The Role of Social Play in the Development of Wild Mountain Gorillas (*Gorilla beringei beringei)* at Bwindi Impenetrable National Park, Uganda

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Abstract of Dissertation

The Role of Social Play in the Development of Wild Mountain Gorillas (*Gorilla beringei beringei)* at Bwindi Impenetrable National Park, Uganda

Social play is found in almost all mammals and many other animals, suggesting it has a high benefit-to-cost ratio, yet there remains little consensus about its evolutionary function. Many different hypotheses have proposed costs and benefits of play, but these hypotheses can be difficult to test in a mutually exclusive framework. The 'motor training hypothesis' posits that play is a platform for honing motor skills. The 'social relationship hypothesis', postulates that the benefit of play has two components; 1) it helps develop and hone skills to interact socially and 2) it is a framework to form social relationships. Other hypotheses have proposed that play behaviour is energetically costly, and its frequency of occurrence is constrained by energy availability. Most research has centred around describing the ontogeny of play which does not provide consistent support for any one hypothesis.

This dissertation presents a new framework to better distinguish between competing hypotheses to further understand the function of social play behaviour, which is then implemented in the study of wild immature mountain gorillas (*Gorilla beringei beringei)* from Bwindi Impenetrable National Park, Uganda. Chapter 1 introduces the subject of social play, what it is and why gorillas are a good model for exploring functional hypothesis of play. Chapter 2 reviews previously published studies of social play across all mammals, examines the current evidence in support of different hypotheses and discusses the difficulties in studying play. Chapter 2 concludes by proposing a study framework to better delineate between the proposed functions of social play. This new

framework is then employed in the subsequent three chapters, which outline novel research on social play in immature mountain gorillas of Bwindi Impenetrable National Park. Chapter 3 investigates the biological, ecological and social correlates of variation in rates of social play, with the aims of examining if patterns of immature play rates support predictions of motor and social development hypotheses based on adult behavioural patterns and to test if social play is energetically constrained. Chapter 4 explores play partnership preferences based on age and sex and examines if play partnerships are stable over time and correlated with immature and maternal partnerships in proximity, with the aim of distinguishing motor development, social skill development and social bond formation functions of play. Chapter 5 analyses the costs and benefits of social play, focusing on how time and energy spent in play trade-off with time spent in other daily activities and energy spent in growth. Chapter 5 also explores the potential benefits of play by examining correlates between play and developmental milestones. Chapter 6 provides a summary of the main findings of the dissertation and the conclusions that can be drawn from this study.

Overall, this dissertation provides a comprehensive framework to study social play from multiple perspectives and presents novel findings for Bwindi mountain gorillas, with broader implications for the study of play behaviour across mammals. We show that sex differences in social play during immaturity may be related to sex differences in reproductive strategies and social behaviour in adult mountain gorillas. We find higher play rates in males than females, particularly during 2-6 years of age, supporting both a social and motor development function of play, as males were predicted to need these skills more for competitive interactions. Additionally, we show that play is likely

energetically constrained as individuals played more before being weaned and during periods of higher fruit consumption. We also show variation in play partnerships patterns; immature gorillas prefer play partners similar to their own age, males prefer male partners, but females have no partner sex-preference. Play partnerships were stable from year to year suggesting that bond formation could be a function of play. Our sex specific patterns suggest that females and males are likely harnessing the behavioural flexibility of play to gain different benefits from it, with males likely gaining more motor and fighting skills beneficial for dominance and physical competition. Furthermore, we show possible trade-offs between play and other functions such as growth and feeding, suggesting that play is at times prioritised over these other activities. Additionally, we show that increased play rates correlate with earlier age of attainment of developmental milestones, specifically agonistic and proximity milestones. Therefore, play ontogenies likely are related to other measures of behavioural development.

We found support for all four major hypotheses tested in this study: motor training hypothesis, social skill development, social bond formation and energetic constraints hypothesis. Specifically, we demonstrate how studying play partnerships can aid in delineating support for the two different social hypotheses for the evolution of play. Furthermore, we show how ecological variables and trade-offs with body size can test the energetic constraints hypothesis. We suggest future research examining structural elements of play, including play types and how these connect with developmental benefits to better distinguish between motor and social hypotheses. Additionally, including more direct measures of energetics and growth will provide better information about energetic trade-offs, beyond what we have already documented.

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Chapter 1: Dissertation Introduction

1.1 Overview

Despite its ubiquity amongst mammals, researchers are yet to fully understand the evolutionary functions and benefits of play (Burghardt, 2005; Fagen, 1978, 1981; Lafreniere, 2011; Power, 2000). Given that play is highly conserved in mammals, this implies that it has a high benefit-to-cost ratio and should have significant fitness benefits (Caro, 1988; Pellis et al., 2015). Play is multifaceted and as such usually is defined by several criteria: 1) has limited immediate function, 2) is spontaneous, rewarding, or voluntary, 3) differs in form or timing from more serious behaviours, 4) is repetitive but occurs in varying forms, and 5) is performed during relaxed periods (Burghardt, 2012). Social play differs from other types of play (e.g. locomotor and object play) in that it involves multiple individuals interacting in an affiliative manner. Thus, as the only type of play that implicitly involves a social interaction component and shows more pronounced sex differences than other types of play (Lafreniere, 2011), social play presents the best opportunity to test for sex differences and how these relate to both motor and social development functions of play.

Two common explanations for the benefits of play are embedded in the 'motor training hypothesis' (Bekoff & Byers, 1981) and the 'social relationship hypothesis' (Baldwin & Baldwin, 1974). The motor training hypothesis posits that play is an opportunity to build and hone physical skills (Bekoff & Byers, 1981). The social relationship hypothesis combines two functions of play: 1) the development of social skills and 2) the formation of social bonds (Baldwin & Baldwin, 1974; Meaney et al., 1985; Poirier & Smith, 1974). Social play is more common in immature individuals than

adults, but the fitness or developmental benefits of play may be seen during immaturity and/or throughout adulthood (Burghardt, 2014; Fagen, 1981). However, the costs of play, including the time spent, energetic costs and risks of play, are likely to be consolidated to the immature period, when play occurs at its highest rates (Caro, 1988, 1995; Miller & Byers, 1991). Other hypotheses of play, such as the Surplus Energy Theory (Spencer, 1872), focus on the costs of play. Therefore, studies of play which include a framework for considering costs and benefits together will be more fruitful in understanding the functions of this behaviour, and how it is prioritised amongst other activities, such as growth (Berghänel et al., 2015). To date, however, studies of social play in mammals have largely focused on describing the ontogeny of play frequency, which often provides insufficient evidence to distinguish between different competing hypothesis for play. Delineating between competing hypotheses is further complicated by studies which treat object, solitary and social play as providing the same function.

1.2 Study species: mountain gorillas *(Gorilla beringei beringei)*.

The goal of this dissertation was to implement a new analytical framework to test competing hypotheses pertaining to proposed benefits and costs of social play behaviour, focusing on immature mountain gorillas from Bwindi Impenetrable National Park in Uganda. Play behaviour is more common in larger brained animals, such as primates (Iwaniuk et al., 2001). Non-human primates live in a large array of habitats and their lives are largely dictated by variation in both ecological and social environments, making them an informative group for simultaneously investigating the variation and multiple proposed costs and benefits of social play. Gorillas specifically, given their biological

variation and close evolutionary relationship to humans (Ruvolo, 1997) provide an excellent species to study the evolution of social play. Gorillas have slow life histories and long developmental periods in which social play is the most common social activity of immatures (Eckardt, 2010; Nowell, 2005). Gorillas are also the most sexually dimorphic great apes, and one of the most sexually dimorphic primates (Leigh & Shea, 1995). Gorillas live in male dominant groups, driven by high levels of male-male competition but female dominance hierarchies are weak (Robbins, 2010; Robbins & Robbins, 2018; Watts, 1992). Females and males have different life history strategies, adult behavioural patterns and levels of reproductive skew (Nsubuga et al., 2007; Robbins, 2010; Robbins et al., 2019, 2023; Vigilant et al., 2015). Therefore, if social play aides in the development of skills, we would expect different sexes to exhibit different patterns in social play and possibly derive different benefits (Lafreniere, 2011). Wild gorillas live in cohesive social groups, in which immature individuals usually cohabit with other immatures of varying ages, to allow a diverse range of play partnerships (Eckardt, 2010; Fletcher, 1994; Grebe et al., 2022).

This study specifically focused on wild mountain gorillas (*Gorilla beringei beringei*) inhabiting Bwindi Impenetrable National Park (BINP), Uganda. BINP is located in South-Western Uganda (0°53'–1°08'N and 29°35'–29°50'E) and covers an area of approximately 331 km^2 (Ganas et al., 2004; Nkurunungi et al., 2004). BINP (extending into Sarambwe Forest in Democratic Republic of Congo) is home to one of only two populations of mountain gorillas, comprising approximately 450 individuals, roughly 40% of the remaining mountain gorillas in the world (Granjon et al., 2020; Hickey et al., 2018). BINP and the only other remaining population of mountain gorillas, inhabiting the

Virunga Massif of Uganda and neighbouring, Rwanda and DR Congo, are separated by approximately 25 km of agricultural land, and are estimated to have split around 5,000 years ago (Roy et al., 2014; van der Valk et al., 2024).

To date, no research has been published on play behaviour of the Bwindi mountain gorillas. However, previous research on the Virunga gorillas demonstrates higher rates of play of immature male than females, specifically rough-and-tumble play (Eckardt, 2010; Fletcher, 1994). Age-and-sex partner preferences suggest that individuals prefer play partners of similar ages and similar sex, particularly male-male dyads (Fletcher, 1994; Grebe et al., 2022). Furthermore, research suggests that play rates are likely constrained by energy availability with higher rates of play pre-weaning and more adult-adult play during the bamboo season, while feeding on this energy dense food (Eckardt, 2010; Fletcher, 1994; Grueter et al., 2016).

Despite their genetic similarities, the two populations of mountain gorillas have divergent life histories where interbirth intervals are longer in Bwindi gorillas (5.1 years) than Virunga gorillas (4.2 years), despite a similar age for adult females at first birth (10.1 and 10.5 years, respectively) (Robbins et al., 2023). Furthermore, weaning ages are later in Bwindi gorillas (4.5 years) than Virunga gorillas (3.3 years) (Eckardt et al., 2016; Robbins & Robbins, 2021). These differences demonstrate that Bwindi mothers invest in their offspring for longer periods, and their offspring become independent later, suggesting a longer developmental period. Whilst mountain gorillas largely subsist on terrestrial herbaceous vegetation, Bwindi gorillas spend an average of 15% (range = 0-70%) of their monthly feeding time consuming fruit, which presents a more temporally and spatially variable food source herbaceous vegetation (Ganas & Robbins, 2005;

Nkurunungi et al., 2004; Ostrofsky & Robbins, 2020; Wright et al., 2015). Whilst Virunga gorillas seasonally consume bamboo, it is not a significant part of the diet of Bwindi gorillas, and fruit seasons in Bwindi provide periods of higher energetic intake than bamboo consumption in the Virunga mountain gorilla range (Wright et al., 2015). Thus, given these life-history differences and greater temporal variation in diet between the two populations of mountain gorillas, the Bwindi gorillas provide an opportunity to examine the relationships between play and both social and ecological variation, particularly when focusing on energetic trade-offs as this population may be more energetically constrained and developing more slowly.

1.3 Research design

In Chapter 2, we reviewed a number of hypotheses that have been developed to explain play behaviour, focusing on those that propose evolutionary costs and benefits of play and have testable predictions: the motor training hypothesis (Bekoff & Byers, 1981); the social relationship hypothesis, broken down into its two component parts, social skill development and social bond formation (Baldwin & Baldwin, 1974; Meaney et al., 1985; Poirier & Smith, 1974); and the energetic constraints hypothesis (surplus energy theory) (Spencer, 1872). We suggested a framework for studying social play, which includes ontogenetic variables of play, structural components of play (such as play partnerships) and analysing costs and benefits, which are necessary components to be able to delineate between the different hypotheses of social play.

We implemented this framework by integrating long-term data with novel data collected from six mountain gorilla groups that have been closely monitored since 1998

in the Eastern, Ruhija Sector of BINP, a higher altitude area of the park (2,100 – 2,500 m). Given prior research on Virunga gorillas found that play is highest during infant (0-3 years) and juvenile stages (3-6 years) (Eckardt, 2010; Fletcher, 1994), this dissertation concentrated on 33 immature Bwindi gorillas, 0-8 years old. Female gorillas are considered adults at 8 years of age (Breuer et al., 2009; Harcourt et al., 1980). We used long-term behavioural records collected since 2000 and novel body size data collected using non-invasive parallel laser photogrammetry since 2017 (including 29 gorillas, of known ages, which reside in other sectors of BINP), to evaluate the objectives outlined below.

1) *Determine how biological, ecological and social factors influence the amount of time spent in social play* ***(Chapter 3)***. Previously reported sex differences are most prominent in social play and likely linked to adult behavioural and reproductive roles (Lafreniere, 2011; Meaney et al., 1985). Furthermore, play can be linked to factors beyond biological characteristics, such as ecological variables (Asensio et al., 2022; Berghänel et al., 2015; Moebius et al., 2019), partner availability (Mayhew et al., 2020; Mendonça et al., 2017; Moebius et al., 2019) and maternal characteristics (Cameron et al., 2008; Gard & Meier, 1977; Wang et al., 2021). Consistent with motor and social development hypotheses, we predicted that males would play more than females, in particular during the juvenile period, to develop motor and social skills, because they exhibit more physical competition and sustain more social affiliative relationships than do females (Robbins, 2010; Watts, 1992). Furthermore, we predicted that play rates would be higher when there were more available play

partners. We predicted that if social play was energetically constrained, rates of play would be positively correlated with periods of higher fruit consumption, when energy intake is higher. We further predicted higher play rates from offspring of multiparous mothers compared to primiparous mothers and higher play rates for individuals that are not yet weaned compared to those that are not weaned, as these states provide more energy supplementation from the mother through breast milk consumption. We analysed over 6000 hours of focal data on 33 immature gorillas from the ages of 0.5 to 8 years, to examine how monthly play rates (proportion of focal time spent in play) varies with biological (age, sex, weaning status, mother parity), ecological (fruit eating), and social factors (partner availability) over a period of 18 years.

2) *Examine how play partnership preferences change based on biological characteristics (age and sex), time and in relation to other affiliative activities* ***(Chapter 4)***. Play during immature development may demonstrate the beginning of adult-like behavioural patterns. For example, play partnerships are likely to mirror adult patterns of social interactions (Fröhlich et al., 2020; Lafreniere, 2011; Maestripieri & Ross, 2004). Play partnership patterns are a useful way to separate out different developmental hypotheses of play. The motor training hypothesis predicts that individuals will prefer same age partners to reduce risk from vigorous play. Furthermore, partnership patterns can help delineate between the two components of the social relationship hypothesis (social skill development and social bond formation). Social skill development predicts sex specific patterns akin to agonistic and affiliative patterns of adult interaction, whilst social bond formation predicts stable dyadic play partnerships over time to create long-lasting affiliative

relationships. To understand what factors (age difference, sex, previous relationships, proximity, proximity of mothers) influence dyadic play partnerships we examined number of partners, evenness of play amongst partners and dyadic play association scores (a measure of strength of dyadic relationships, relative to how much each individual played with other individuals and in total) from yearly social networks of dyadic play relationships, in 32 immature Bwindi mountain gorillas (0.5 – 8 years old) over a 10 year period.

