2006). This is also true for humans, where boys display higher levels of testosterone compared to girls throughout various stages of development (Matchock, Dorn and Susman, 2007; Lamminmäki et al., 2012). This is likely to be relevant to development and the expression of RTP behaviours, as hormones including testosterone have been implicated in higher levels of RTP, in both animal and human studies (Jarvis, 2007; Grebe et al., 2019). I suggest that future studies focus on modelling the reciprocal interactions between individual predispositions for RTP with environmental constraints and facilitators of the behaviour, potentially considering the mechanisms which mediate such interactions, which could include the hormonal mechanisms which underlie RTP, all of which are affected by sex and gender. An example of how future models of RTP could be constructed is seen in Figure 7.1, which shows the interactions between ultimate and proximate factors which may contribute to RTP, across evolutionary, developmental, and short-term timescales.

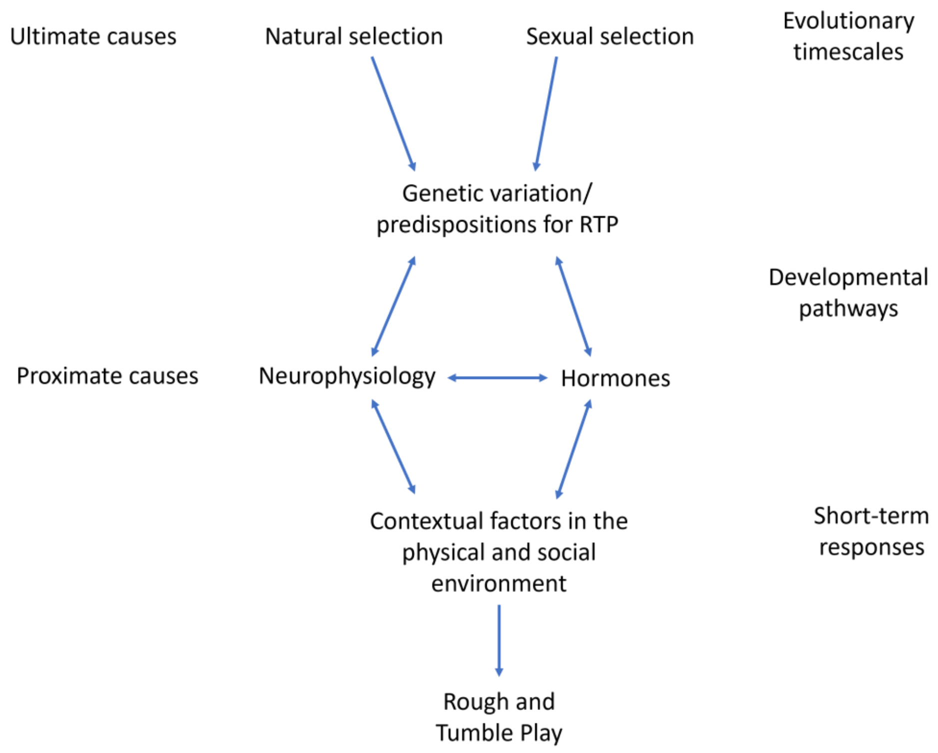

Figure 7.1 *Example of a potential theoretical model for determining rates of RTP in relation to sex and gender differences.*

Limitations of the Research

There were various methodological issues affecting the data used in this thesis, for both the non-human and human analyses, such as small sample sizes. Although I took care to maximise the sample size for both non-human and human analyses, various factors resulted in limitations on sample size. For the non-human mammal data, I chose to undertake a systematic review in order to ensure that as many studies, and therefore the largest range of species, could be included in my analyses. However, factors such as taxonomic bias, which I explored in Chapter 3, were reflected in the data gathered by systematic review, as mammalian orders such as primates and carnivora were over-represented to a statistically significant degree. This limited the number of species which could be included in subsequent analyses, and led to species being classified based on limited data. Similarly, for the cross-cultural studies, although all cultures within the SCCS were considered, sample size was limited based on a lack of data, as many of the ethnographies which were considered when coding the data did not contain enough information to make a judgement on the presence of RTP, particularly for girls (see Figure 5.1). This led to the decision to take a subset of ethnographies to explore the data in further detail, as the limited sample size may have been an issue when quantitatively analysing the data.

Another example of methodological issues comes from the limitations of using secondary data, as many of the studies and ethnographies included in data collection were not longitudinal, and did not capture variation in RTP over time. Developmental change is continuous, and it is likely that the function of a behaviour can change throughout ontogeny (Bateson and Laland, 2013), which should be taken into account when studying the adaptive function of RTP. Due to issues with sample size, I decided to include data concerning all non-adult RTP, to maximise the amount of data included in each analysis. This was also a pragmatic decision for the human data, as ethnographers often did not specify ages of the children involved in the play they were describing. However, where possible, I have included data on age of the individuals involved in each study or ethnography, as seen in Table 3.2, where the age of the animals included in each study is recorded if possible, and in the qualitative analysis of the ethnographic data, where I consider changes to play regarding age differences.

Noise in the data may also have been introduced by the various measurements and definitions of RTP that were used in both non-human and human studies. Table 3.2 summarises the studies included in the systematic review of sex differences in mammalian RTP, showing the range of measurements of RTP. Within these measurements, ethograms differed between studies, as various components of RTP were only relevant to certain species, or changed depending on the interests of the researcher. Care was taken to exclude studies which included definitions of RTP that did not match that used in this thesis, and the definition of RTP is given for each study, but it is possible that the behaviour which was measured varied by species and/or study. For the human studies, I took great care to be consistent in my own definitions (see the coding scheme in Chapter 5 and Appendix F), but it is possible that other researchers may define each category differently, leading to inconsistencies with the wider literature. It is also possible, particularly due to the age of the ethnographies used, that definitions of play varied to those used in this thesis, and were therefore excluded from the data.

Finally, I consider the methodological limitations introduced by variation in sampling in both the animal and human literature, including differences in sample sizes and the time scale of research. Animal studies ranged from observation of sessions which lasted minutes, to years spent observing the same group of animals. This is further compounded by the range of settings in which data was collected. For example, animal studies included wild, provisioned, and captive groups, and there were large amounts of variation even within these groups, such as enclosure size and enrichment provided, which was difficult to assess and compare between studies. Similarly, although ethnographies are based on longitudinal data collection, the collection of ethnographies in Chapter 6 describe time periods ranging from 1 year to over 50 years, and describe various types of subsistence society, including variation in subsistence style. However, these variations have been discussed throughout, and may contribute to differences in RTP.