3) *Investigate proposed trade-offs and developmental outcomes of social play* ***(Chapter 5)***. Play has been linked to long-term fitness and reproductive benefits (Fagen & Fagen, 2009; Lee & Moss, 2014; Théoret-Gosselin et al., 2015). In the absence of data spanning several decades, we can measure more immediate costs and benefits by examining trade-offs between play and growth and correlations between play and the age at key developmental milestones (Berghänel et al., 2015; Bründl et al., 2020; Heintz, 2014). Reproductive skew is high in male gorillas, and female gorillas shoulder the majority of the energetic costs of reproduction. Therefore, we predicted that greater time spent in play would be correlated with smaller than expected body size, particularly in females. Furthermore, we expected a trade-off between time spent in play and time spent resting. Finally, we expected individuals with higher play rates to attain physical and social developmental milestones sooner. To investigate the costs and benefits of social play in immature Bwindi mountain gorillas (0.5-8 years), we analysed 11 years of behavioural data from 30 individuals. We calculated monthly activity budgets, extracted 31 developmental milestones, and calculated body size-for-age variation using non-invasive parallel laser photogrammetry.

This dissertation provides a comprehensive framework for the study of social play and a methodology to link different ontogenetic patterns and structural variation (e.g. play partnerships) with different developmental functions. Furthermore, we provide the first detailed account of social play in Bwindi mountain gorillas, which is an important addition to the study of social play in gorillas, given their divergent life-history patterns compared to other previously studied gorilla populations.

Chapter 2: Background. Evaluating the hypotheses for the function of social play: Evidence from mammals.

Abstract

The evolution of social play in mammals continues to be an enigma. Play is ubiquitous in immature mammals, yet the immediate and/or long-term functions remain unclear. Despite many hypotheses suggested for the function of play, research has not produced a clear consensus on what the benefits are for this common behaviour. Research on play is marked by multiple difficulties, such as the lack of agreement on the definition of play, a large number of studies being focused on captive animals, small samples sizes, and a lack of longitudinal studies. Above all, a lack of standardisation in the research framework to test functions has led to many descriptive studies with inconsistent conclusions. The goal of this paper is to present a framework for the study of play to distinguish among its proposed functions, by reviewing past literature and variation in social play from multiple perspectives. The conclusions we see from this literature review strongly supports the need for multi-faceted research. Firstly, research must shift to focus on linking the variation in play to species specific behavioural, socio-ecological, and reproductive variation. Secondly, research must explore how the structural elements of play (e.g. play partnerships) can vary, as a mechanism to delineate different functions of play. Third, we must better understand the energetics of play and trade-offs between play and other activities such as growth. Finally, to examine the ultimate benefits of play, we must examine correlations between play rates and short-term developmental measures, and within long-term studies we must link play variation with direct measurements of

fitness. With new technology and more interdisciplinary research, there is increasing optimism that we can find consistent support for the functions of social play.

2.1 Introduction: What is play?

Play has been highly conserved within the tree of life (Fagen, 1981). However, there is little agreement on how it functions to provide an evolutionary benefit. Despite the universal ability to recognise play, a standardised working definition of play has not been reached. Some researchers argue that a definition is superfluous, given it is an easily identifiable behaviour (Chalmers, 1980); others suggest play will be easier to define when its functions are better known (Burghardt, 2005; Fagen, 1981). Both of these arguments pose limitations and a lead to the circular nature of the study of play. Researchers have created a suite of descriptions and categorisations focusing on structure and/or function, some of which are only specific to humans (see Table 2.1, formatted from Burghardt, 2005). Most researchers agree on a polythetic definition, in which an action must satisfy a suite of characteristics to be understood as play (Martin & Caro, 1985). One of the most popular definitions involves Burghardt's five criteria stating that play: 1) is a repeated behaviour 2) has limited immediate function, 3) is incompletely functional differing from more serious versions structurally, contextually, or ontogenetically, 4) is initiated voluntarily, 5) in displayed in a relaxed or low-stress setting (Burghardt, 2005).

In addition to difficulties in defining play, the arbitrary grouping of different types of play further complicates its study. Play has been categorised into three main types. (1) Solitary/locomotor play involves individuals moving around alone, without a

clear goal of the movement. (2) Object play involves play with an inanimate object, such as a ball or branch. (3) Social play involves interactive play between two or more individuals (Fagen, 1981; Graham & Burghardt, 2012). Different types of play are likely to have different functions and different evolutionary histories (Burghardt, 2014). Given the versatility of social play, it is an ideal behaviour to study as it can adapt to the different developmental needs of different species and individuals (Lafreniere, 2011). Play has been linked with the development of motor and social skills (Berghänel et al., 2015; Heintz et al., 2017). Furthermore, social play has been shown to improve children's social skills, an important finding when the recent pandemic limited social interaction (Arinalhaq & Mayar, 2022). Social play is seen as a platform to enhance cooperation, positive emotions and adaptability, all of which would have been highly advantageous to our human ancestors (Behncke, 2015).

Over the last century, increasing research has improved our understanding of the variation in play frequency (Burghardt, 2005). However, the question of the function of play remains largely unanswered. The conservation of social play in many lineages would suggest that it has a high benefit-to-cost ratio and has either been conserved across many species or evolved independently multiple times. For a behaviour to be preserved through evolution, there needs to be an overall net worth, i.e. the costs of performing a behaviour are outweighed by the benefits gained from performing it (Martin & Caro, 1985). However, the evidence that has been presented has little commonality across the wide breadth of study species. Furthermore, social play is not present in all species e.g. aardvarks (Burghardt, 2005), or all populations of the same species, e.g. squirrel monkeys (Baldwin & Baldwin, 1974).

Table 2.1: Descriptions of play compiled and quoted from Burghardt (2005), The Genesis of Animal Play.

Author	Definition	Structural / functional
Barnett (1998): Child Playfulness Scale (CPS)	"Consists of twenty-three statements grouped into five categories: cognitive spontaneity, social spontaneity, physical spontaneity, manifest joy, and humor." Pg 68	Structural
Bekoff and Byers (1981)	"Play is all motor activity performed postnatally that appears to be purposeless in which motor patterns from other contexts may often be used in modified form and altered temporal sequencing." Pg 55	Structural
Burghardt's (2005): 5 criteria of play.	"Limited immediate function" Pg 81	Functional
	"Endogenous component" Pg 81	Functional
	"Structural or temporal difference" Pg 81	Structural
	"Repeated performance" Pg 81	Structural
	"Relaxed field" Pg 81	Structural
Carr (1902): 5 special utilities of play	"Ease of reaction" Pg 43	Structural
	"Increased activity" Pg 43	Structural
	"Greater intensity of reaction, including emotions" Pg 43	Structural
	"Greater stimulation to growth and development" Pg 43	Functional
	"Increased variability or reactions and ideas" Pg 43	Functional
Clark and Millar (1998): children's play	"Non-literality transformation of meanings and actions, taking an 'as if' stand toward reality." Pg 66	Structural
	"Intrinsic motivation, activity done for its own sake, rather than being externally motivated." Pg 66	Functional
	"Positive affect - enjoyment or pleasure." Pg 66	Functional
	"Process flexibility - flexible use of an object as means, rather than action directed by the object." Pg 66	Structural
Fagen (1981)	"Behavior that functions to develop, practice, or maintain physical or cognitive abilities and social relationships, including both tactics and strategies, by varying, repeating, and/ or recombining already functional sub-sequences of behavior outside their primary context" Pg 45-46	Functional

Author	Definition	Structural / functional
Fagen (1993)	"Play is improvised performance, with variations, of skilled motor and communicative actions in a context separate from the environment in which behavior including these actions proximately increases reproductive success." Pg 56	Structural
Huizinga (1995)	"Play is voluntary (related to freedom), distinct from ordinary life, disinterested (unconnected with any immediate satisfaction of biological wants or needs; not goal directed), and dependent on some order or rules." Pg 69	Structural
Immelmann & Beer (1989)	"Behavior performed without the 'serious point' that such behavior has in its normal context." Pg 56	Structural
Kortmulder (1998)	"A free and creative form of individual or social behaviour, in which many motor and role patterns may be mixed in a graceful manner, often occurring without obvious external provocation." Pg 55	Structural
Maier (1998)	"An activity that imitates elements of goal-directed behavior but does not lead to an immediate goal." Pg 56	Structural
Martin and Caro (1985)	"Play is all locomotor activity performed postnatally that appears to an observer to have no obvious immediate benefits for the player, in which motor patterns resembling those used in serious functional contexts may be used in modified form. The motor acts constituting play have some or all of the following structural characteristics: exaggeration of movements, repetition of motor acts, and fragmentation or disordering of sequences of motor acts." Pg 55	Structural
Millar (1981)	"Voluntary" Pg 70	Structural
	"Paradoxical (out of context/ has no goal)" Pg 70	Structural
	"Exaggerated" Pg 70	Structural
	"May be accompanied by play signals" Pg 70	Structural
	"Random sequences of activities from different adult functional behaviour systems" Pg 70	Structural
	"May be repeated, ritualized or involve rules" Pg 70	Structural
Porter and Bundy (2001): Test of Playfulness (ToP)	"Scale is based on thirty-two observational items derived from four qualities felt to contribute to playfulness: intrinsic motivation, internal control, framing, and suspending reality" Pg 67	Structural

2.2 The goal of this paper: A framework to delineate between proposed benefits of play.

The goal of this paper is to present the main hypotheses for the function of play and consider how future studies can distinguish among them and test them more rigorously, the second part of which has largely been lacking in previous reviews of functional hypotheses (Burghardt, 2014; Graham & Burghardt, 2012). This review will focus solely on evidence for the function of social play. Whilst solitary and object play may serve important motor functions, they are unlikely to serve a social function due to their solitary nature. Social play is most common in mammals (Burghardt, 2005; Power, 2000). Whilst observations of play do occur in birds, fish, reptiles and amphibians, social play is not always the most common and observations of play are not as concentrated in the developmental stage, suggesting other potential drivers (Burghardt, 2005, 2015). Therefore, this review will mainly focus on mammals. Across species there are patterns of increased play in animals with larger relative brain sizes (Iwaniuk et al., 2001) and increased social complexity (Graham & Burghardt, 2012), suggesting social benefits. The amount of social play and size of play group also increase with social group size (Asensio et al., 2022; Baldwin & Baldwin, 1971; Toinon et al., 2022). This social component makes it particularly important to review mammalian literature given the heightened value of social connections in mammalian species, particularly primates (Silk, 2007). One can compare human social play with other mammals, to inform our understanding of the impact of play on human development (Burghardt, 2005). However, comparison between human and non-human primate play must be done with considered attention to the unique cultural and social environment in which human social play occurs. Therefore, a thorough

analysis of human play literature is outside the scope of this review, but some studies will be highlighted, (for a more comprehensive overview of human play literature see Johnson et al., 1999; Power, 2000; Sutton-Smith, 2000). Given the behavioural flexibility of social play, a comparative review of current available research enables us to see large scale patterns across species to help us understand the function of play.

We will review the hypotheses that have been presented to explain the evolution of play (Section 2.3), specifically focusing on ultimate and proximate hypotheses which present testable predictions about: motor skill development, social skill development, social bond formation and energetic constraints (but see Appendix A Table S2.1 for a list of classic theories). We will examine evidence for these hypotheses (Section 2.4), in three main categories: 1) evidence of fitness benefits - research that has directly tested long-term fitness or reproductive success (see Appendix A Table S2.2); 2) correlates of fitness - research that has examined correlation between play and metrics of fitness (such as skill acquisition; see Appendix A Table S2.2); and 3) pattern of variation – studies which analyse patterns of variation in play and link them to predictions that follow hypotheses for the functions of play (see Appendix A Table S2.3). All studies unless specifically stated are focusing on play in immature individuals, and we will be linking the variation in play to social structure and behavioural competences outside of play as adults. Table S2.2 and Table S2.3 (Appendix A) indicate the species studied, whether it was captive, wild or domesticated, the response variable, the explanatory variable and the relationship that was found between them. After reviewing the evidence, we will discuss common difficulties encountered in the study of play (Section 2.5) and offer potential solutions as a way forward (Section 2.6). Finally, we will suggest a proposed framework to study play

(Section 2.7), to improve our understanding of the evolutionary significance of this behaviour.

2.3 Hypotheses for the benefits of social play

2.3.1 Ultimate hypotheses

For play to have evolved one expects an increase in reproductive success or fitness related to the amount of time individuals spend in play. This could be driven by improvements in competitive ability, survival, or reproductive ability. Furthermore, for social play to be so highly conserved implies that it provides an increase in reproductive success, or costs are at least equal to its benefits. Studies detailing how play correlates with these developmental and behavioural changes are rare as they require larger longitudinal datasets (Berghänel et al., 2015; Heintz et al., 2017). However, given the many factors that contribute to survival and reproduction, the mechanisms underlying the relationship between play and these measures are not yet clear. Therefore, when examining correlations between play and fitness benefits it is difficult to separate out the support for either social or motor hypotheses.

Motor development benefits

Motor development hypotheses posit that play provides a context for physiological development related to performing motor functions such as building muscle, strength, coordination, and neural connections. These skills can impact survival and fitness as adults, because they play a large role in competition, movement, feeding and predator avoidance.

The **Exercise Theory** (Table 2.2) stresses that the function of play is centred on building strength and muscle and not developing specific motor skills, which are thought to be innate (Brownlee, 1954). Play makes up a large proportion of exercise for immature animals. Therefore, play could increase muscle development and strength, because of its energy intensive nature. A secondary prediction of the exercise theory is that the amount of play increases during periods of higher energy intake. It also predicts sex differences in play, if muscular development or strength is prioritised differently amongst the sexes, for instance for physical competition. Muscle development could be gained from locomotor or object play, not just social play (Smith, 1982).

The **Motor-training Hypothesis** (Table 2.2) has adapted the ideas of the exercise theory to encompass four areas involved in motor skills: bone thickening and remodelling, muscular development, cardiopulmonary development, and neural development (Bekoff & Byers, 1981). Motor training predicts that individuals prefer play partners of a similar age, size, and experience. Peers allow for more vigorous play with less risk of harm from older more powerful individuals (Byers, 1980). Similar to the exercise theory, sex differences in social play are expected when adult roles or morphology are sexually distinct. Given that the predictions of the exercise theory are encompassed within the motor training hypothesis, it is not possible to distinguish between them using correlational studies alone. Therefore, our review will refer to the motor training hypothesis only.

Social development benefits of play

There are two aspects to the **Social Relationship Hypothesis** of play (Baldwin & Baldwin, 1974, Table 2.2): 1) developing social skills and 2) building individual relationships (Meaney et al., 1985). These functions can be difficult to track and quantify and often studies do not clearly differentiate between these two aspects. We will refer to these two separate functions as 1) social skill development and 2) social bond formation and attempt to parse out the literature based on which of the two components each article supports.

Social skill development

The hypothesized **Social Skill Development** (Table 2.2) function of play posits that play is a platform to learn the skills that are necessary to interact socially with other individuals. This can involve refining social behaviour cues, creating a behavioural repertoire, learning about dominance and practising communication (Baldwin & Baldwin, 1974; Meaney et al., 1985; Poirier & Smith, 1974). This hypothesis suggests that individuals will develop some social skills innately but that provides an opportunity to improve these skills so that they become more effective. Beyond the prediction that younger individuals play more to learn social skills, this hypothesis predicts that if one sex has more social interactions as an adult, we would expect this sex to play more frequently and preferentially partner with the sex with whom they affiliate more with as adults.

Social Bond Formation

Social Bond Formation (Table 2.2) is a proposed acculturation function of social play, to establish bonds and strengthen relationships between different individuals within a social group (Meaney et al., 1985). This goes beyond learning the behaviours performed during social interactions (social skill development) and instead proposes that play is more important in facilitating the bonds to form individual relationships. Adult mammals, particularly primates display differentiated affiliative relationships and formation of social bonds can improve survival and reproduction (Feldblum et al., 2021; Ostner & Schülke, 2018; Schülke et al., 2010; Silk, 2007). If the primary benefit of social play is building dyadic social bonds among pairs of individuals, we would expect play partners to mirror partners for other affiliative behaviours. Additionally, we would expect individual play partners to be stable over time, in a similar degree to adult relationships are stable in that specific species. This hypothesis focuses on patterns of variation at the level of the individual. Therefore, studies that investigate play at individual scale are necessary to distinguish between the two proposed social functions.

2.3.2. Proximate hypotheses

Proximate drivers of play are another focus for hypotheses. Proximate drivers are not mutually exclusive from the ultimate hypotheses discussed above, but present new frameworks.

Energetic constraints

The idea that play is energetically costly links to the **Surplus Energy Theory** (Table 2.2), which suggests that play is a behaviour performed only when excess energy is available (Spencer, 1872). This theory posits that there are no functional benefits to play, explaining the behaviour instead as a by-product of excess energy. Play being under energetic constraints does not exclude it from also having functional benefits. Therefore, whilst we will discuss energetic constraints of play, it will not be in the original framework laid out by the Surplus Energy Theory.

Self-assessment theory

The **Self-assessment Theory** (Table 2.2) was proposed by Thompson (1996) in accordance with play preference research in sable antelopes. It posits that social play does not help develop skills, but it is a time to evaluate skill development in relation to other individuals. Accordingly, it is predicted that partners of the same age are preferred and in species with large differences in adult sex roles or morphology, play partners of the same sex would be more suitable to compare developmental progression. Additionally, the stability of play partners is important to be able to track developmental competence over time. The predictions of this hypothesis largely overlap with other theories (social skills development and social bond formation). For that reason, evidence for the self-assessment theory will not be focus of this review.

Training for the unexpected

The **Training for the Unexpected Hypothesis** (Table 2.2) proposes that skills learnt in play help in unforeseen circumstances during adulthood (Špinka et al., 2001). Training for the unexpected assumes that individuals purposely put themselves at a disadvantage during play (self-handicapping). Therefore, they are expected to play more with relatives, as known individuals are less at risk of cheating when self-handicapping occurs. If one sex is more likely to encounter novel situations, they would be expected to play more. As such, the dispersing sex may be predicted to play more frequently than the philopatric sex. Finally, when play partners are of differing ages and sizes, younger individuals are expected to initiate play because they have more to gain from the situation than older individuals who are more developed in their skills (Špinka et al., 2001). This theory only gives predictions that can be measured indirectly in patterns of variation in play behaviour. It is very difficult to measure the proposed direct benefits (performance in an unexpected circumstance), and therefore will not be discussed further.

Table 2.2: Ultimate and proximate hypothesis of play that present testable predictions. * denotes hypotheses reviewed in this manuscript.

Hypothesis	Conceptualisation	Major Predictions
Exercise Theory	Brownlee, 1954	Play is a mechanism to build muscle through exercise. More play when more energy. Sex differences according to the muscular differences in adults.
Motor-training Hypothesis*	Bekoff & Byers, 1981	Play improves bone thickening and remodelling, muscular development, cardiopulmonary development, and neural development. Individuals prefer play partners of a similar age, size, and experience.
Social Relationship Hypothesis	Baldwin & Baldwin, 1974	Play improves the development and learning of social behaviours and can help build social relationships.
Social Skill Development*	Baldwin & Baldwin, 1974, Piorier et al. 1978	Play allows for the development of social skills and social behavioural repertoire. Preference for same sex partners in play, similar to social partners in adulthood.
Social Bond Formation*	Meaney et al. 1985	Play helps to establish social bonds and strengthen relationships. Play partners should be stable over time and correlate with partners in other affiliative activities.
Surplus Energy Theory	Spencer, 1872	Play has no benefits and occurs when an individual has excess energy.
Energetic Constraints*		Play is dependent on energy availability and will occur more when energy availability is higher.
Self-assessment Theory	Thompson, 1996	Play is a means to evaluate one's own development relative to other individuals. Predicts partners of similar age and sex (in dimorphic species). Play partners would be stable over time.
Training for the Unexpected Hypothesis	Špinka et al. 2001	Play is a time to learn how to behave in unforeseen circumstances as adults. Assumes self-handicapping by older individuals. Peers and age-mates are preferred partners. Younger individuals initiate play more.

2.4 Evidence in support of hypotheses

2.4.1 *Evidence of fitness benefits*

Improved reproductive ability as a result of play has not been well studied and is not well supported. Neither reproductive age in African elephants (Lee & Moss, 2014) nor copulation rates in mink (Dallaire & Mason, 2017) showed relationships with amount of time in social play. However, chimpanzee males showed an earlier age of first mating with increased play (Heintz et al., 2017). Male mink showed a positive relationship between the amount of play and longer copulation durations, although female mink that played more had a longer latency to begin each bout of copulation, which is suggested to be a result of mate choice (Dallaire & Mason, 2017). Male dolphins that spent a larger time in the actor role in play herding conceived more offspring as adults (Holmes et al., 2024). Additionally, the presence of play in populations of squirrel monkey populations correlated with a larger repertoire of sexual behaviours, which potentially could be gained through socially learning within play (Baldwin & Baldwin, 1973).

The effect of play on survivorship has similarly been understudied. Increase in frequency of play has been shown to have a positive correlation with survival to independence in brown bears (Fagen & Fagen, 2009), and age of mortality in African elephants (Lee & Moss, 2014) and mountain goats (Théoret-Gosselin et al., 2015). Many factors contribute to survival and reproductive success such as dominance rank, social bonds, size and competitive ability, so if play is not directly linked to reproductive fitness and survival, it may be linked indirectly by impacting these other factors which correlate with fitness. In marmots (Blumstein et al., 2013) and wolves (Cafazzo et al., 2018), individuals that were more dominant in play achieved higher ranks outside of play.

However, given dominance is likely to be acquired differently in different species, through physical strength or coalitions, species specific predictions are beneficial when looking at dominance.

2.4.2 Evidence for motor development benefits

2.4.2.1 Correlates of fitness: motor skill acquisition

Experimental studies demonstrated that cerebellar synapse development and muscle fibre type differentiation coincide with periods of increased play in rats, cats and mice (Byers & Walker, 1995). A correlation also occurs between increased play and increased dendritic pruning (a maturation period, in which the strongest neurones are selected), in rats (Ham & Pellis, 2023; Stark, 2021). These physiological changes remained for the rest of their lives, and thus strongly support that motor skills development goes beyond just muscle development and strength.

Researchers have tested for the effects of time spent in social play with competence of motor behaviours later in life. Social play is linked with earlier attainment of specific motor skills, namely independent travel and riding dorsally in chimpanzee offspring (Heintz et al., 2017) and motor skill acquisition (jumping, running, hanging) in macaques (Berghänel et al., 2015). Social play is also linked with improved feeding competition and sensorimotor skills (obstacle negotiation test) in marmosets (Chalmers & Locke-Haydon, 1984) and improved motor skills in ground squirrels (Nunes et al., 2004). However, in marmosets the improvement after 3 weeks was no longer there after 10 weeks (Chalmers & Locke-Haydon, 1984). This would suggest that the improvement was a short-term benefit.

Competitive ability can depend on motor skill development, which can be correlated with play rates. Cheetahs showed a positive relationship between number of predation behaviours (crouching and stalking) observed in a play context with the number of these behaviours aimed at prey outside of play (Caro, 1995). Additionally, higher rates of contact play correlated with higher rates of patting, biting and grasping live prey that was presented to cubs from their mothers (Caro, 1995). In slow loris, aggressive postures in play mirrored those outside of play (Barrett et al., 2021). However, long-term correlations between play and competitive ability are less strong. Time spent play-fighting for immature meerkats had no correlation with fighting success as adults (Sharpe, 2005c). Similarly, white face capuchin monkeys that played more did not reach alpha position earlier (Perry et al., 2017). Other studies investigated aggression and found negative correlations between the amount of social play and aggression rates outside of play in humans (Saad et al., 2022), hamsters (Kyle et al., 2020) and wolves (Cafazzo et al., 2018). However, one cannot rule out social skill development in this context. Playing could be a platform to learn to mediate confrontation, which may have the effect of reducing levels of aggression outside of play.

2.4.2.2. Patterns of variation: implying motor development benefits from patterns of variation

a) Age partner preferences

Play partners of the same age are preferred for sifaka (Lutz et al., 2019), baboons (Lutz et al., 2019; Owens, 1975), Rhesus macaques (Kulik et al., 2015), Tibetan macaques (Mayhew et al., 2020), western lowland gorillas (Palagi et al., 2007), mountain

gorillas (Fletcher, 1994; Grebe et al., 2022), vervet monkeys (Fairbanks, 1993), oryx (Pfeifer, 1985), antelopes (Thompson, 1996), Siberian ibex (Byers, 1980), gazelles (Gomendio, 1988), bighorn sheep (Hass & Jenni, 1993), African elephants (Freeman et al., 2021), Belding's ground squirrels (Nunes et al., 2004) and wallabies (Watson, 1993). Contrastingly studies of slow loris (Barrett et al., 2021), golden lion tamarins (De Oliveira et al., 2003), and chimpanzees (Markus & Croft, 1995) revealed that individuals prefer partners of different ages. No partner preferences based on age were observed in captive squirrel monkeys (Biben, 1989), capuchins (Lutz et al., 2019) or adult bonobos (Palagi & Paoli, 2007). For species with greater levels of sexual dimorphism, it appears more common for individuals to prefer partners of the same ages; this does not hold true for sifaka. It may be that species which are more sexually dimorphic as adults have a tendency for associating with similar age partners during immaturity, because interacting with similar age and size peers will become more important for gain motor skills as individuals age.

b) Play-types: amount of energetic social play

We see an overarching pattern of more play in males, particularly in primates (Forster & Cords, 2005; Lonsdorf et al., 2018; Moebius et al., 2019; Shimada & Sueur, 2018; Wang et al., 2021; Winkler & Perry, 2022). However, given the overlapping predictions of motor and social skills development hypotheses, play frequency alone is not enough to separate out support for each of them, as in many primates the more competitive sex and the more social sex are often the same. However, examining time spent in more energetic types of play more closely aligns to motor skill acquisition. We

would expect sex-biases in aggression as adults to be mirrored in sex-biases of time spent in more energetic play types. More vigorous play categories include rough-and-tumble play and play fighting (sparring). This contrasts with the less intense categories of gentle play, rest play, mother infant play (Burghardt, 2005; Fagen, 1981; Power, 2000).

Most primates have male-led dominance hierarchies (Miller, 1993) and almost all primate studies showed that males immature engage in vigorous play more, as seen in hamadryas baboons (Abegglen, 1984), squirrel monkeys (Aghababian et al., 2021), baboons (Chalmers, 1980; Owens, 1975), blue monkeys (Forster & Cords, 2005), rhesus macaques (Gard & Meier, 1977), Tibetan macaques (Wang et al., 2021), mountain gorillas (Fletcher, 1994) and western lowland gorillas (Hoff et al., 1981; Palagi et al., 2007; but see Nowell, 2005). These patterns appear to be related to adult sex-specific behaviour and patterns vary between species. For instance, adult female bonobos have more agonistic interactions between them than adult males and the sexes are co-dominant; bonobo adult females showed a higher amount of contact play (Palagi & Paoli, 2007). Titi monkeys, which live in monogamous pairs, showed no sex differences in play wrestling (Chau et al., 2008). Baboon immature females demonstrated a higher frequency of mauling play (when one individuals is passive and being 'mauled' – females more commonly took both the passive and active role of mauling) (Owens, 1975). However, this was separate from wrestling play which was seen to be more common in males. An additional study on rhesus macaques (Hinde & Spencer-Booth, 1967) demonstrated no sex-bias in rough-and-tumble play contrary to Gard & Meier's (1977) results. Both these studies were on captive individuals and had small sample sizes (<15) (See Appendix A Table S2.3).

Studies of other mammals, similarly to primates, suggest the dominant or larger sex as adults performs more energetic play as immatures, while in monomorphic species no sex difference is observed. For instance, bighorn sheep (Berger, 1980), cattle (Brownlee, 1954), and oryx (Pfeifer, 1985), showed a male-bias for more energetic style social play or more contact behaviours within play, whilst, female hyenas spent more time than males in rough-and-tumble play than males (Pedersen et al., 1990). Beagles (Bekoff, 1974), coyotes (Bekoff, 1974), wolves (Bekoff, 1974), prairie voles (Chau et al., 2008), squirrels (Pasztor et al., 2001) and meerkats (Sharpe, 2005c) did no show a sex preference for more energetic types of play.

2.4.3 Evidence for social skills development

2.4.3.1 Correlates of fitness: social skill parameters

One way of testing social skills development is through social isolation studies, in which individuals are prevented from playing with others, to look at the impact on their social skills (Panksepp & Beatty, 1980). However, it is very difficult to stop individuals playing with one another without limiting other social interactions, and this methodology presents ethical questions. Therefore, it is difficult to understand the underlying causation. Population level comparisons where levels of play differ, are a natural and more ethical way to test this hypothesis. Wild populations of squirrel monkeys in which social play was present showed increased affiliative behaviours (Baldwin & Baldwin, 1973). Earlier ages of commencing grooming in wild chimpanzees correlates with greater play frequency (Heintz, 2014). Wild dolphins which had higher frequency of cooperative play were more successful in cooperative enrichment tasks (Matrai et al., 2021).

2.4.3.2 Patterns of variation: implying social development benefits from patterns of variation

a) Play partner sex preference

In primates, most species show sex-specific play patterns that are consistent with adult social relationships, specifically dominance relationships. Males showed preferences for play with other males, as in squirrel monkeys (Aghababian et al., 2021), western lowland gorillas (Brown, 1988; Maestripieri & Ross, 2004), mountain gorillas (Fletcher, 1994; Grebe et al., 2022), baboons (Cheney, 1978; Owens, 1975), sifaka (Lutz et al., 2019), Tibetan macaques (Wright et al., 2018), white headed langurs (Yang et al., 2022) and rhesus macaques (Kulik et al., 2015; Yanagi & Berman, 2017). However, capuchins males were shown to prefer female partners (Lutz et al., 2019) and titi monkeys (Chau et al., 2008) showed no play partner sex preferences, both of which were captive studies (See Appendix A Table S2.3). However, group demography in a captive setting may not reflect natural variation in group structure in the wild because of movements of individuals between captive populations by humans, which could bias results. For instance chimpanzees showed no overall sex preference in play in captivity (Markus & Croft, 1995), but wild male maternal siblings played more than female siblings (Lonsdorf et al., 2018). Similarly wild western lowland gorillas showed sex preferences but these largely appeared to be driven by the group sex ratio of play partners (Nowell, 2005).

Female preferences for play partner sex were not so clear cut. Western lowland gorilla (Brown, 1988; Maestripieri & Ross, 2004) and titi monkey (Chau et al., 2008)

females preferred to play with males but sifaka (Lutz et al., 2019), Tibetan macaque (Wright et al., 2018), bonobos (Palagi, 2006), white headed langurs (Yang et al., 2022), mountain gorillas (Fletcher, 1994) and rhesus macaque (Yanagi & Berman, 2017), females preferred to partner with other females. The difference in gorilla species may be explained by western lowland gorilla females having weaker inter-female relationships as adults compared to mountain gorilla females (Young & Robbins, 2022) and female-female adult grooming is not observed in western gorillas (Robbins et al., 2016). Baboon studies showed contradictory results; one study demonstrated female preference for male partners (Owens, 1975) and the other showed female preference for female partners (Cheney, 1978).