Overall, although I acknowledge that noise in the data may be an issue, I am fairly confident that the analyses included are still reliable, and that the conclusions drawn from analysing the data are still useful for shaping future research. Where issues with noise in the data may have been introduced, I have endeavoured to be as transparent as possible about the data which were included in the analyses, and have undertaken qualitative analysis to further explore the conclusions drawn from the quantitative analyses. Future studies could focus on longitudinal data, to explore sex and gender differences throughout juvenility and childhood, which could address the issues with the use of secondary data analysis. In addition to this, I recommend that future studies on RTP move towards using a standardised definition of the behaviour, and that more studies are generated regarding sex and gender differences so that future comparative studies have larger banks of data to draw from.

Significance of the Research

With regards to mammalian RTP, this research is significant as no prior study has systematically investigated the extent to which male biases in RTP are consistent across species. Through the process of systematic review, I have presented evidence that although RTP is commonly male biased, findings were highly variable both within- and between-species, and sex differences were both smaller and less consistent than expected. Analyses of the distribution of sex differences in RTP showed low levels of phylogenetic signal, which suggests that sex biases in RTP have evolved independently, rather than as a result of shared history between species. Although the narrative synthesis of the systematic review findings points to a range of potential factors which may underlie sex differences in RTP, including intrasexual competition, sexual dimorphism, and sex-biased dispersal, phylogenetically informed quantitative analyses suggest that these factors may not be strongly associated with sex biases in RTP, and that it instead may be a rapidly changing trait. Both quantitative and qualitative analyses suggest that factors such as changes to the environment, whether physical or social, may be more likely to affect sex differences in RTP, although other methodological considerations which introduced noise to the data must also be considered.

With regards to human RTP, reviews of ethnographies in the eHRAF database also found male biases, with boys being more likely than girls to engage in RTP across cultures, especially for wrestling rather than chasing behaviours. This confirmed previous analyses of gender differences in RTP which suggested male biases, with a wider range of cultures. The distribution of gender differences in RTP did not seem to be patterned by phylogenetic history, as phylogenetic signal was consistently low, or spatial proximity, as spatial autocorrelation was also low, suggesting that long term vertical and horizontal transmission of social norms may not underlie gender differences in RTP. I investigated various cultural factors that may have been associated with gender differences in RTP, including marriage and descent system, food uncertainty, ideologies of male toughness, and the age of marriage for girls, all of which were unlikely to be associated with gender differences in RTP. This may have been a result of biased data, limited sample size, or again due to the rapidly changing nature of RTP. Further investigation of gender differences in RTP across cultures using qualitative methods suggests that engagement in RTP is related to the function of the behaviour, as RTP was linked to physical development, gaining knowledge about the environment, and practicing skills which were necessary for adulthood, which was often tied into gendered roles within that culture, such as hunting. However, qualitative analyses also supported the link between engagement in RTP and contextual factors which may change rapidly, including proximity to adults, environmental conditions, and social settings.

Conclusions

Overall, this thesis provides evidence that sex differences in RTP are unlikely to be distributed across mammalian species according to shared evolutionary history, and that gender differences in RTP across human societies are unlikely to be distributed according to shared cultural history or spatial proximity. I have investigated various biological and cultural factors which are thought to underlie the sex and gender differences in RTP, none of which seem to be likely to contribute according to these models. This may be due to various methodological factors, including issues with the measurement and definitions of RTP, variation in sampling, or issues with sample sizes, or could be due to the rapidly changing nature of sex and gender differences in RTP due to variations in the environment. These are significant findings as they contribute to understanding of sex and gender differences in RTP, and call for a number of improvement to future research in the area, including carrying out further research with more mammalian species and a wider range of human cultures, using stricter and more consistent definitions and measurements of RTP. Future studies should consider the interactions between biological and cultural factors which affect RTP across development for both males and females, potentially considering models such as epigenetic landscapes to capture the interactions between genetics, physiological mechanisms, and factors which affect RTP over the course of development and short-term timescales. I suggest that future studies make use of systematic review and mixed methods analyses of data, to ensure that data sets used in comparative methods are comprehensive, high quality, and appropriately used.

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Appendices

Appendix A – Data Sources for Chapter 4

Variable	Species	Source
Male body mass	**All species**	Myhrvold 2015
	except:	
	Suricata suricatta	Kappeler et al. 2019
	Alouatta palliata	Rowe & Myers 2016
	Alouatta pigra	
	Ateles geoffroyi	
	Callicebus cupreus	
	Gorilla gorilla	
	Lemur catta	
	Pan troglodytes	
	Pongo abelii	
	Pongo pygmaeus	
	Leontocebus fuscicollis	
	Saimiri sciureus	
	Capra ibex	Loison et al. 1999
	Odocoileus hemionus	
	Gazella cuvieri	Pérez-Barbería and Gordon 2000
	Ovid candansis	
	Canis latrans	Johnson et al. 2017
	Lynx lynx	
	Prionailurus bengalensis	
	Microtus ochrogaster	Dewsbury et al. 1980
	Marmota flaviventris	Schulte-Hostedde 2007
	Urocitellus beldingi	
	Urocitellus columbianus	
	Desmodus rotundus	Delpietro & Russo 2002
	Marmota marmota	Sartorelli et al. 2004
	Mesocricetus auratus	Gatterman et al. 2002
Female body mass	**All species**	Myhrvold 2015
	except:	
	Suricata suricatta	Kappeler et al. 2019
	Alouatta palliata	Rowe & Myers 2016
	Alouatta pigra	
	Ateles geoffroyi	
	Callicebus cupreus	
	Gorilla gorilla	
	Lemur catta	
	Pan troglodytes	
	Pongo abelii	
	Pongo pygmaeus	
	Leontocebus fuscicollis	
	Saimiri sciureus	
	Capra ibex	Loison et al. 1999
	Odocoileus hemionus	
	Gazella cuvieri	

	Ovid candansis	Pérez-Barbería and Gordon 2000
	Canis latrans	Johnson et al. 2007
	Lynx lynx	
	Prionailurus bengalensis	
	Callithrix jacchus	Rowe & Myers 2016
	Microtus ochrogaster	Dewsbury et al. 1980
	Marmota flaviventris	Schulte-Hostedde 2007
	Urocitellus beldingi	
	Urocitellus columbianus	
	Desmodus rotundus	Delpietro & Russo 2002
	Marmota marmota	Sartorelli et al. 2004
	Mesocricetus auratus	Gatterman et al. 2002
Mating system	*Odoceilus hemionus*	Mabry et al. 2013
	Canis latrans	
	Canis lupus	
	Lynx lynx	
	Hydrochoerus hydochaeris	
	Microtus ochrogaster	
	Urocitellus columbianus	
	Capra ibex	Loison et al. 1999
	Odocoileus hemionus	
	Alouatta palliata	Rowe & Myers 2016
	Alouatta pigra	
	Ateles geoffroyi	
	Callicebus cupreus	
	Callithrix jacchus	
	Felis catus	Cohas & Allainé 2009
	Marmota marmota	
	Suricata suricatta	
	Oryx dammah	Lukas & Clutton-Brock 2013
	Ovis canadensis	
	Sus scrofa	
	Tayassu pecari	
	Arctocephalus australis	
	Arctocephalus galapagoensis	
	Halichoerus grypus	
	Phoca vitulina	
	Desmodus rotundus	
	Equus caballus	
	Marmota flaviventris	
	Mesocricetus auratus	
	Rattus norvegicus	
	Urocitellus beldingi	
Sex-biased dispersal	*Alouatta palliata*	Greenwood 1980
	Macaca mulatta	
	Macaca fuscata	
	Chlorocebus aethiops	
	Colobus guereza	
	Erythrocebus patas	