Many non-primate species, including maned-wolf, crab-eating fox, bush dogs (Biben, 1983), prairie voles (Chau et al., 2008), oryx (Pfeifer, 1985), meerkats (Sharpe, 2005a), antelopes (Thompson, 1996) and big horn sheep (Hass & Jenni, 1993), presented no sex preference in play partners. However, red-necked wallabies (Watson, 1993) demonstrated both males and females had preferences for male partners. Siberian ibex males also preferred male partners (Byers, 1980). Watson (1993) suggest that the lack of preference for female-female play dyads is evidence for a lack of social function of play as they would expect females to engage more in play as they are the philopatric sex. This argument is an important example of the need to distinguish between building skills for socialisation (social skills development) and building social relationships (social bond formation). Predictions that an individual would play more with others that they are likely to co-reside with as adults would only support the latter.

2.4.4 Evidence for social bond formation

2.4.4.1 Patterns of variation: Play partnership patterns

Japanese macaques (Shimada & Sueur, 2018) and wild squirrel monkeys (Baldwin & Baldwin, 1974) showed association preferences outside of play for the same individuals with whom they spent the most time in social play. Similarly, preferred partners during adulthood in other affiliative behaviours (grooming, touching, feeding) predicted social play partners in adulthood in bonobo (Palagi & Paoli, 2007), sifaka, baboons and capuchins (Lutz et al., 2019). Geladas played more with those that they groomed (Mancini & Palagi, 2009). Chimpanzees that played more had started to groom non-kin earlier (Heintz et al., 2017). Increased play in wolves correlated with increased affiliative behaviours outside of play (Cafazzo et al., 2018). However, this same relationship was not found in meerkats (Sharpe, 2005b). Similarly, red-necked wallabies (Watson, 1993) and captive squirrel monkeys (Biben, 1986), did not show any such associations. Social bond formation as a hypothesis would also predict that partner preferences were stable over time, which has not been investigated in these studies, but is the case in sable antelopes (Thompson, 1996).

2.4.5 Evidence for energetic constraints

2.4.5.1 Correlates of fitness: Trade-offs with growth

Trade-offs between play and growth would be most relevant to the energetic constraints hypothesis as play is most common in immature individuals, who are investing energy in growth but not yet in reproduction. In Assamese macaques, locomotor play explained up to 50% of the variance in growth, with individuals that

played at higher rates growing less (Berghänel et al., 2015). This provides strong evidence to counter the surplus energy theory that predicts that play consumes only excess energy (Spencer, 1872). Furthermore, this trade-off was seen to play out differently between sexes. During periods of increased food availability there was a greater increase in amount of time spent playing for male individuals, whereas for females there was an increase in rates of body size growth (Berghänel et al., 2015). Thus, the cost and benefits of play are not equal for all individuals.

2.4.5.2 Patterns of variation: implying energetic constraints from patterns of variation

a) Ecological factors

Researchers have predicted the energetic costs of play based on oxygen consumption rate (Martin, 1984) and metabolic rate based on mass (Miller & Byers, 1991). However, such measures are only possible in captive populations, or those in which body mass is already known. More commonly, researchers estimate energetic costs based on contextual information (see below). Variation in the environment can mediate energy consumption and expenditure, because of spatial and temporal variation of food, which can in turn impact individual behaviour. Levels of social play are thought to change based on energy availability so should correlate with environmental variables. Baldwin and Baldwin (1974) showed that in low quality habitats squirrel monkeys ceased playing completely. However, this appears to be rare as most species continue to play even during times of lower food availability, strongly supporting a beneficial function of play (Sabbi et al., 2024).

Multiple environmental variables have been examined across studies (food allocation / supplementation, food availability, habitat quality, season, drought). All these variables have been treated as proxies for energy availability/intake. Nearly all these variables showed a positive correlation of increased social play during periods of higher energy availability, as observed in squirrel monkeys (Baldwin & Baldwin, 1974, 1976; Stone, 2008), macaques (Berghänel et al., 2015; Loy, 1970), mountain gorillas adults (Grueter et al., 2016), langurs (Sommer & Mendoza-Granados, 1995), adult howler monkeys (Asensio et al., 2022), chimpanzees (Moebius et al., 2019; Sabbi et al., 2024), rats (Siviy & Panksepp, 1985), cattle (Brownlee, 1954), African elephants (Lee & Moss, 2014) and in Bornean orangutans, but not Sumatran orangutans (Kunz et al., 2024). However, tamarins exhibited no differences in amount of play with food supplementation (De Oliveira et al., 2003). Energy availability can also interact with other factors. In chimpanzees the effect of partner availability interacted with fruit availability; at times of low fruit availability, the number of potential play partners had a higher impact on social play frequency than at high fruit availability (Moebius et al., 2019).

Other environmental variables which have been investigated in rhesus macaques have been cloud cover, which showed no relationship with social play frequency, and temperature, which positively correlated with social play frequency (Gard & Meier, 1977). In comparison, temperature showed a negative correlation with play frequency in big horn sheep (Berger, 1980). Temperature variables may also be connected to energetic constraints of play as play may be more costly during hotter than average temperatures.

b) Maternal Characteristics

The hypotheses reviewed in Section 2.3 do not incorporate specific predictions about the role of maternal characteristics on offspring social play. However, immature behaviour is heavily informed by maternal characteristics, and we would expect play to be no different. Higher ranking individuals often have access to a higher quantity and quality of resources (Murray et al., 2006). This is turn can produce more energy for offspring, through providing high quality and/or quantity of milk or providing them access to these resources as well. We address studies of maternal rank and weaning periods with play in the context of energetic constraints of play.

A correlation between maternal rank and increased play has been recorded in female baboons (Cheney, 1978), Japanese macaques (French, 1981), rhesus macaques (Gard & Meier, 1977; Tartabini & Dienske, 1979) and hyenas (Holekamp & Smale, 1998). Tibetan macaque mothers of higher rank also had offspring that played more frequently during the juvenile stage, but not during infancy (Wang et al., 2021). There was no relationships between maternal rank and play in wild provisioned Tibetan macaques providing further support that rank is linked to energy availability, because provisioned individuals are not as energetically constrained (Mayhew et al., 2020). Rhesus macaques preferred play partners whose mothers were of the same rank as their own (Tartabini & Dienske, 1979). Chimpanzees showed no correlation between mothers' rank and play frequency (Moebius et al., 2019). Going beyond maternal rank, matriline rank showed no relationships with offspring play frequency in Rhesus macaques (Tartabini & Dienske, 1979), nor did matriline size in orangutans (Kunz et al., 2024).

Additionally, mother's condition showed a positive correlation with amount of social play in male horses (Cameron et al., 2008).

Studies on the effects of weaning on play are also useful to ascertain if changes in available energy from the mother affect social play rates. This is suggested by studies in which mountain gorilla (Eckardt, 2010; Fletcher, 1994) individuals played less the period directly after weaning compared to the 6 months before weaning. However, suckling in African elephants (Lee & Moss, 2014) and oryx (Pfeifer, 1985) showed no relationship with amount of play. Furthermore, primiparous mothers who are having to balance energy for growth and milk production for offspring may produce less milk, e.g. in rhesus macaques (Charnov & Berrigan, 1993; Pittet & Hinde, 2023). Thus it has also been observed that offspring of primiparous rhesus macaque mothers play less (Mitchell et al., 1966)

2.5 The difficulties in studying play

In the introduction we discussed how the lack of definition for play and the treatment of all play as the same has impaired research into its function. Furthermore, availability of data and methodological frameworks further complicate our ability to clearly test the function of play. To effectively reframe research to explore the function of play we must first acknowledge the difficulties that we have in its study.

2.5.1 Limitations of short-term studies and studies in captivity

Studies of play have historically been limited by small sample sizes and a large proportion of studies have been conducted on captive animals (See Appendix A Table

S2.2 and Table S2.3 for list of captive and non-captive studies). Whilst the study of captive animals makes data collection much easier, the controlled setting could be impacting natural variation in play behaviour. Most importantly, group compositions that are human controlled (e.g. animals in the zoo) are likely to exert an influence on who individuals play with, the way in which they play and the space available. These may severely diminish the value of conclusions drawn from captive studies particularly about play partner preferences. For instance, wild rhesus macaque studies showed that males play more (Kulik et al., 2015; Yanagi & Berman, 2017), whereas captive studies reported no sex difference (Hinde & Spencer-Booth, 1967). Wild populations could be more appropriate for making more informed conclusion about the function of play, because of natural variation in group demography and ecological variation.

2.5.2 Temporal mismatch of costs and benefits of play

The benefits of social play could be immediate or delayed to a later point in an individual's development. The potential delayed impact of play creates difficulties in its study and remains a major reason why we struggle to understand its function. Immediate benefits would improve individuals' likelihood of survival in their current life-history stage. For example, immature cheetahs which played more were observed to be more effective at catching prey, and increased predatory behaviour correlated with increased performance of these same behaviours during play (Caro, 1995). Short-term benefits of social play could be developed during immaturity, but these benefits could be advantageous in the long-term, during adulthood.

Unlike the benefits, the costs of social play are likely concentrated during immature stages of life. Despite huge variation in social play between species, play frequency has a general ontogenetic pattern in most animals. Social play is most common in the infant and juvenile stages of development of mammals, implying a developmental function (Burghardt, 2005; Fagen, 1981). This relationship holds true across orders; Primates (Aghababian et al., 2021; Mendonça et al., 2017), Rodentia (Pellis & Pellis, 1987), Artiodactyla (Berger, 1980; Thompson, 1996) and Carnivora (Antonevich et al., 2020; Bekoff, 1974; Biben, 1983; Caro, 1995). Play is proposed to be a risky behaviour, during which individuals are thought to be less aware or vigilant (Fagen, 1981). For example, the majority of South American fur seal pups killed outside of the breeding season were caught by predators during play (Harcourt, 1991). Slow lorises were observed to play more in moonlight, when they are more easily seen, and during rain when it is slippery which are arguably more risky periods (Barrett et al., 2021) and golden lion tamarins chose to play more on branches than on the ground or in the canopy (De Oliveira et al., 2003). Similarly, immature Siberian ibex preferred risky surfaces such as sloped terrain for play, which could be because these are more suitable places to learn and develop skills for movement on those terrains navigated by adults (Byers, 1977).

2.5.3 Difficult to delineate between proposed functions through studies of play frequency alone

Most indirect approaches to examine the functions of play fail to clearly delineate between different hypotheses for the benefits of play and instead infer support for specific hypotheses post-hoc. The quantity and style of social play varies dramatically

both on population and individual scales, suggesting that it is a highly flexible behaviour, and may serve different functions in different species (Baldwin & Baldwin, 1974). Most research on play presents data on variation in frequency of play. This first step provides extremely important information to understand driving factors that can impact a specific behaviour. However, studies describing play frequency patterns can only imply the functions of social play by linking patterns of variation in play to variation in adult behavioural and reproductive strategies, and many hypotheses for the function of social play outline predictions in social play frequency that intersect with one another and are not mutually exclusive (Wang et al., 2021; Winkler & Perry, 2022).

Even with more direct measures such as assessing development through the attainment of motor milestones, it can be difficult to differentiate between hypotheses. For example, not all motor functions are mutually exclusive from the social development that occurs concurrently. Most social behaviours and many skills which can improve survival have both a motor and social component. Furthermore, it is possible that play could perform multiple functions. Therefore, studying only the variation in frequency of play is unlikely to provide clear support for a single specific hypothesis.

2.5.4 We cannot expect the same patterns across species

When studying play we need to take the behavioural, ecological, social, and life history characteristics of a species into account when making predictions about patterns of variation. Not only do some of the proposed hypothesis provide overlapping predictions, but these predictions cannot be implemented without careful attention to the variation in social behaviour and life-history within and among the study species. Males

and females diverge in their reproductive strategies, and as such their life-histories and developmental priorities are different. Female mammals must invest larger amounts of time and energy in their offspring (Charnov & Berrigan, 1993). They must strike a balance between reaching a large size, to increase energetic reserves to support reproduction, versus maturing sooner, to reduce pre-reproductive mortality (Charnov & Berrigan, 1993). Males, whose direct energetic investment in offspring growth is more limited, prioritise those traits (e.g., large body size, strength, competitive abilities) that allow them to gain access to mates (Leigh, 1995). If social play is informative for development, then we would expect to see sex differences in social play that reflect sexual differentiation in adult behaviour and life-history.

2.6 Discussion: Moving forward

We have outlined the literature that provides support for different hypotheses regarding the benefits of play and outlined general difficulties in testing proposed functional hypotheses. The evidence presents a wider variety of approaches for studying the functionality of play, and thus it is difficult to delineate between different hypothesis and it seems most likely that play supports several functions. The evidence reviewed here suggests that across species there are patterns of variation in play and correlations with developmental functions which support both a motor and social function of play, but it is unclear that one of these sets of hypotheses has stronger support than the other. Social bond formation is the easiest function to delineate, because these predictions are specific to individuals (e.g. stability or correlations with other affiliation parameters) rather than population patterns. Additionally, there is some evidence for ultimate benefits of play

(survival and reproduction) that could be gained through the mechanism of improved skills development, although research is minimal. It is important to consider both ultimate and proximate causes in future studies. Although currently there can be no clear answer to what the function of play is, we move forward with new knowledge and suggestions for future research.

2.6.1 Long-term studies on wild population are most valuable

Long-term data sets are the only way in which we can test if increased social play is correlated with specific developmental changes later in life. Choosing appropriate developmental milestones is difficult but will allow us to have a deeper insight into how certain structures of play may be linked to specific developmental outcomes. Furthermore, these long-term datasets will be more fruitful if they are coming from wild populations. We have witnessed that different species exhibit different patterns within social play rates, types and partnerships, which likely links to that fact that its function is also variable. Therefore, to understand the function we need to analyse play in its natural context. The need for studies on wild populations is even more pressing when we study variation in play partnerships, as only in wild populations can we see natural occurring group compositions that reflect the availability of play partners, that individuals would be accustomed to during their development in the wild.

2.6.2 Trade-offs of costs and benefits

The temporal mismatch in costs and benefits of play have led to the development of hypotheses focusing on only the costs of play, which suggest that there are no specific

benefits. Research on play frequency suggests that energy availability is one of many factors influencing play frequency, but this relationship does not exclude that social play likely also has beneficial consequences, contrary to some hypotheses (Spencer, 1872). Considering how social play is recruited in trade-offs can help reveal its function. Life-history theory posits that energy is balanced between growth, reproduction, and maintenance (Kappeler & Pereira, 2003). If individuals are directing energy into play at the cost of other physiological functions this would suggest play has beneficial outputs. Studies of energetic constraints of play have not differentiated between proposed social and motor benefits of play. However, the trade-offs that occur strongly support that there is a beneficial function that is worth the costs of less energy investment in other activities.

2.6.3 *Research must connect structural components of play with function*

One outcome of this review is that study design has a huge influence on the conclusions that can be drawn, and thus on our ability to accurately assess the function of social play. When only considering play frequency it is effectively impossible to distinguish between different hypotheses. Multifaceted studies that integrate the frequency of social play and the structure of play (play partners, play type) to test relationships with specific long-term behaviours or functions are necessary. Studies examining motor skill development were more successful in finding expected sex-specific patterns when they examined specific types of social play. For example, sex more strongly predicted the amount of energetic social play, than total amount of social play.

Studies which examine structural elements of play such as play types or play partnerships highlight that more nuanced study and additional data are necessary to tease apart the different hypotheses considered here. For example, to understand when motor-training is important is it necessary to assess sex differences in type of play occurring, such as play-fighting versus affiliative play. However, to understand the importance of play as a foundation for developing social skills it is more important to examine partner preferences. To clearly understand interactions between motor and social functions, it would be beneficial to be able to study how social play structures change with different play partners. For example, are behaviours and play types of male-male dyad play bout different from play bouts of male-female dyads? This would help explore how different structural elements of play can be useful for interpreting development of different social functions.