	Papio anubis	
	Papio hamadryas	
	Theropithecus gelada	
	Pan troglodytes	
	Gorilla gorilla	
	Urocitellus beldingi	
	Marmota flaviventris	
	Microtus ochrogaster	
	Loxodonta africana	
	Ovis canadensis	
	Cercopithecus mitis	Dobson 1982
	Lemur catta	Handley & Perrin 2007
	Saimiri sciureus	
	Lophocebus albigena	
	Papio cynocephalus	
	Ateles geoffroyi	
	Alouatta palliata	
	Macaca nigra	Faust & Thompson 2000
	Rattus norvegicus	Stenseth et al. 1992
	Cercopithecus ascanius	
	Tursiops truncatus	Natoli et al. 2005
	Felis catus	Devillard et al. 2004
	Suricata suricatta	Doolan & Macdonald 1996
	Desmodus rotundus	Wilkinson 1985
	Macropus rufogriseus	Cockburn 1989
	Alouatta pigra	Van Belle & Di Fiore 2022
	Callicebus cupreus	Mayeaux 2008
	Callithrix jacchus	Jack et al. 2009
	Cercocebus atys	
	Procolobus rufomitratus	
	Pongo abelii	Sugiyama 2017
	Rhinopithecus roxellana	
	Leontocebus fuscicollis	Goldizen et al. 1996
	Elephas maximus	Vidya & Sukkumar 2005
	Marmota marmota	Farand et al. 2002