To understand how play may be adapted to multiple functions across different contexts, finer structural analysis is necessary. For example, exploration of specific behaviours, movements, and communication during play bouts and how these relate to later life developmental parameters will be important. As data this specific are very difficult to collect in real time, it is likely that researchers will need to rely more on recordings of play behaviour to be coded afterwards. Particularly, researchers need to connect more specific motor behaviours that occur in play with their presence in adulthood. For instance, do male-specific behaviours occur more often in male-male vigorous play and does the rate of occurrence of these behaviours in play correlate with the rate of occurrence in adulthood? With increasing longitudinal datasets, particularly

from long-term research focusing on natural mammal populations, this is becoming more feasible.

Additionally, data on individual movement patterns, for example, could be quantified in videos using movement tracking software. With these more detailed analyses it will be possible to assess of how play structure varies depending on the individuals involved. For instance, using video footage researchers discovered that initiation configuration (face-to-face) in Japanese macaques determined the length and asymmetry of agonistic behaviours during play attacks (Iki & Hasegawa, 2021). Coding video footage will also allow a more standardised approach to study play structure. However, coding video footage is very time consuming and labour intensive.

2.6.4 Research needs to be hypothesis driven

It is important to operationalize the hypotheses for play (Section 2.3) in terms of specific predictions relating to adulthood, contextualising adults' morphology and behavioural roles. For instance, if adult females hold positions of higher rank, social development hypotheses would expect females to spend more time in vigorous social play. We may expect play to be utilised differently when there is variation in sexual dimorphism, philopatry, dominance hierarchies, developmental timescale and research should contextualise these factors as necessary.

Many hypotheses for the functions of play are not mutually exclusive and it can be difficult to tease them apart. Our research design needs to adapt, knowing that functions are unlikely to be the same in every species or even every individual. Hypotheses for social play are usually framed in very broad terms, and it is necessary to

break down these broad categories of social skills and motor skills, for example, into smaller testable frameworks. On a species-level scale, comparisons between more social to less social mammals would be beneficial. This would help distinguish between social and motor development functions. Similarly, studying sister taxa which are physiologically similar but have different social structures (e.g., bonobos and chimpanzees) would provide a strong framework for differentiating between these set of hypotheses.

2.7 Suggested framework to study social play

This review of research allows us to produce a new framework to study play which will be implemented in the following chapters, using Bwindi mountain gorillas as a model. When creating this framework, we are focusing on – where possible - creating mutually exclusive predictions to delineate hypotheses. Whilst the framework is suitable for different species, it is important to contextualise the predictions by species specific behavioural, socio-ecological, and reproductive variation. Given the varying proposed functions of social play we can expect varying results based on sex and age, and in species where dominance, competitive ability, dispersal and social roles differ by sex as well. Furthermore, the socio-ecological environment varies between captive and wild groups which may change predictions even within species.

First, environmental drivers must be considered if we are to fully understand inter- and intraspecific (including population level) variation in play behaviour. For many species, play frequency predictions by sex and age are not enough to distinguish between the motor and social development hypotheses and thus it is an important to go beyond

these biological factors. In Chapter 3 we will explore biological, ecological and social correlates of play. Second, to begin to delineate the different functions of social play we must explore how the structural elements of play vary. Play partnerships provide a more important avenue to differentiate between the two social functions of play (social skills development and social bond formation). In Chapter 4 we will focus on the latter, examining how play partnerships vary with age and sex and if these relationships are stable through time to differentiate between the two social functions of play. Due to the complex nature of defining play types and the time needed to code videos, examining patterns of play-types is outside the scope of this dissertation. Third, we must better understand the energetics of play and trade-offs between play and other activities such as growth, before we can achieve a comprehensive understanding of the benefits of play. In Chapter 5, we will examine trade-offs of time spent in play and other activities. Additionally, we will examine energetic trade-offs by looking at the trade-off between play and body size. Finally, more direct measures of motor and social skill development should be incorporated into research designs. In short-term studies, we can do this by examining correlations between quantity of play and developmental milestones in immature individuals. In long-term studies, linking play variation with direct measurements of fitness will be important to understand the evolutionary significance and reproductive benefits of play. Unfortunately, we do not currently have longitudinal data allowing for the quantification of fitness benefits for the Bwindi gorilla population. Therefore Chapter 5 will focus on shorter-term developmental milestones to understand the benefits of play and how these link to motor and social development.

2.8 Conclusion

Play is an extremely diverse behaviour. Not only does it vary in structure from species to species, but it can vary within an individual, depending on their age, the partners with whom they are playing and the context in which they are playing. Thus, methods of quantifying play and study designs need to take in to account this level of variation and flexibility. This body of research is unlikely to yield just one definitive answer for the function of play. Current data give support for both motor and social functions of play. With methodological advances and availability of new data, this is enabling researchers to ask more specific questions about how to connect structure with function. Understanding this connection along with designing more robust research protocols is imperative to answer question about the evolutionary benefits of play.

Chapter 3: Biological, ecological, and social correlates of social play behaviour in immature Bwindi mountain gorillas (G*orilla beringei beringei*).

Keywords: social play, *Gorilla beringei beringei, motor training hypothesis, social relationship hypothesis*

Abstract

Social play is a widespread behaviour within the mammalian order. Multiple hypotheses have been developed to explain the proximate costs and ultimate benefits of play for immature individuals, but their predictions are often non-mutually exclusive. The motor training hypothesis and the social relationship hypothesis are two frameworks for exploring how play during immaturity can improve skill development. Furthermore, play is hypothesised to be under energy constraints and will vary depending on socioecological factors. To assess how play varies with biological (age, sex, weaning status, mother parity), ecological (fruit eating), and social factors (partner availability), we analysed over 6000 hours of focal data on 33 immature Bwindi mountain gorillas (*Gorilla beringei beringei*; aged 0.59-8 years) spanning 18 years. We found that male and female mountain gorillas have different ontogenies of social play. Male gorillas, particularly between 2-6 years old, played more than females, adhering to our prediction that male strategies in this species would be under stronger selection pressure to enhance development of social and motor skills. Social play rate is also corelated with the number of other immature individuals present. Furthermore, social play rate positively correlated with fruit consumption and weaning status, but not mother's parity. Variation in social

play in gorillas is consistent with predictions for both a motor and social development function and suggests that social play is under energetic constraints. Our results demonstrate the need to study social play in a framework of trade-offs between proximate energetic costs and potential long-term ultimate benefits of skill development.

3.1. Introduction

Play is ubiquitous in the mammalian order (Burghardt, 2005). Play is most common in immature individuals (Burghardt, 2005; Fagen, 1981; Power, 2000) and involves exaggerated and repeated locomotor activity without clear immediate function, but resembles serious functional behaviours (Martin & Caro, 1985). Burghardt (2005) outlined five criteria that define play and encapsulate its multiple facets as a behaviour that 1) has limited immediate function, 2) is spontaneous, rewarding, or voluntary, 3) differs in form or timing from more serious behaviours, 4) is repetitive but occurs in varying forms, and 5) is performed during relaxed periods. A multicomponent definition of play exemplifies that the behaviour is extremely structurally variable. As such, different types of play may have different cost and benefits and evolutionary histories (Pellis et al., 2015). Three common categories of play have been identified: social play (involving two or more individuals), object play, and locomotor play (also referred to as solitary play) (Burghardt, 1984). Biologists have yet to clearly demonstrate the ultimate benefits of social play because linking social play to long-term fitness is difficult and needs large longitudinal datasets. Such long-term studies to date have shown that play frequency is positively correlated with survival, lifespan and reproduction (e.g. brown bears: R. Fagen & Fagen, 2009; African elephants: Lee & Moss, 2014; mountain goats:

Théoret-Gosselin et al., 2015). Furthermore, higher overall play rates during immaturity have been correlated with number of paternities (dolphins: Holmes et al., 2024) or other measures of improved adult reproductive fitness, such as earlier ages at first mating (male chimpanzees: Heintz et al., 2017) and increased copulation durations (male mink: Dallaire & Mason, 2017).

Multiple hypotheses propose possible beneficial functions of play. The 'motor training hypothesis' links play to the improvement of motor skills during immaturity to enhance competitive ability and reproductive success in adults (Bekoff & Byers, 1981). Play has been linked to learning skills which are beneficial throughout life such as predation skills (e.g. cheetahs, Caro, 1995), improved travel proficiency (e.g. chimpanzees, Heintz et al., 2017), and feeding proficiency (e.g. marmosets, Chalmers & Locke-Haydon, 1984). Skills gained may improve survival during different stages of development. However, these skills may not always translate to reproductive advantages in adulthood, such as obtaining the alpha position or improved fighting success (e.g. capuchins Perry et al., 2017; meerkats Sharpe, 2005). The 'social relationship hypothesis' posits that play is a platform to practise adult behaviours and to learn how to interact with other individuals (Baldwin & Baldwin, 1974; Poirier & Smith, 1974). Consistent with this hypothesis, increased social play during immaturity is correlated with earlier development of social skills, such as grooming of others and first mating in chimpanzees (Heintz et al., 2017). Furthermore, developing social skills could result in higher dominance rank in adulthood as is seen in marmots and wolves (Blumstein et al., 2013; Cafazzo et al., 2018). Hypothesizing about the proximate costs of play, Spencer (1872) suggested that, given it is a behaviour that often encompasses apparently vigorous or

strenuous movements (Miller & Byers, 1991), social play has no benefits and occurs only during times of 'surplus energy', which is linked to current ideas that play is energetically constrained due to trade-offs with other activities (Graham & Burghardt, 2012). These hypotheses for play are not mutually exclusive and difficult to rigorously test because studies are often conducted in captive settings and/or do not examine variation of play in relation to its costs and benefits. Here, we examine these hypotheses by analysing social play rates during immaturity (0.5-8 years) in a wild gorilla population, which shows distinct sex-biases in life-history and behaviour and undergoes natural variation in socio-ecological variables.

Studying variation in the frequency of social play is broadly informative for understanding its potential costs and benefits in different contexts and how they may change over ontogeny and for different sexes. Differences in physical size, social behaviour, and reproductive strategies of adults appear to manifest in species-specific differences in immature play (Kunz et al., 2024; Lafreniere, 2011), providing support for both motor and social developmental hypotheses, which may ultimately relate to fitness. Social play is also likely constrained by energy availability, which may vary depending upon an individual's ecological and social environment. Thus, it is important to go beyond examining only age and sex-based variation to understand how individual play behaviour differs depending on biological, ecological, and social variation. Despite the large socio-ecological variation within and between primates, few studies have examined the ontogeny of social play in relation to ecological (diet variation) and social variation (group size and structure) to understand both its ultimate benefits and proximate costs (Asensio et al., 2022; Kunz et al., 2024).

If playing as an immature enhances competitive ability through the development of motor skills, we expect the sex that experiences more competition in adulthood to play more as immatures. In most primates, competition involving physical contact is typically greater between male adults than females. In fact, immature male primates spend more time in social play than females (e.g. vervets: Fedigan, 1972; blue monkeys: Forster & Cords, 2005; gorillas: Meder, 1990; chimpanzees: Lonsdorf, Anderson, et al., 2014; capuchins: Winkler & Perry, 2022; langurs: Yang et al., 2022). Furthermore, this sex bias becomes stronger when concentrating on more competitive types of play (rough-and-tumble, fighting/sparring) (Abegglen, 1984; Aghababian et al., 2021; Caine & Mitchell, 1979; Chalmers, 1980; Fletcher, 1994; Gard & Meier, 1977; Marley et al., 2022; Palagi & Paoli, 2007), supporting the idea that play is used for enhancing motor skills and results in improved competitive ability as adults. Similarly, female meerkats show high levels of reproductive skew stemming from competitive ability, and immature females win at higher rates during play-fights with males (Clutton-Brock et al., 2006). In monogamous species in which competition is more balanced between the sexes, such as titi monkeys and prairie voles, we see little sex difference in immature play (Chau et al., 2008). Sex biases in immature play frequency appear to be linked to adult reproductive competition, and it is important to contextualise this based on the species being studied.

Patterns of play frequency also relate to patterns in social dominance. Play fighting is female-biased in hyenas, in which females are dominant (Pedersen et al., 1990), and also in captive adult bonobos (Palagi & Paoli, 2007) who have intersexual dominance hierarchies (Surbeck & Hohmann, 2013). Similarly, in most primates in which males are generally dominant over females, males show higher play rates (squirrel monkeys:

Baldwin & Baldwin, 1974a; gorillas: Eckardt, 2010; Hoff et al., 1981; chimpanzees: Moebius et al., 2019; baboons: Owens, 1975, But see gorillas: Brown, 1988; Fletcher, 1994 and chimpanzees: Heintz et al., 2017). Other primates with less despotic hierarchies, such as geladas, have shown no sex biases in play frequency (Mancini & Palagi, 2009). These patterns in immaturity appear to be related to dominance roles in adulthood, and the dominant sex tends to exhibit a greater rate of play.

Social skill development encompasses learning about dominance, practicing communication, refining social behaviour cues, and creating a behavioural repertoire (Poirier & Smith, 1974). This hypothesis suggests that individuals will develop some social skills innately but play acts as a conduit to improve effectiveness of these skills. Therefore, individuals that have more varied social relationships as adults would be expected to spend more time in play, learning from an array of partners and establishing relationships with other individuals. Thus, the availability of play partners may also influence the occurrence of play because high partner availability provides more social opportunities. Species with larger average group sizes show higher rates of play (Burghardt, 2005; Power, 2000) and within species, group size positively correlates with individual play rates (howler monkeys: Asensio et al., 2022; squirrel monkeys: Baldwin & Baldwin, 1971; chimpanzees: Moebius et al., 2019). These results support that individuals play more when there are more individuals around to play with. Assuming that having more individuals to play with equates to an increased number of play partners, this implies a potential social benefit to play, in which social skill development is linked to play with different partners.

Others have proposed that energetic constraints influence play. Berghänel et al., (2015) found that half of the variation in body size growth of macaques was explained by variation in play, with slower growth rates associated with higher rates of play, providing evidence that individuals trade-off their energy allocation between growth and play. Furthermore, proxies for energy availability correlate with variation in play, lending support to play being under energetic constraints. The comparatively rare occurrence of play in adulthood (Grueter et al., 2016; Palagi & Paoli, 2007) suggests that during immaturity, benefits must outweigh any energetic costs. The energetic costs for unweaned individuals may also be lower because they can be offset by milk supply from the mother. Higher energy supplementation by the mother and reduced foraging time allows more time and energy to be allocated to social activities such as play (Dunbar & Dunbar, 1988; Eckardt, 2010). A reduction in play, in the period post-weaning occurs among individuals that are weaned earlier than average (gorillas: Eckardt, 2010; Fletcher, 1994), but not in all cases (elephants: Lee & Moss, 2014; Oryx: Pfeifer, 1985). Furthermore, primiparous mothers who have not yet attained final adult body size may face a trade-off between investing energy in their own growth and the growth of their infants (Charnov & Berrigan, 1993). Macaque primiparous mothers provide less milk energy to their firstborns (Pittet & Hinde, 2023), which may reduce energy available for social play. Parity was not correlated with weaning age in Bwindi gorillas (Robbins & Robbins, 2021), which could suggest that primiparous mothers are not providing less milk than multiparous mothers, or if they are offspring are allocating more energy to growth than other activities. This trade-off may continue beyond weaning, as adolescent

offspring of primiparous macaque mothers have been shown to play less than offspring of multiparous mothers (Mitchell et al., 1966).