Appendix B – Density and Trace Plots for Chapter 4

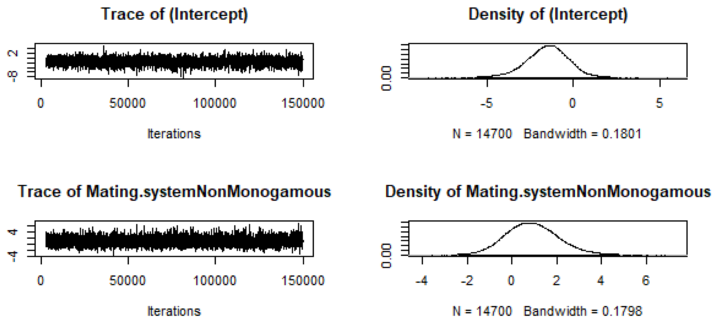

Figure B.1. *Mating system model diagnostic plots.*

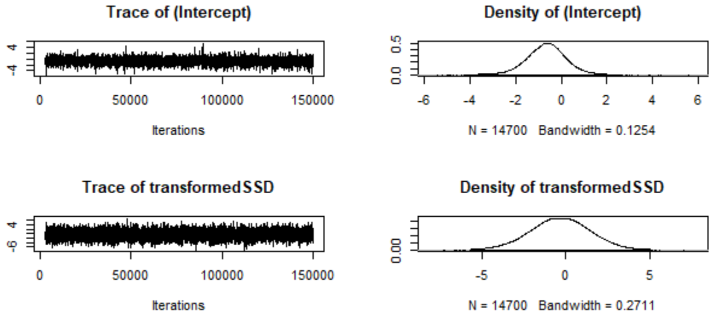

Figure B.2. *SSD model diagnostic plots.*

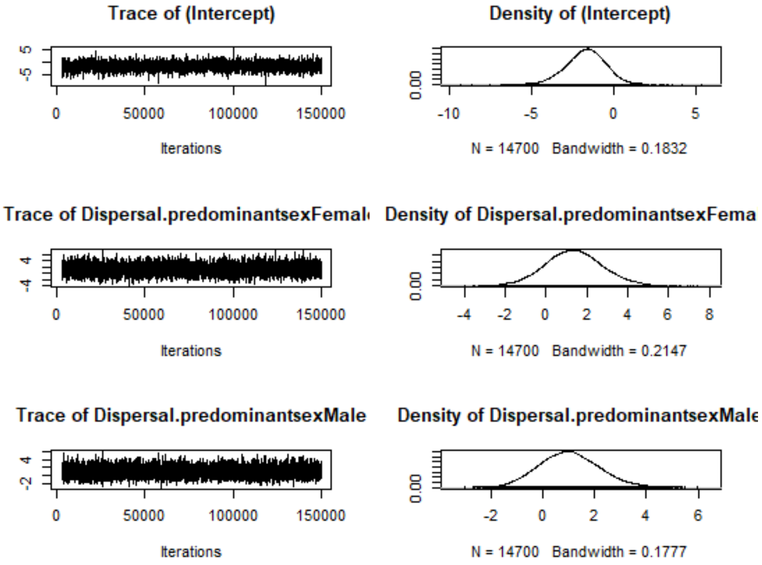

Figure B.3. *Dispersal model diagnostic plots.*

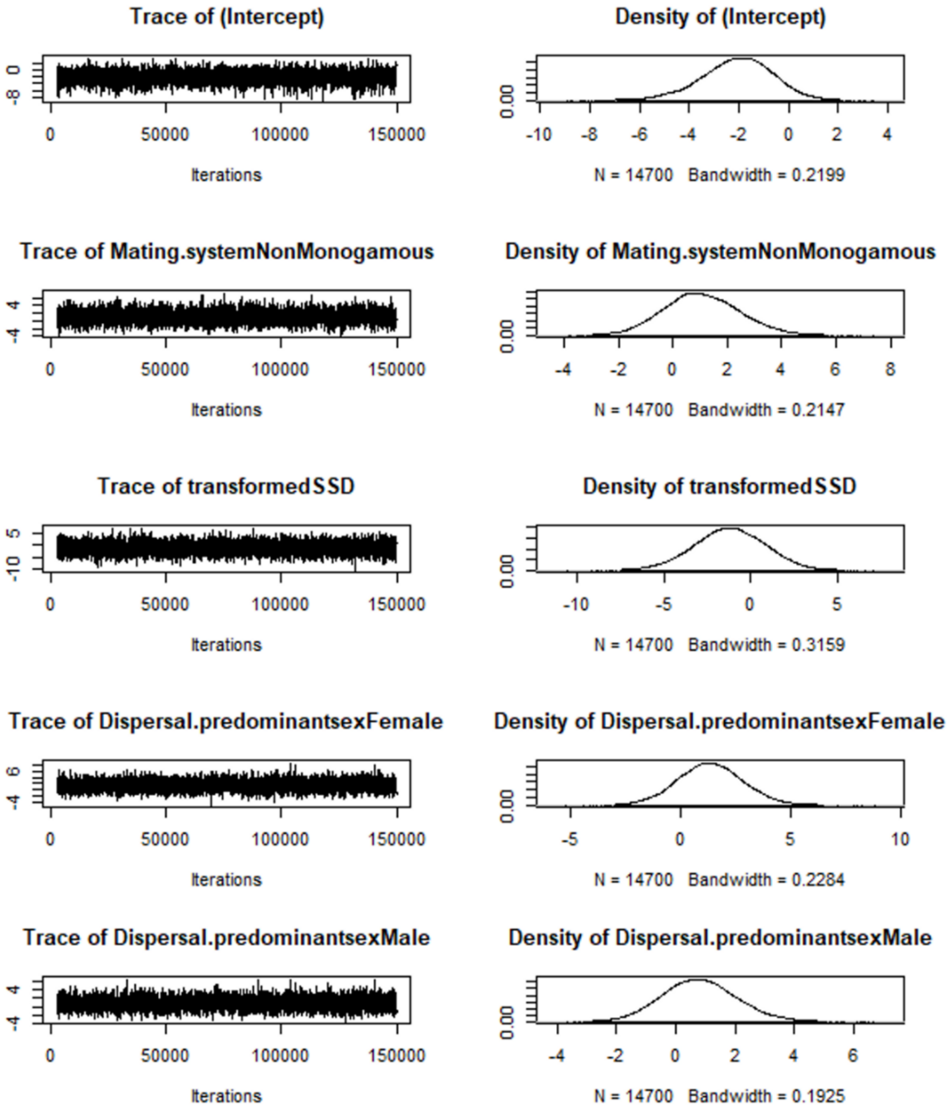

Figure B.4. *Full model diagnostic plots.*

Appendix C – Correlation Matrix for Chapter 4

Correlation matrix of predictor variables.

Variable	Mating System	Dispersal	SSD (transformed)
Mating System		0.31*	0.41**
Dispersal	0.31*		0.13
SSD (transformed)	0.41**	0.13	

* denotes significance, p<.05, ** denotes significance, p<.01

Appendix D – Single Variable Model Results for Chapter 4

Results of single variable models.

Model	Parameter	Mean	Lower 95% CI	Upper 95% CI	ESS
1	Intercept	-1.5271	-3.9713	0.9233	4171
	Mating System (Non-Monogamous)	0.9537	-1.2737	3.3006	3597
2	Intercept	-0.6710	-2.5503	0.9979	7284
	SSD	-0.2662	-3.7908	3.0968	0.885
3	Intercept	-1.6383	-4.1136	0.7966	3969
	Sex-biased Dispersal (Female)	1.3183	-1.5599	4.0090	3626
	Sex-biased Dispersal (Male)	1.0082	-1.2233	3.3213	3234

Intercept = a mathematical constant; Parameter = explanatory variables included in the model; Mean = mean value of the posterior distribution; 95% CIs = the true value of a parameter with a probability of 0.95, given the data; ESS = effective sample size, the information content of a sample MCMC chain.

Appendix E – Heritability Plots for Chapter 4

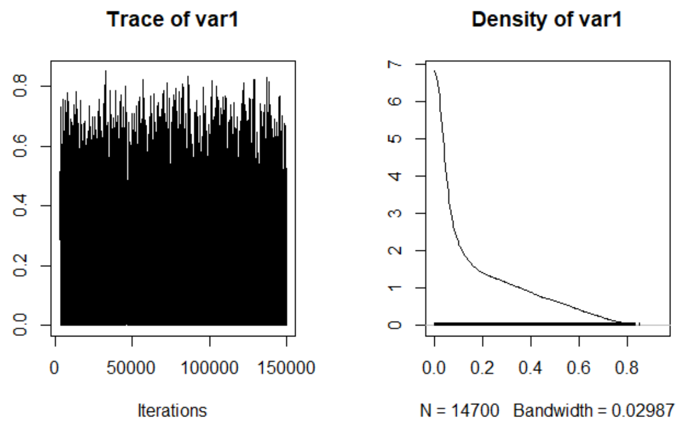

Figure C.1. *Mating system model heritability plots.*

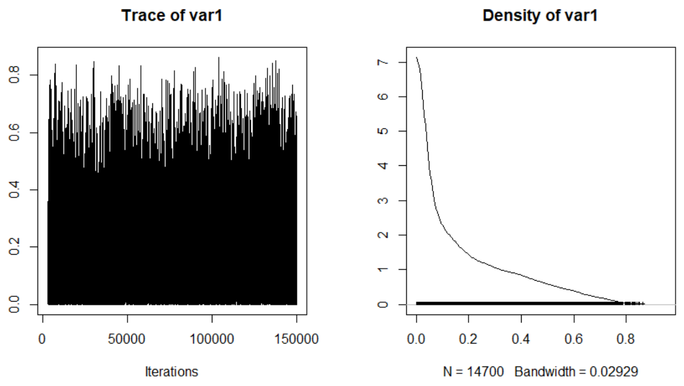

Figure C.2. *SSD model heritability plots.*

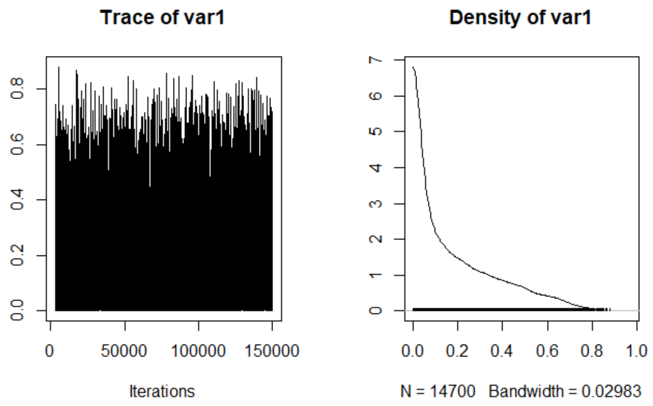

Figure C.3. *Dispersal model diagnostic plots.*

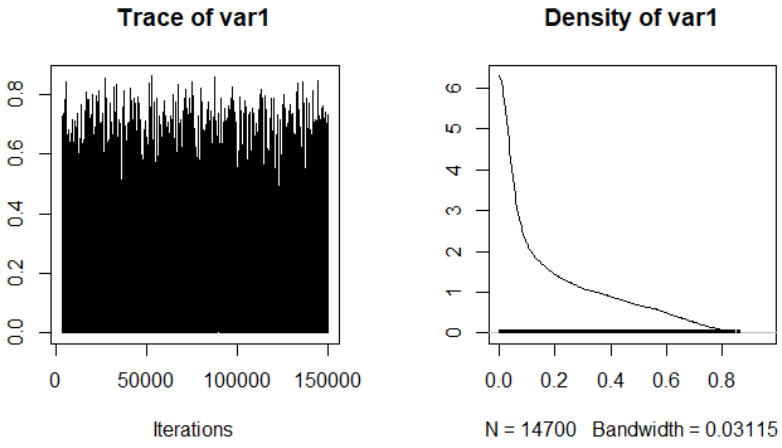

Figure C.4. *Full model diagnostic plots.*

Appendix F – Coding Scheme for Chapter 5

Theoretical definition of variable – Rough and tumble play (RTP)
(Pellegrini, 2002)
R&T typically composed of: run, chase, flee, wrestle, open hand hit – generally accompanied by smiles or play face – afterwards, children generally stay together and/or move towards other cooperative/social games or behaviours – children often alternate roles (e.g. self-handicapping)
NOT aggression, which is composed of: closed hand hits, shoves, pushes, and kicks – generally accompanied by frowns or crying – afterwards, children generally separate – children will not alternate roles (the aggressor remains the aggressor throughout)

(Pellegrini and Smith, 1998)
Rough-and-tumble play refers to vigorous behaviours such as wrestling, grappling, kicking, and tumbling that would appear to be aggressive except for the playful context; chasing is sometimes included within this definition

Operational definition of variable – split into chasing and wrestling
Behaviours described for children/non-adults. Both behaviours must occur exclusively within a playful context, either described as play or accompanied by a display of enjoyment (e.g. laughing, smiling, play face, etc.). Interactions should not be categorised as RTP if they appear aggressive (accompanied by frowns and/or crying). May include descriptions of playing war and/or sham combat as RTP if the following behaviours are described as components of that behaviour. Include descriptions of RTP which are included as part of purely physical games e.g. wrestling or racing within a contest, but do NOT include organised sports or games as part of ceremonies/rituals.

Wrestling RTP
Contact behaviour (e.g. wrestling, grappling, kicking, tumbling, pushing) that appears within a playful context and with alternation of roles.

Chasing RTP
Descriptions of running, chasing and fleeing behaviours which occur within a playful context and with alternation of roles.

Coding Schemes:

Boys Wrestling RTP
0. No wrestling RTP – ethnographer states that boys do not, or rarely, engage in wrestling RTP behaviours
0.5. Inferred absence – ethnographer describes the typical play activities of boys in sufficient detail to be able to infer that if wrestling RTP is not mentioned it probably is absent or rare
1. Boys participate in wrestling RTP – ethnographer describes boys engaging in wrestling RTP behaviours
9. Not enough information – ethnographer does not mention wrestling RTP of boys, or does not provide enough information to make a judgement

Girls Wrestling RTP
0. No wrestling RTP – ethnographer states that girls do not, or rarely, engage in wrestling RTP behaviours

0.5. Inferred absence – ethnographer describes the typical play activities of girls in sufficient detail to be able to infer that if wrestling RTP is not mentioned it probably is absent or rare
1. Girls participate in wrestling RTP – ethnographer describes girls engaging in wrestling RTP behaviours
9. Not enough information – ethnographer does not mention wrestling RTP of girls, or does not provide enough information to make a judgement

Boys Chasing RTP

0. No chasing RTP – ethnographer states that boys do not, or rarely, engage in chasing RTP behaviours
0.5. Inferred absence – ethnographer describes the typical play activities of boys in sufficient detail to be able to infer that if chasing RTP is not mentioned it probably is absent or rare
1. Boys participate in chasing RTP – ethnographer describes boys engaging in chasing RTP behaviours
9. Not enough information – ethnographer does not mention chasing RTP of boys, or does not provide enough information to make a judgement

Girls Chasing RTP

0. No chasing RTP – ethnographer states that girls do not, or rarely, engage in chasing RTP behaviours
0.5. Inferred absence – ethnographer describes the typical play activities of girls in sufficient detail to be able to infer that if chasing RTP is not mentioned it probably is absent or rare
1. Girls participate in chasing RTP – ethnographer describes girls engaging in chasing RTP behaviours
9. Not enough information – ethnographer does not mention chasing RTP of girls, or does not provide enough information to make a judgement

General Instructions

Using the eHRAF database, use the Advanced Search function. Add all cultures and add the subjects ‘childhood activities [857]’ OR ‘Games [524]’ OR ‘Athletic Sports [526]’. After searching, use the narrow results function to restrict results to the Standard Cross Cultural Sample (SCCS). Then, begin to randomly sample cultures from this list.

Record meta-data, coding, and relevant quotes using the coding sheet, which contains the columns: Name of Society, Sample, Identifier, Alternative Society Names, Time Frame, Location, Data Sources, Conder Name, Date Coded, Boys Wrestling, Boys Wrestling Quotes, Girls Wrestling, Girls Wrestling Quotes, Boys Chasing, Boys Chasing Quotes, Girls Chasing, Girls Chasing Quotes, Other Notes.

The same activity can be recorded as both chasing and wrestling RTP, if it contains both components of the behaviour. Do NOT use intermediate scores. Absence of RTP for boys or girls can be inferred if the ethnographer describes the typical play activities of that gender, but does not mention RTP.