Once individuals are independent, their energy intake becomes entirely dependent on their own foraging and food availability. Ecological variables treated as proxies for energy availability or intake (food supplementation, food availability, habitat quality, season, drought) show a positive correlation between energy intake and increased social play in numerous studies (e.g howlers: Asensio et al., 2022; squirrel monkeys: Baldwin & Baldwin, 1974a, 1976; Stone, 2008; macaques: Berghänel et al., 2015: Loy, 1970; cattle: Brownlee, 1954; mountain gorillas: Grueter et al., 2016; African elephants: Lee & Moss, 2014; chimpanzees: Moebius et al., 2019; rats: Siviy & Panksepp, 1985; langurs: Sommer & Mendoza-Granados, 1995). Correlation between ecological variables and variation in play frequency provides support for energetic constraints of social play behaviour. However, ecological variables have rarely been studied alongside biological and social factors which also drive variation in play.

In the current study, we examine variation in the rate of social play in wild Bwindi mountain gorillas. Gorillas have high levels of male-male reproductive competition, leading to high reproductive skew (Nsubuga et al., 2007; Vigilant et al., 2015). A male-bias in social play rates could be linked to development of motor skills for competition and social skills for affiliation. Gorillas are the most sexually dimorphic great ape, and one of the most dimorphic primates (Leigh & Shea, 1995). Therefore, if play acts as a platform for solidifying the motor skills related to reproductive strategies, male-bias in play rates would be more apparent in gorillas than other great apes. Furthermore, gorillas live in male-dominant hierarchies, and females exhibit weak dominance hierarchies

(Robbins, 2010), suggesting the need for social and physical skill development to be greater in males. Male-female affiliative relationships are seen to be more important than female-female association; therefore males must maintain more social relationships (Morrison et al., 2019; Watts, 1992). Research to date has shown a potential male bias in play frequency in gorillas (Eckardt, 2010; Hoff et al., 1981; Maestripieri & Ross, 2004; Meder, 1990; Nowell, 2005; Palagi et al., 2007; but see Brown, 1988; Fletcher, 1994). However, previous gorilla studies have predominately used play rates based on instantaneous sampling (e.g. no. of play bouts/scan sampling), not total time spent in play (minutes/seconds of play per observation time), which gives a less accurate representation of total play amount. Gorillas, like humans, live in highly cohesive social groups, with between group social variation. This variation allows a natural experiment to understand how group size predicts play rates. Most studies have focused on captive western lowland gorillas (Brown, 1988; Hoff et al., 1981; Maestripieri & Ross, 2004; Meder, 1990; Palagi et al., 2007; but see Nowell, 2005), which present a difficult environment to assess social variation because partner availability is controlled, and sample size is usually limited. Furthermore, captive studies cannot test ecological variation as food availability because diets are human controlled. Studies of wild mountain gorillas populations (Eckardt, 2010; Fletcher, 1994; Grebe et al., 2022), focused on the Virunga mountain gorillas which show little annual dietary variability. Conversely, Bwindi mountain gorillas demonstrate monthly dietary variation in frugivory between 0-70% (Ostrofsky & Robbins, 2020), which presents an opportunity to study ecological variation alongside biological and social variables.

Here we test if biological, ecological, and social factors influence variation in play rates (% of focal time spent in social play) of immature mountain gorillas of Bwindi Impenetrable National Park, to determine if the variation in social play is consistent with predictions of 1) a motor developmental function of play, 2) a social development function of play, and/or 3) the role of energetic constraints (see Table 3.1 for a list of all parameters and predictions). We test the following hypotheses and predictions:

- Biological factors (age, sex, weaning status and maternal parity): We predict that play rate will show a quadratic relationship with age interacting with sex. We expect males will play at higher rates than females and this difference will be greater during the juvenile period (3-6 years) and then decrease again. A male bias in social play rate would be consistent with both motor and social hypotheses of play. We predict unweaned individuals and offspring of multiparous mothers will play at higher rates because they are less energetically constrained than weaned individuals or offspring of primiparous mothers.
- Ecological factors (fruit consumption): We expect play rate to be positively correlated with fruit consumption. Fruit provides a more readily available source of energy (Rothman et al., 2008), and therefore high fruit consumption may fuel periods of increased social play.
- Social factors (partner availability): The motor training hypothesis would predict an asymptotic relationship between partner availability and play rate, as individuals reach a threshold amount of play needed to develop motor skills. The social relationship development hypothesis would predict a positive correlation

between partner availability and play rate, as to develop social relationships with multiple partners depends on playing with all available individuals.

Table 3.1: List of biological, ecological, and social correlates tested in this study and their corresponding hypotheses and predictions. The final column demonstrates if these hypotheses were supported by the results of the study.

Correlate Type	**Variable (definition)**	**Prediction**	**Hypothesis supported**	**Result**
Biological	Age^2 * sex interaction	Males will have higher social play rates than females; this gap will increase at later ages.	Motor and social	**Significant; supports prediction.**
	Weaning status (weaned / not weaned)	Unweaned individuals will have higher social play rates than weaned individuals.	Energetic constraints	**Significant; supports prediction.**
	Maternal Parity (primiparous / multiparous)	Offspring of multiparous mothers will have higher social play rates than offspring of primiparous mothers.	Energetic constraints	No relationship.
Ecological	Fruit consumption (% of monthly scans feeding on fruit)	Months of higher fruit consumption will correlate with higher social play rate.	Energetic constraints	**Significant; supports prediction**
Social	Partner $availability^2$ (No. of other immature individuals in the group <8 years of age)	Motor skills: Partner availability will have an asymptotic relationship with social play rate. Social skills: Partner availability will have a positive relationship with social play rate.	Motor or social	**Significant; but with parabolic relationship.**

3.2. Methods

Study Population and Subjects

This study was conducted on five habituated mountain gorilla (*Gorilla beringei beringei)* groups in Bwindi Impenetrable National Park, Uganda from 2005 until 2023, with the majority of the data being collected after 2012 (see Appendix B: Table S3.1). Data were collected by several researchers (see Acknowledgements), who were trained according to the same protocol and supervised on a routine basis to ensure uniformity. Specific data for this study were extracted from a general long-term behavioural database, which includes behavioural observation of play behaviour. A total of 33 immature individuals between the age of 0.59 (~7 months) and 8 years were included. Female gorillas are categorised as adults from 8 years onwards (Breuer et al., 2009).

Data collection

The gorillas were observed for approximately 4 hours per day, according to regulations set out by Uganda Wildlife Authority. Data collection was in the form of focal sampling (Altmann, 1974) and individuals were focalled for 5-60 minute periods, with the goal of obtaining five hours of focal time per individual per month, for a total of 6,278 hours of focal time. Total focal time per individual was recorded throughout the month, and focal periods were a maximum of 60 minutes to maintain balanced sampling across individuals through the day and month. If individuals were out of view for more than 60 seconds, the focal period was ended. Focal periods per individual were grouped on a monthly basis, creating one datapoint per month for each individual. Months with less than 3 hours of focal time were excluded, to limit the weight of months with shorter

observation periods, because longer observation periods should give a more accurate sample of proportion of time spent in play over a month. We had a total of 1,115 monthly datapoints. Monthly data points had a mean of 338 minutes of focal time (range: 180-998, 90% of data points involved between 180-480 minutes). Each individual was represented by a mean of 34 monthly datapoints (range: 5-67).

Social play behaviour was defined in the data collection protocol as: when two individuals wrestle, tickle, chase, hit, etc. in a non-aggressive manner, it is often accompanied by a 'play chuckle' vocalization by immatures (Heintz et al., 2017; Winkler & Perry, 2022). Solitary play behaviour was excluded as other studies show it to have different ontogeny and likely different evolutionary origins (Eckardt, 2010; Winkler & Perry, 2022). Play behaviour was recorded for play bouts with durations greater than a minimum of 5 seconds, and the duration was recorded to the nearest second by electronic tablet timer (or nearest 5 seconds pre 2016 when data were collected on paper with a digital watch). Play bouts ended when another behaviour occurred, or individuals stopped playing for more than 60 seconds. A total of 348 hours of social play behaviour was recorded.

Concurrent with focal sampling, scan sampling occurred at fixed intervals (pre-May 2015: every 5 mins, post-May 2015: every 10 mins), during which the activity (feeding, fruit feeding, resting, or travelling) of every individual in view at the time the scan was recorded. Due to the vegetation and group spread individuals in view at any one scan ranged from 5-40m. When individuals were feeding, the species name was recorded when known. For our analysis, all plants were assigned as fruit or non-fruit.

Response Variables

Monthly play rate – was the total number of seconds an individual spent in social play during focal observation, with any other individual. This was represented as a proportion of observation time by adding an offset of total focal time in the model.

Explanatory variables

Age - was assigned as of the 15th day of the month for each monthly data point. Only individuals below 8 years of age and whose birthdate was known within +/- 15 days, were included in the analysis.

Sex – was known for all individuals, representing 20 males and 13 females. More males were born later in the study, leading to less data points per male individuals but total number of monthly data points for males and females were roughly equal.

Weaning status - weaning ages were used from Robbins et al. (2021), based on last observed suckling date, and the same methods were used to calculate weaning ages for 8 additional individuals who were weaned after the study period of Robbins et al. (2021). Weaning status was recorded as binary value, weaned or not weaned, for each month, based on if their age on the 15th day of the month was younger or older than their weaning age.

Maternal parity – the mother of each offspring was binary coded as primiparous or multiparous.

Partner availability – was the number of other individuals in the group less than 8 years old. We tested the model with both a linear and quadratic term for partner availability and

the model with quadratic term provided better diagnostics. Thus, partner availability was added as a quadratic term.

Fruit consumption – was the proportion of each individuals' total time that was spent feeding on fruit. It was calculated by dividing the number of scans an individual was recorded feeding on fruit by the total number of scans in which an individual was present per month. Using the total number of scans as the denominator accounts for variation in how much individuals are present during the scans. We chose a proportion of total time in the scans because it is a better representation of the amount of fruit consumed, compared to a proportion of feeding time, because younger individuals spend less time feeding overall. This gives a better measure of total energy consumption through fruit, even for those individuals which are not feeding as often. To reduce bias of short observation times, we excluded days in which fewer than 5 scans of an individual were recorded and excluded months in which fewer than 5 days of scans were recorded.

Statistical Analysis

Model structure

R was used to perform all statistical analyses (R Core Team, 2022).

A Generalized Linear Mixed Model (GLMM) with a negative binomial distribution was used to analyse correlations between the response and explanatory variables, using the GLMMtmb package (Brooks et al., 2017). GLMMs are suitable for longitudinal observational studies as they allow for random effects of individuals and other factors which are repeated in the dataset. Preliminary analyses indicated that our data were overdispersed, so we constructed models using the negative binomial family, which is

appropriate for overdispersed count data. The monthly play rate was specified as the response variable. Linear and quadratic terms for age (age^2) were included as fixed effects because age was expected to have a non-linear effect on play rate. This relationship is unlikely to be perfectly symmetrical which is why having both terms is important. Sex and an interaction between sex and the quadratic term for age were included (age^2*sex), to account for variation in the ontogeny of play between the sexes. Other fixed effects included weaning status, maternal parity, partner availability[2] and fruit consumption.

All variables were centred and standardised (z-transformed). Categorical variables were first dummy coded with numerical values, and then for each variable the mean value was subtracted from each value and then divided by the standard deviation. Z-transformation of variables allows for all variables to be compared on the same scale (mean = 0 and SD = 1) without changing their distribution. This allows for better convergence of models and comparison of effect sizes between each variable (Schielzeth, 2010). Random intercept terms were added for individual, mother, and year. The random effect term for individual was nested within mother. The model was first run with a random intercept term for group. However, model diagnostics indicated deviation between the model predicted and observed values and demonstrated a presence of heteroscedasticity (see Appendix B: Figure S3.1). Therefore, the group random intercept was removed. An offset term was included for focal time in seconds, which accounts for variable observation amount per month for each individual. A zero-inflation term for age was included in the models to account for higher than expected zero counts disproportionally distributed by age.

Model diagnostics and selection

Variance inflation factors (VIFs) were calculated using the package performance (Lüdecke et al., 2021), and showed no presence of collinearity amongst the fixed effects (all VIFs < 4). Further model diagnostics were performed using the DHARMa package (Hartig, 2020). The DHARMa package transforms residual checks for non-Gaussian distributed models, to allow for checks of normality and homoscedasticity. Visual inspection of quantile-quantile plots determined that the residuals corresponded to the assumption of normality (see Appendix B: Figure S3.2), which was confirmed statistically (KS test for uniformity: D = 0.0280, p-value = 0.349). The KS test confirms the model did not show significant deviation of the residuals from the expected normal distribution. The model did not show significant dispersion between the standard deviation of the residuals in the fitted vs. simulated data (dispersion parameter = 0.744, p-value = 0.224, ideal dispersion value is 1). Test for outliers was non-significant (p-value = 0.402), indicating that there were no more outliers than expected. Visual checks and statistical tests confirmed no heteroscedasticity when predicted values were plotted against fitted values (see Appendix B: Figure S3.2). The distribution of the data were checked at each quartile, and fitted vs predicted values were not significantly different (quartile 0.25, p-value: 0.274; quartile 0.5, p-value 0.191; quartile 0.75, p-value: 0.073). The zero-inflation test indicated the ratio of expected to observed zeros was not significant (ratio = 1.0313, p = 0.808, ideal ratio is 1), which signifies the zero-inflation term was correctly assigned in the model. We checked that the zero-inflation model provided significantly more predictive power than the non-zero inflated model. Then a

full-null model comparison was performed, using an ANOVA test, with the test statistic set to chi squared, comparing the model against a null model comprised of only the random effects.

Ethical note

Data used as part of this study were collected non-invasively from nonhuman primates. Permission was granted for the study by Uganda Wildlife Authority and Uganda National Council of Science and Technology, and we adhered to all protocols and guidelines set by these institutions.

3.3. Results

The zero-inflated model was significantly better at predicting the patterns observed (p-value: <0.001). Comparisons of AIC values show that the full model had higher predictive power than the null model ($\chi 2$ = 125.45, df = 10, p-value <0.001).

Amongst biological correlates, we found the interaction of the quadratic age term and sex was significant (Beta = -2.592, SE = 1.015 and, p-value = 0.011) (Table 3.2). Immature males and females had similar (overlapping 95% confidence interval ranges) rates of social play below 2 years and above 6 years, but males had higher rates of play between the ages of 2-6 years (Figure 3.1). Play rate was higher in unweaned individuals than weaned (Beta = -0.192, SE = 0.065 and, p-value = 0.003) (Figure 3.2, Table 3.2). There was no relationship between maternal parity and the rate at which offspring play (Beta = -0.011, SE = 0.071 and, p-value = 0.877) (Table 3.2).

Table 3.2: Results of the GLMM for the intercept, random intercepts, and each fixed effect term in the play rate model. Significant relationships (P <0.05) are in bold, * = an interaction term.

Term	Estimate	SE / SD	p
mother:id	Random intercept	0.341	
year	Random intercept	0.237	
intercept	-2.848	0.103	**<0.001**
age	-6.788	2.244	**0.002**
sex	0.280	0.080	**<0.001**
age^2	-1.587	1.178	0.178
age*sex	-0.108	1.137	0.924
age^2*sex	-2.592	1.015	**0.0107**
weaning status	-0.192	0.065	**0.003**
maternal parity	-0.011	0.071	0.877
fruit consumption	0.060	0.024	**0.014**
partner availability	-0.108	1.137	0.924
partner availability^2	-0.075	0.032	**0.021**

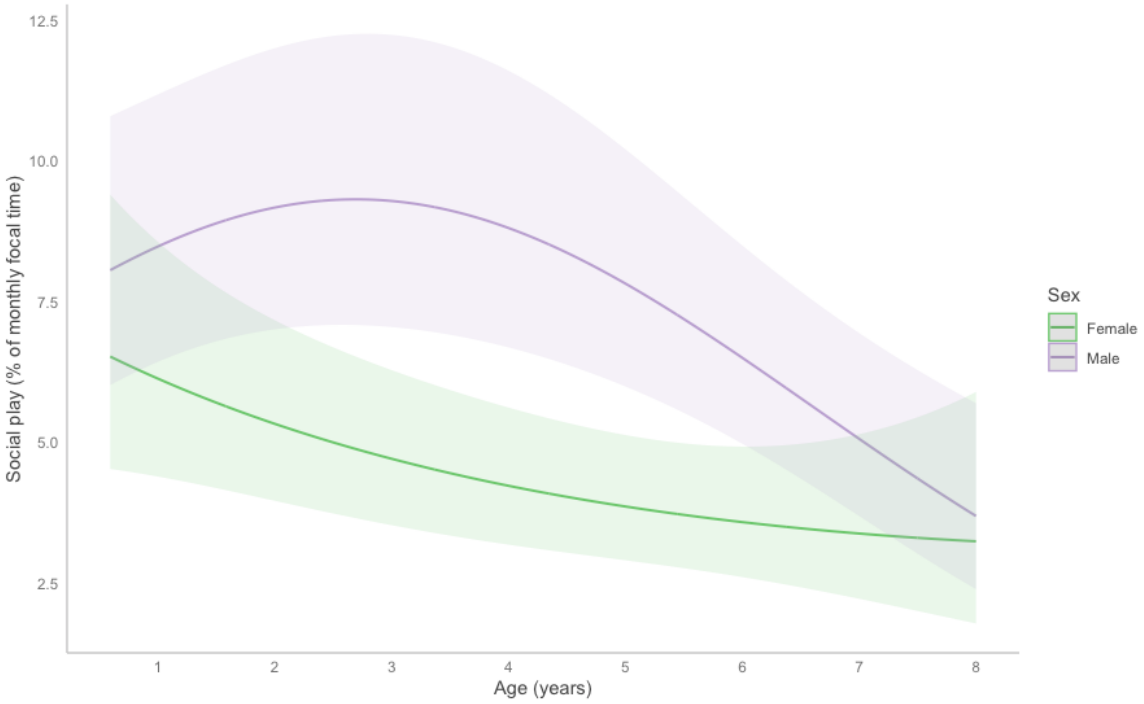

Figure 3.1: Model predictions for the interaction term of age and sex and social play rates. Male (purple) and female (green) immature gorillas from ages 0.59-8 years. Shaded areas = 95% confidence intervals. To allow the model to create predictive values, all other variables were fixed, and focal time was set by the model at a value of 5.3 hours, to allow predictive comparative proportions based on a static observation amount. Model prediction values have been back transformed for easier interpretation.

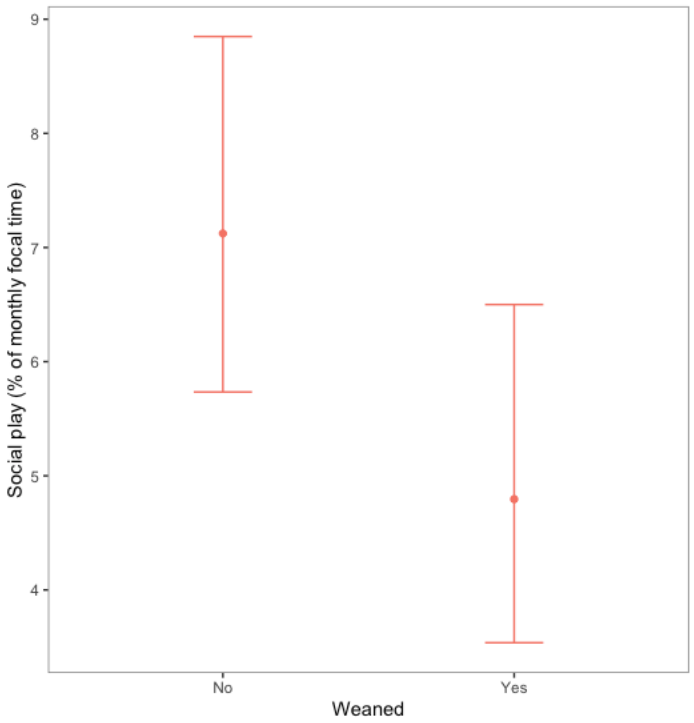

Figure 3.2: Model predictions for the variation in social play rate by weaning status, mean and 95% confidence intervals, as in Figure 3.1. Model prediction values have been back transformed for easier interpretation.

Play rate increased during periods of higher fruit consumption (Beta = 0.060, SE = 0.024 and, p-value = 0.014) (Figure 3.3, Table 3.2). The quadratic term for partner availability was significantly correlated with an increase in play rate (Beta = -0.075, SE = 0.032 and, p-value = 0.021) (Figure 3.4, Table 3.2). The rate of play increased as the number of available partners increased, up to a peak of five partners, after which it decreased.

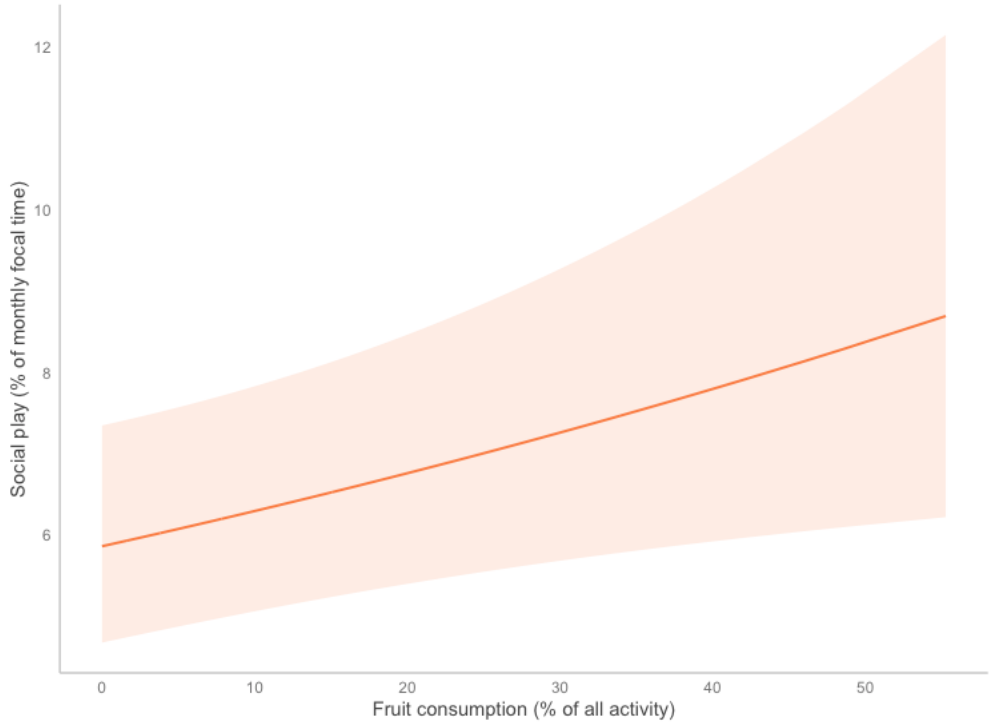

Figure 3.3: Model predictions for the relationship between proportion of an individual's time spent feeding on fruit and social play rates, as in Figure 3.1. Shaded area denotes 95% confidence intervals. Model prediction values have been back transformed for easier interpretation.

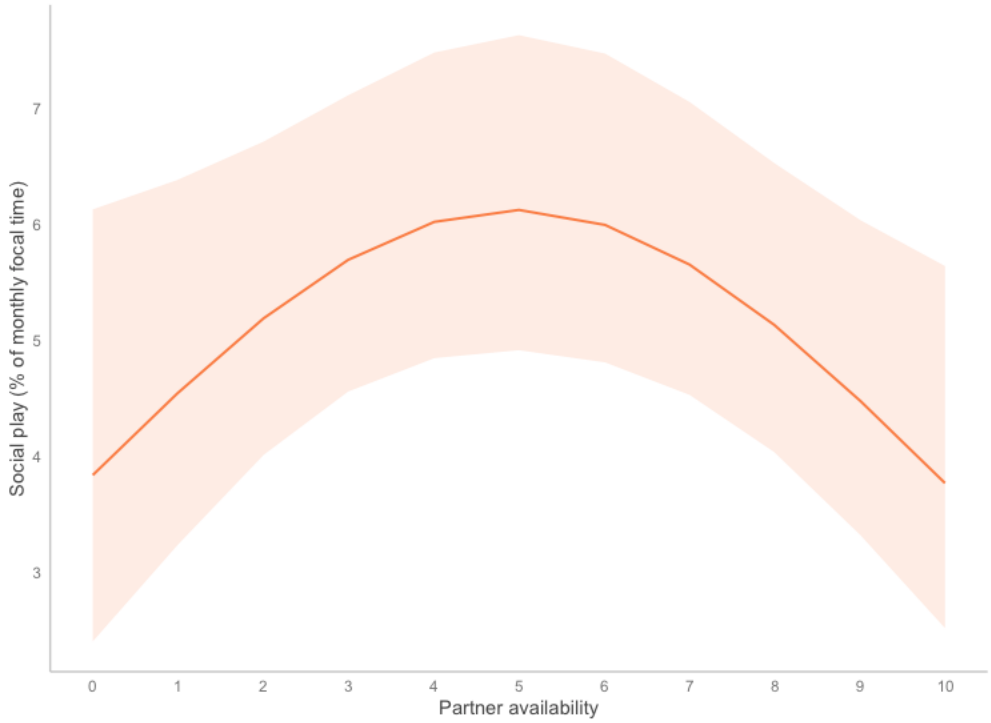

Figure 3.4: Model predictions for the relationship between partner availability and social play rates, as in Figure 3.1. Shaded area denotes 95% confidence intervals. Model prediction values have been back transformed for easier interpretation.

3.4. Discussion

Our results indicated that the amount of time immature Bwindi mountain gorillas spend in social play is correlated with biological, ecological, and social factors, pointing to likely costs and benefits of play. We observed a positive male-bias in play rates, which was predicted for both a social and motor function of play. The relationship between social play and partner availability further provides support for a social function of play, although it did not conform exactly to our predictions. Additionally, social play rates were higher during times of high fruit consumption and before weaning, which is in accordance with predictions that social play is energetically constrained. Our dataset used rate of play (seconds of play per focal time), which provides a more accurate representation of play amounts than more common methods of play frequency, calculated by scan samples or number of play bouts (Moebius et al., 2019; Winkler & Perry, 2022; Yanagi & Berman, 2017). The patterns we observed in play rate variation were consistent with predictions from all three of the non-mutually exclusive hypotheses tested (motor training, social relationship, energetic constraints).

Motor training hypothesis

Gorillas exhibit high levels of male-male competition, whereas female-female competition is relatively weak (Doran & McNeilage, 1998; Robbins, 1996; Stoinski, Rosenbaum, et al., 2009; Watts, 1994). The positive male sex bias in play observed here in mountain gorillas, and in several other primate species in which male-male physical competition is a large component of gaining reproductive access (Aghababian et al., 2021; Owens, 1975; Wang et al., 2021), fits predictions for the motor training hypothesis

and is similar to results of previous gorilla studies (Eckardt, 2010; Maestripieri & Ross, 2004; Nowell, 2005, but see Brown, 1988; Fletcher, 1994). This suggests that play is a platform to improve competitive ability. Age had a quadratic effect on play rates in males, with a peak between 2-3 years of age. Males had higher rates of play than females throughout most of immaturity, and larger sex differences occurred between 2 and 6 years old, which follows other studies demonstrating sex-differences between the sexes are greater after infant period (0-3 years) (Hutchinson & Fletcher, 2010). Females showed a steady decline of social play rate from 0.6 years to 8 years. The sex-specific ontogeny of play further highlights different developmental needs of the two sexes related to adult behavioural strategies (Lonsdorf, 2017). Previous studies reported that sex biases in play become stronger when concentrating on more vigorous types of play (rough-and-tumble, fighting/sparring) (Abegglen, 1984; Aghababian et al., 2021; Caine & Mitchell, 1979; Chalmers, 1980; Fletcher, 1994; Gard & Meier, 1977; Palagi & Paoli, 2007), suggesting motor skill development may be greater from more intense play types and more necessary for males. However, increased time in play fighting was not linked with fighting success in adulthood in meerkats (Sharpe, 2005c). This could be because of self-handicapping (individuals purposely limiting their ability) in play (Petrů et al., 2009; Schank et al., 2018), or that individuals are more likely to initiate play fights with individuals that are disadvantaged compared to themselves (Biben, 1989; Iki & Hasegawa, 2021). This indicates that focusing on a structural element of play e.g. play-types, play partnerships and play initiation may be more fruitful to understand function.

Social relationship hypothesis

A male-bias in play rates within gorillas is also consistent with a social skill development function of play because of the greater importance for males than females of developing skills to attain and retain dominance status as well as male-female affiliative relationships being key to social group patterns (Robbins, 2010; Watts, 1992; Young & Robbins, 2022). Furthermore, some species demonstrate a link between dominance in play and dominance outside of play (wolves: Cafazzo et al., 2018). Studying partner preferences in play would be an additional way to test if affiliative sex-preference as adults is exhibited in social play behaviour of immatures. Studies of captive western gorillas show both male and females had a preference for male partners (Brown, 1988; Maestripieri & Ross, 2004), whilst wild mountain gorillas studies show higher rates of male-male partnerships in play (Fletcher, 1994; Grebe et al., 2022), supporting a social skill development role of play.

Contrary to our predictions for both motor skill and social skills development, there was a parabolic relationship between social play rate and play partner availability which was also contrary to studies in wild western gorillas which showed a positive correlation (Nowell, 2005). Social play rate increased up to a peak at around five available partners, then declined. However, this relationship could still indicate a social function of play. As gorilla group size increases so does the spread of individuals, due to feeding competition (Robbins et al., 2021). Therefore, as group spread increases, immatures may spend more time searching for play partners, which would reduce their overall time spent in play. If individuals are spending more time searching out different play partners to achieve a larger repertoire of partners, at the costs of a lower overall rate of play, this may indicate that playing with more partners is more valuable for social

skills development. The relationship between group size and group spread may be more relevant to mountain gorillas than western gorillas as they tend to have larger group sizes, however food is also more spatially dense in mountain gorilla habitat (Robbins & Robbins, 2018). Social skills and relationships are developed through interactions with different individuals, whereas the motor training hypothesis emphasises play as a platform to practice and develop motor skills, which does not rely on learning from different partners. Here we did not examine specific play partnerships, but a follow up study (Chapter 4) will examine play partner preferences and repertoires to delineate between social and motor skills functions of play.

Energetic constraints

Our results are consistent with our predictions that play is under energetic constraints. Social play rates were higher before weaning than after (by an average 2%, or nearly a 50% decline in play rates) and during months of higher fruit consumption. Contrary to the surplus energy theory (Spencer, 1872), which focuses on the energetic costs without any beneficial function of play, we believe there are both proximate costs and ultimate benefits of play. Our study supports a need to study play in the framework of both costs and benefits, because the costs of play may constrain the potential benefits. Specifically, males played at higher rates between 2-6 years compared to later in life, suggesting that the benefits-to-cost ratio is higher at younger ages despite also needing to invest more energy in growth. Once weaned, individuals need to invest heavily into feeding and growth, which may limit the energy they should invest in play. However, older individuals in this study between 7-8 years of age were still spending approximately

3% of their time in social play (compared to 4-7% at 2-3 years olds) indicating there may still be benefits to social play past the juvenile period (Asensio et al., 2022; Norscia & Palagi, 2011). Furthermore, different play-type show different energetic levels and likely different energetic costs. Therefore, spending time in different play types during ontogeny may exacerbate or reduce overall costs of play and energetic trade-offs with other activities.