Appendix G – Density and Trace Plots for Chapter 5

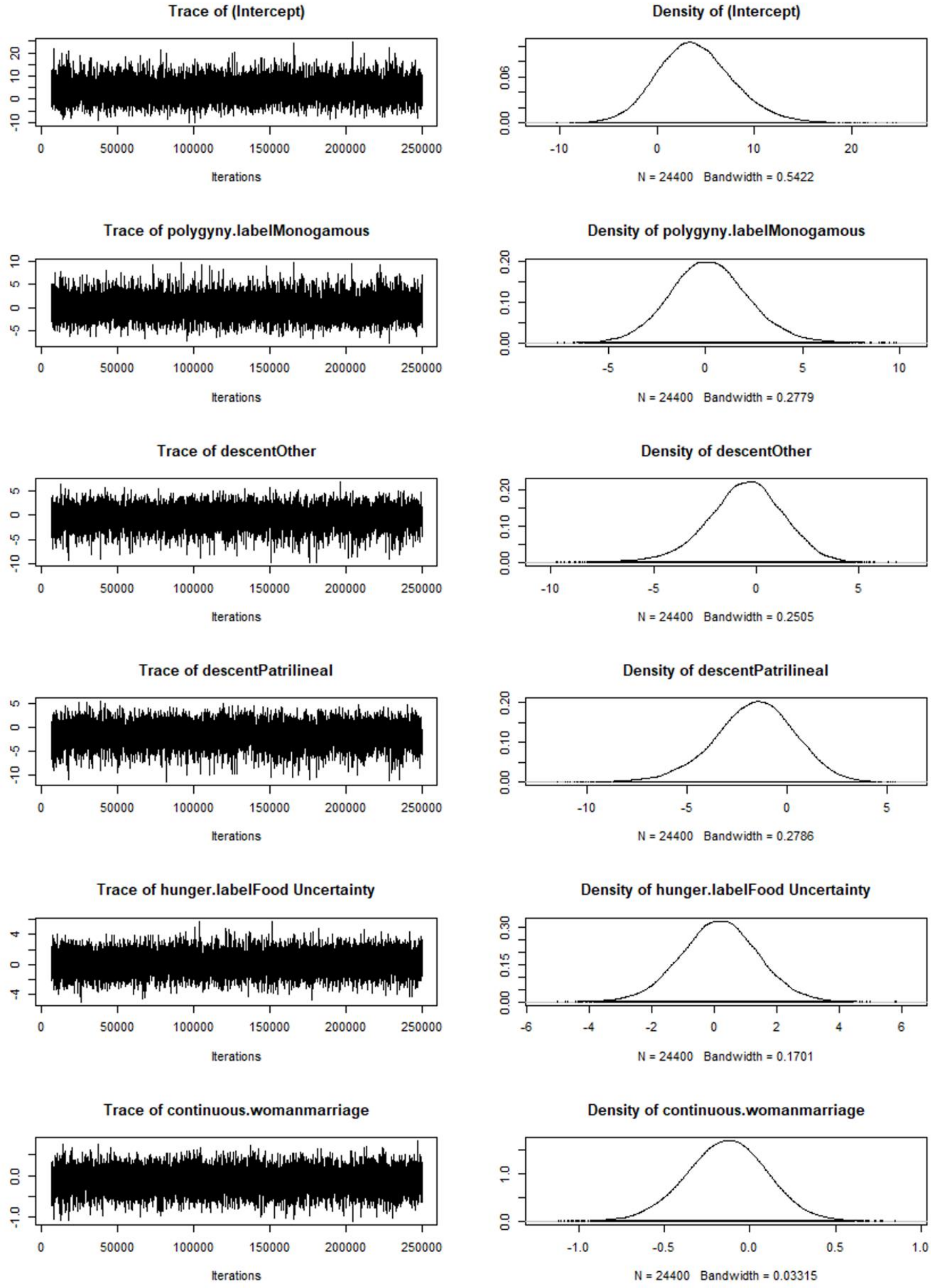

Figure E.1. *Density and trace plots of each model parameter in the girls RTP regression model using genetic and linguistic data.*

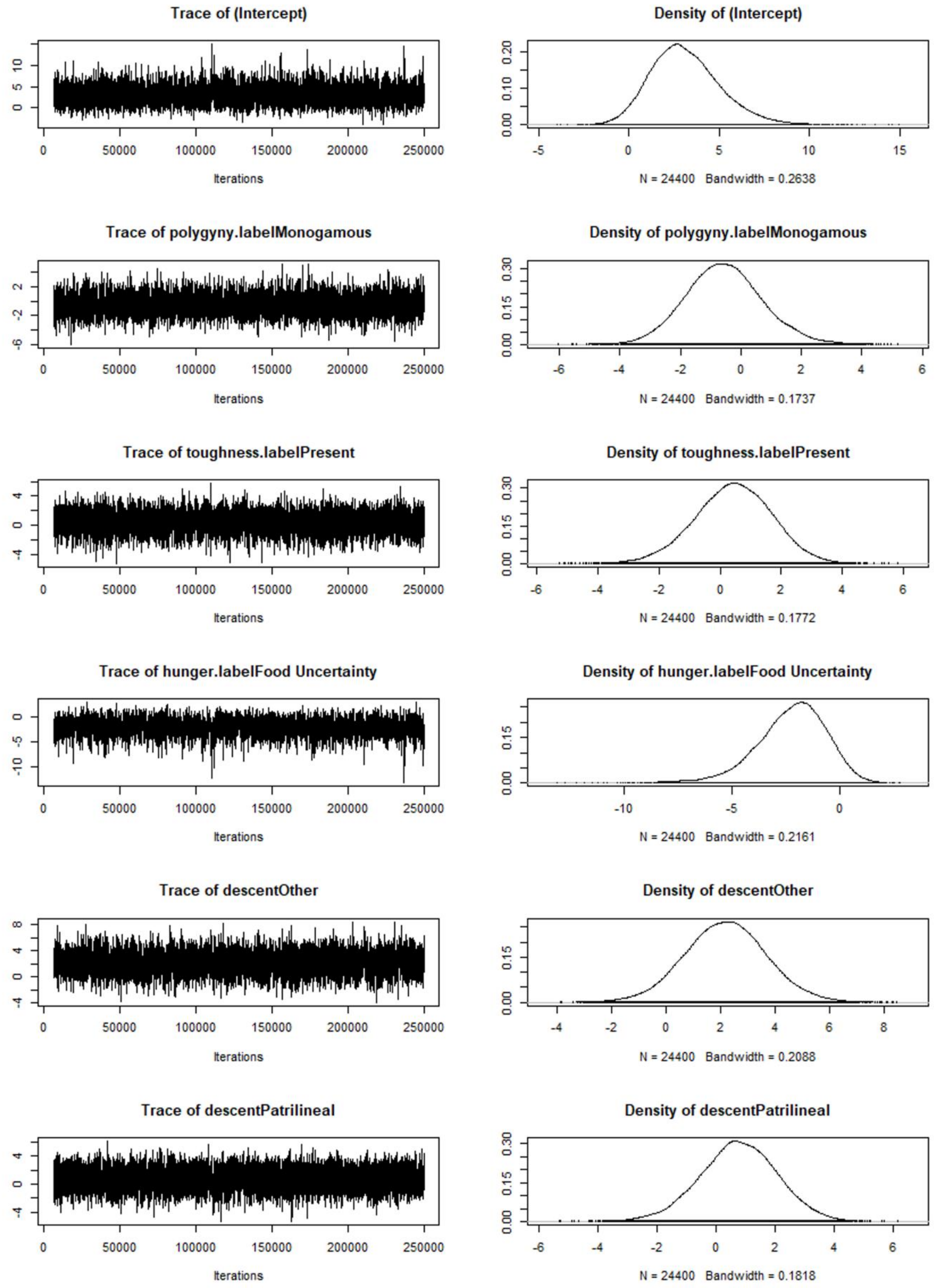

Figure E.2. *Density and trace plots of each model parameter in the boys RTP regression model using genetic and linguistic data.*

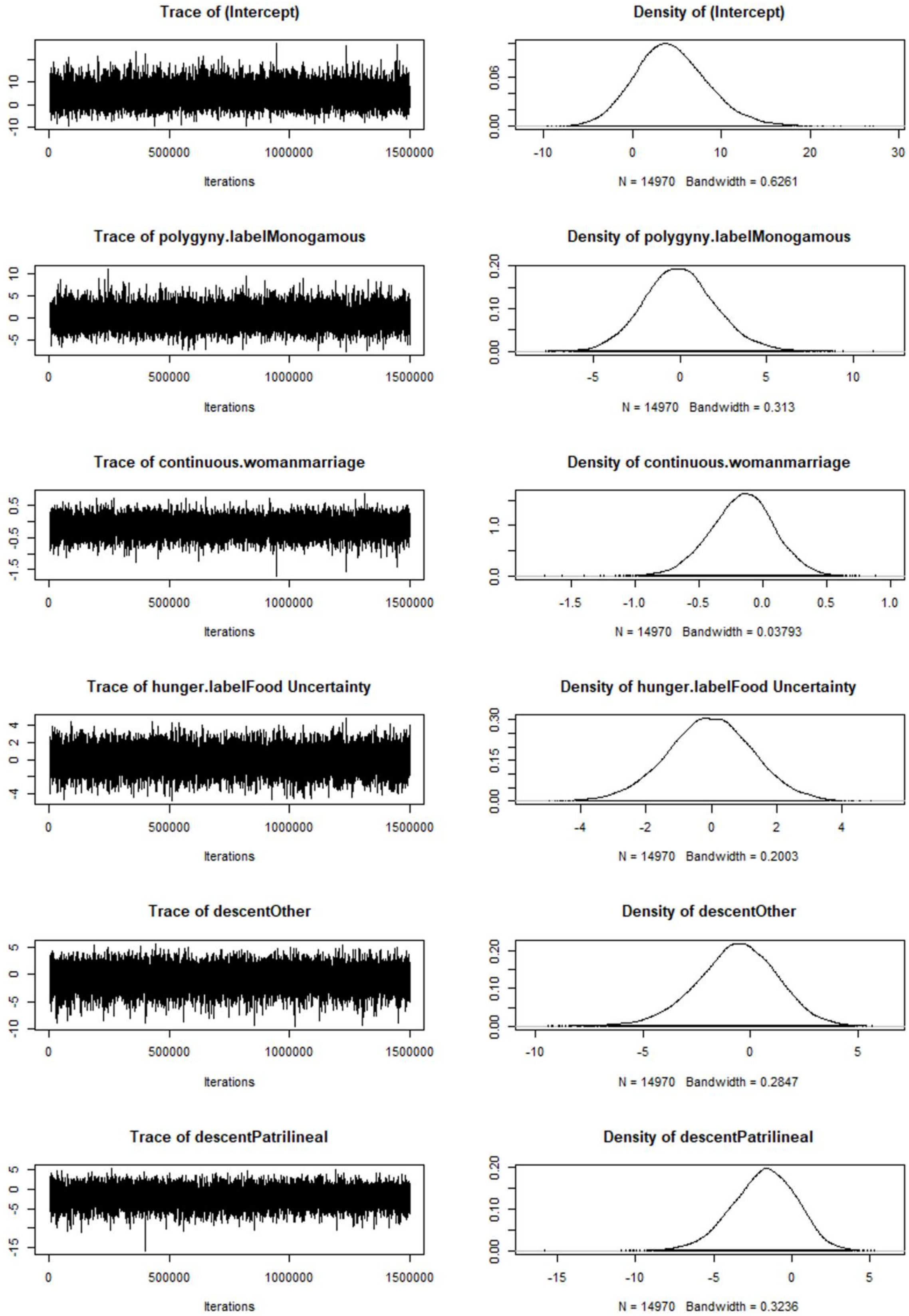

Figure E.3 *Trace and density plots for the girls RTP regression model using spatial data.*

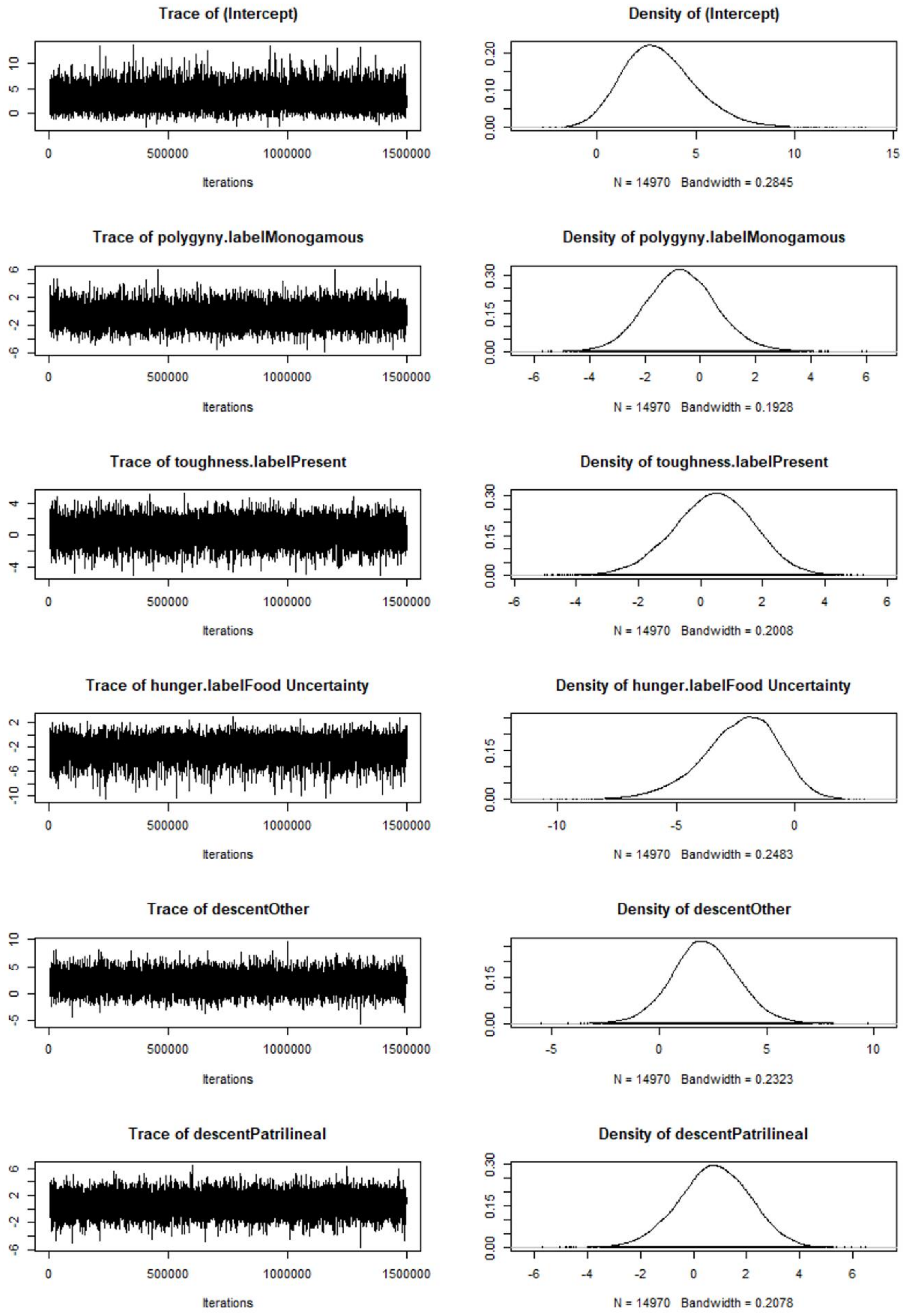

Figure E.4. *Trace and density plots for the boys RTP regression model using spatial data.*

Appendix H – Correlation Matrix for Chapter 5

Correlation matrix of predictor variables.

Variable	Polygyny	Ideology of Male Toughness	Hunger	Age of women at marriage	Descent
Polygyny		-0.04	-0.06	0.13	-0.05
Ideology of Male Toughness	-0.04		0.27*	-0.12	0.12
Hunger	-0.06	0.27*		-0.09	0.14
Age of women at marriage	0.13	-0.12	-0.09		-0.22
Descent	-0.05	0.12	0.14	-0.22	

* denotes significance, p<.01

Appendix I – Heritability Plots for Chapter 5

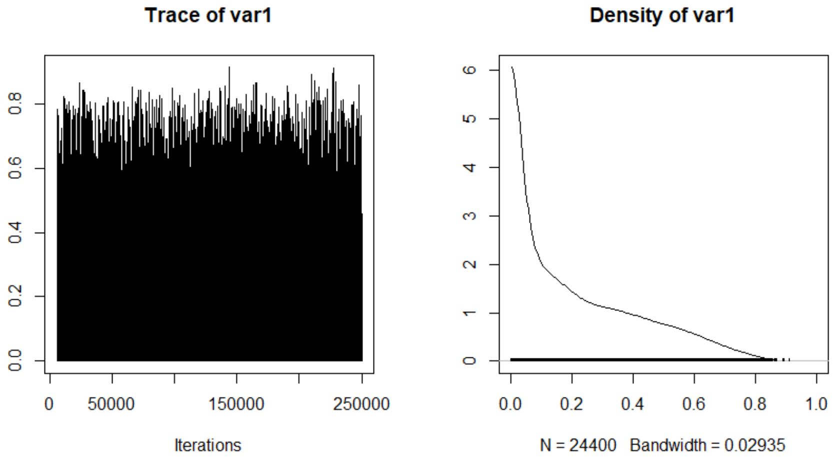

Figure 7. *Heritability plots for the girls RTP regression model using genetic and linguistic data.*

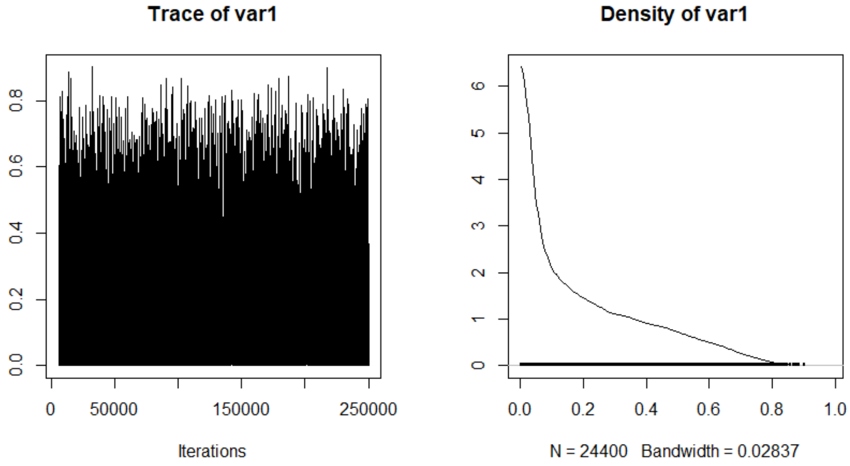

Figure 9. *Heritability plots for the boys RTP regression model using genetic and linguistic data.*

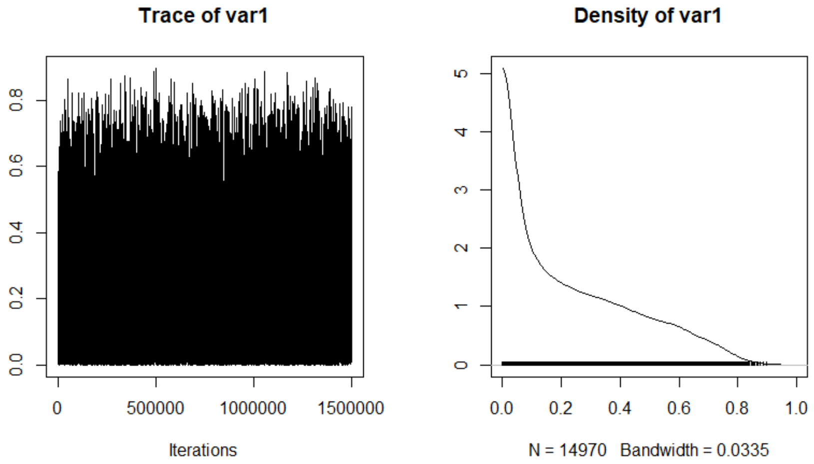

Figure 11. *Heritability plots for the girls RTP regression model using spatial data.*

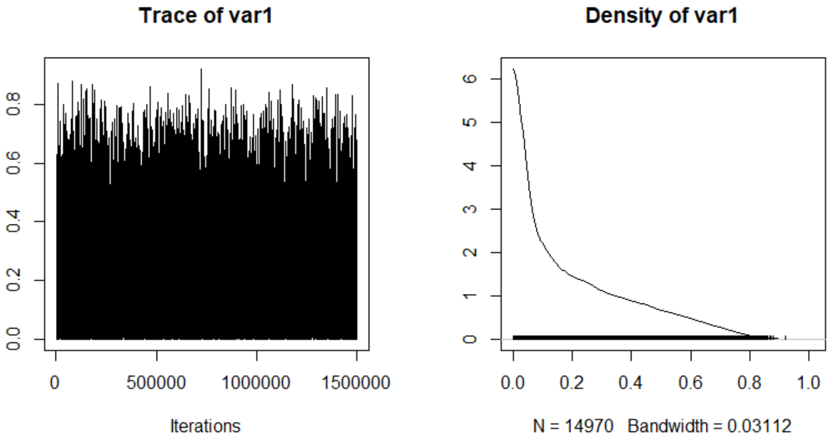

Figure 13. *Heritability plots for the boys RTP regression model using spatial data.*

Appendix J – Link to figshare

See https://figshare.com/projects/A_Cross-Species_and_Cross-Cultural_Comparative_Analysis_of_Sex_and_Gender_Differences_in_Rough_and_Tumble_Play/161254 for R code and data