Fruit consumption, our proxy for increased energy availability, has higher energy return rates than non-fruit foods (Wright & Robbins, 2014). However, fruiting periods also lead to higher daily travel rates in Bwindi gorillas (Ganas & Robbins, 2005; Seiler et al., 2018), which could counteract this higher energy intake. Although, this may be less consequential for younger individuals which save energy by being carried more often, energy which could be spent on play. Nonetheless a positive correlation between increased fruit consumption and amount of play conforms with previous primate and great ape studies (Asensio et al., 2022; Kunz et al., 2024; Moebius et al., 2019), including the finding that adult gorillas play more during the bamboo season, in which energy intake rates may be higher (Grueter et al., 2016).

Weaning is also considered to be a key developmental milestone linked to large changes in energy acquisition (Lee, 1997), which will influence energetic availability for play. As previously reported we observed that social play rate was higher in unweaned individuals (Eckardt, 2010; Fletcher, 1994), but in our study play rate had already started declining at around 3 years (for males), which is before weaning at mean of 4.8 years in Bwindi gorillas (Robbins & Robbins, 2021). Contrary to our predictions that primiparous

mothers may be providing less energy supplementation to offspring, we found no effect of mother parity on offspring play rate.

Future directions

Longitudinal studies of wild primates are invaluable for understanding how natural ecological variation relates to behavioural variation, and they are necessary for linking behavioural development to fitness benefits. Alongside examining variation in biological, ecological, and social factors, we suggest that future studies should incorporate other metrics of play behaviour, such as developmental metrics (Berghänel et al., 2015; Heintz et al., 2017), which in turn can impact dominance and reproductive fitness. These relationships provide support and can help delineate between motor and social skills hypotheses of play. Furthermore, the social relationship hypothesis encompasses 1) development of social skills and 2) formation of dyadic social relationships (Meaney et al., 1985). Teasing apart these two components of the social relationships hypotheses is not possible in this study that examined only play rates; a finer scale analysis that incorporates other metrics such as play partner preference, is needed. Partner preference and development may also be interconnected as individuals become more independent from the mother they may prioritise other play partners, and mother-offspring play may compensate for lower levels immature-immature play when other immature are not available (Sabbi et al., 2024).

Through using long-term data, studying how the trade-off between play and other factors, such as growth (Berghänel et al., 2015; Heintz et al., 2017), would allow us to understand which functions are being prioritised in primate development. Assamese

macaques showed a sex-specific trade-off between body growth and play, whereby males increased play more than females during periods of high fruit availability (Berghänel et al., 2015). These findings strongly support that the benefits of play are at times being prioritised over growth. To understand the interplay between the energetic costs of play and its potential benefits, more direct measures of energy balance would further elucidate our understanding of the energetic costs of play. We were not able to measure energy balance directly in this study.

3.5. Conclusion

Mountain gorillas provide an important context for studying play behaviour as they are one of our closest living relatives, and their high degree of sexual dimorphism allows for clear testing of sex-biases in behaviour. Male gorillas, which are dominant over females and have more affiliative relationships, are expected to benefit from developing motor and social skills more than females. Our finding of a male-bias in play rates is consistent with play being a platform to develop either motor or social skills, based on the needs of adults. However, while these different hypotheses focus on different aspects of play, they are not mutually exclusive. Furthermore, engaging in play likely has energetic costs, suggested by its higher rates before weaning in months of high fruit consumption. Documenting the variation and complex nature of play will help elucidate the necessity of play in development and why it has been highly conserved in the tree of life.

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Chapter 4: Differentiated and stable play partnerships in Bwindi mountain gorillas.

Keywords: social play, *Gorilla beringei beringei*, social relationships

Abstract

Social play is ubiquitous amongst mammals and is likely to be a key component of immature social relationships. Differentiated social relationships amongst adults are an important part of primate social structure, yet we know little about relationships amongst immatures. Frequency of play has been the most commonly studied aspect of animal play behaviour, but challenges still remain in understanding immature social relationships and delineating non-mutually exclusive hypotheses for the benefits of play. Two common frameworks for the function of play include the motor training hypothesis (building motor skills) and the social relationship hypothesis (social development). The social relationship hypothesis can be further delineated by its two proposed functions, building social skills (social skill development) and establishing social relationships (social bond formation). To differentiate among these hypotheses and understand what factors (age difference, sex, previous relationships, proximity, proximity of mothers) influence dyadic play partnerships, we analysed nine years of play behaviour amongst 32 immature Bwindi mountain gorillas (*Gorilla beringei beringei;* age 0.5-8 years). We used network analysis to calculate play association scores, a relative measure of how much time each dyad spends in social play. Bwindi gorillas chose partners of similar ages, in support of the motor training hypothesis. Male-male dyads had higher play association scores than female-female or male-female dyads, suggesting that social play could be beneficial for males to build motor skills and skills related to social dominance behaviours. We found

that Bwindi gorillas have differentiated social relationships in play and proximity, which are not driven by mother-mother proximity. In support of the social bond formation hypothesis, play association scores correlated with proximity and were stable from one year to the next. However, play partnerships did not correlate with proximity partnerships in subsequent years. Play partnership patterns support a motor, social skill development and social bond formation function of play. Our results suggest the benefits of play may be sex- and age-dependent. Examining play on a dyadic level may help us differentiate between these benefits and provide evidence of a key feature of social relationships amongst immature mammals.

4.1 Introduction

The function and long-term advantages of social play are unclear, despite it being reported in almost all mammal species and a large number of birds and reptiles (Burghardt, 2005; Fagen, 1981; Power, 2000). Two frameworks for examining the evolutionary function of social play are the 'motor training hypothesis' (Bekoff & Byers, 1981) and the 'social relationship hypothesis' (Baldwin & Baldwin, 1974). Social play, unlike other types, has the potential to develop both social and motor skills, because it involves the interaction between two or more individuals (Burghardt, 2014). Predictions of motor and social development hypotheses of play for variation in play rates are non-mutually exclusive (Chapter 2). However, examining differentiation in play partner preferences may be more fruitful for distinguishing between the hypotheses (see Table 4.1). Furthermore, partnerships in play may be the foundation for building relationships and social skills for immature individuals, both of which may continue into adulthood (Fagen, 1981; Palagi, 2018), particularly in species in which play is the predominant

social activity for infants, such as gorillas (Eckardt, 2010; Nowell, 2005). Yet, little attention has been paid to the differentiation in social affiliation amongst unrelated immature-immature dyads.

The 'motor training hypothesis' posits that play is a platform to refine motor skills and enhance competitive ability (Bekoff & Byers, 1981). To develop motor skills, we expect individuals to prefer to play with similar aged and sized peers and kin, to safely engage in more vigorous play (Bekoff & Byers, 1981). The desire for lower risk interactions presents itself in choice of play partner. Many species demonstrate the preference for similar age partners [e.g., sifaka (Lutz et al., 2019), baboons (Lutz et al., 2019; Owens, 1975), western lowland gorillas (Palagi et al., 2007), mountain gorillas (Fletcher, 1994), vervet monkeys (Fairbanks, 1993), oryx (Pfeifer, 1985), antelopes (Thompson, 1996), Siberian ibex (Byers, 1980), gazelles (Gomendio, 1988), bighorn sheep (Hass & Jenni, 1993), African elephants (Freeman et al., 2021), and wallabies (Watson, 1993)]. This pattern appears more common in more dimorphic species, with some more monomorphic species exhibiting no play partner preferences based on age [e.g., wolves, bush dog, foxes (Biben, 1983), capuchins (Lutz et al., 2019) and bonobo (Palagi & Paoli, 2007)]. Furthermore, as motor skills are most relevant in competitive interactions, we would expect a sex-bias in partner preference based on competition as adults.

Adult primates exhibit differentiated social relationships and the development of these social bonds can impact survival and reproduction (Feldblum et al., 2021; Ostner & Schülke, 2018; Schülke et al., 2010; Silk, 2007; Silk et al., 2006). However, we do not know if these differentiated relationships begin during immaturity or how immature

individuals learn to form social bonds. Immature primates spend more time in play than other taxonomic groups (Burghardt 2005), and social play is the primary social activity amongst immature primates (Smith, 1978; Watts & Pusey, 1993). Therefore, play is an important activity to examine when investigating immature social relationships. In some primates social interactions of offspring appear to be largely driven by maternal behaviour (Murray et al., 2014). Similarly, the presence of older kin in chimpanzees can impact play rates, particularly for male-male siblings (Lonsdorf et al., 2018). Play partnerships in Virunga mountain gorillas are shown to be differentiated by age and sex (Fletcher, 1994; Grebe et al., 2022). However, it is unclear if gorilla immature relationships are driven by maternal behaviour. Furthermore, we do not know if play partnerships are stable over time for immatures in their natal groups, which would suggest they act similarly to adult affiliative relationships (Young & Robbins, 2022).

The 'social relationship hypothesis' (Baldwin & Baldwin, 1974) pertains to social benefits of play and learning how to interact with other individuals. The 'social relationship hypothesis' incorporates two components of social development: 1) developing social skills (referred to here as social skills development) and 2) building individual social relationships (social bond formation) (Meaney et al., 1985). Whilst not mutually exclusive, these two components can be differentiated by examining different aspects of partner preference patterns.

A social skill development role of play suggests that play is beneficial to cultivate skills relevant to interacting socially as an adult. Primate social relationships consist of both affiliation patterns and patterns of social dominance, both of which create social environments within the group that immature primates need to learn to navigate. Adult

social skills often vary between sexes therefore, partner preferences in play would likely be present in a pattern akin to adult social relationships. In species in which females have stronger affiliative relationships with males during adulthood, immature females prefer immature male play partners, such as Western lowland gorillas (Brown, 1988; Maestripieri & Ross, 2004) and monogamous Titi monkeys (Chau et al., 2008). Primates in which females are dominant have shown a female-female preference for dyadic play (e.g. Sifakas, Lutz et al., 2019; bonobos, Palagi, 2006). Similarly, in wild studies of male-dominant squirrel monkeys (Aghababian et al., 2021), baboons (Cheney, 1978; Owens, 1975), Tibetan macaques (Wright et al., 2018) and rhesus macaques (Yanagi & Berman, 2017), males preferred to play with other males. However, it is important to account for partner availability because some studies indicated that sex preferences were not greater than would be expected from group composition alone (Nowell, 2005). Contrastingly, non-primates such as maned-wolf, crab-eating fox, bush dog (Biben, 1983), prairie voles (Chau et al., 2008), oryx (Pfeifer, 1985), sable antelopes (Thompson, 1996), big horn sheep (Hass & Jenni, 1993), do not display strong sex preferences for play partners, only preferences for similar age individuals. This contrasting pattern indicates that social skill development through play may be more relevant for primates, which have longer juvenile periods than mammals.

A social bond formation function of play would suggest that individuals playing together aids them in developing long-lasting dyadic relationships. This would present as the same dyads playing together over time and dyadic partnership preferences in play to be correlated with dyadic partnerships preferences in other affiliative activities. Dyadic partnerships in play have been shown to mimic dyadic preference in other affiliative

activities, suggesting bond formation translates between different affiliative activities. This appears to be the case in primates, as Japanese macaques (Shimada & Sueur, 2018), geladas (Mancini & Palagi, 2009) and wild squirrel monkeys (Baldwin & Baldwin, 1974) associated more in other activities with their play partners. Similarly, in bonobos (Palagi & Paoli, 2007), sifaka, baboons and capuchins (Lutz et al., 2019), preferred partners in other affiliative behaviours (grooming, touching, feeding) were correlated to their preferred play partners. In contrast, meerkats (Sharpe, 2005b) and red-necked wallabies (Watson, 1993) show little correlation between partnerships in play versus other affiliative behaviours, suggesting this function of play may be more important for primates. Affiliative measures in these studies were taken during overlapping time periods, therefore, it is difficult to ascertain if there is a causation between play partner preference and partner preference in other affiliative activities. However, social play behaviour occurs before grooming in chimpanzees (Bründl et al., 2020) and the amount of social play has been shown to correlate with age of first grooming (Heintz, 2014), suggesting play can occur before the initiation of other affiliative activities. If play is a component of social bonds in immatures, we would expect partnerships to be stable over time (Thompson, 1996) as observed for adult affiliative behaviours, e.g. grooming and proximity (Bray & Gilby, 2020; Mitani, 2009). However, the stability of play relationships has not been examined in immature primates.

Social play during development could provide an opportunity to learn how to build motor skills, social skills and/or begin to form bonds with other individuals. However, there has been little focus on play partnership patterns in immature primates. Gorillas are an excellent model in which to examine this topic because they live in

cohesive social units, creating a stable environment of play partner opportunities for immature individuals over their long developmental periods (Robbins, 2010). Gorillas are the most sexually dimorphic great ape and the sexes have different life history and social strategies (Leigh & Shea, 1996; Watts, 1992). If play is beneficial for developing skills necessary for adulthood, sex differences in play should be most apparent in gorillas as they show sex-differences in behaviour from the juvenile stage onwards (Hutchinson & Fletcher, 2010). Gorillas live in male-dominant social groups with high levels of male-male competition (Robbins, 2010). Therefore, males should prefer other males as play partners if building motor skills is the priority. Similarly, male-male play preferences would be expected if play was an opportunity to practise competitive skills and to test one's developing motor skills against a similar sized individual. Competitive skills are related to dominance, which involves both motor skills to engage in competitive interactions and social skills to understand dominance hierarchies. Previous studies support male-male preference in play (Brown, 1988; Fletcher, 1994; Grebe et al., 2022). In contrast, since female-female competition and affiliation are low in gorillas (Watts, 1994; Young & Robbins, 2022), we would expect female-female play to be less important.

Affiliative interactions are also an important social skill to learn. Male-female relationships are the most important affiliative relationships during adulthood in gorillas (Harcourt, 1979; Watts, 1992, 2001). Therefore, if play serves as a format for learning social affiliation skills, we expect both sexes to prefer opposite sex play mates, akin to adult preferences. Furthermore, due to mountain gorilla groups typically having more adult females than males, males have to sustain more affiliative relationships. Therefore,

males would be expected to have more play partners and play more evenly with those partners, to learn how to maintain multiple affiliative relationships. Social bond formation goes beyond just learning skills in play and suggests that individuals are building specific dyadic relationships. Therefore, we would expect partnerships preferences at the dyadic level to be stable over time and should correlate with partner preferences in other affiliative activities. In gorillas, since both sexes may disperse, bonds developed during immaturity are unlikely to last into adulthood. However, play could enable social bond formation, on a short-term basis, amongst immatures before age of dispersal.

Here we examine partner preferences of immature Bwindi mountain gorillas (*Gorilla beringei beringei*) to distinguish between three proposed functions of play (see Table 4.1): 1) motor training, 2) social skill development and 3) social bond formation. We will test six different components of partner preference (see Table 4.1): 1) Number of play partners – if sex predicts the percentage of available play partners that an individual plays with, 2) Evenness of play – if sex predicts how evenly distributed time spent in play is split among available play partners (e.g. do individuals spend the same amount of time playing with all play partners), 3) Age preference – if individuals prefer to play with partners of the same age, 4) Sex preference – if individuals prefer to play with partners of the same sex, 5) Play preference stability – if preferred play partners on a dyadic level are the same from one year to the next, and 6) Correlation with social proximity – if play partnerships are correlated with immature proximity partnerships, mother-mother proximity partnerships and immature partnerships one year later.

Table 4.1: Predictions of play partnerships attributed according to the three hypotheses tested (predictions in bold are supported by the results). *Play evenness is a measure of how time spent in play is distributed between all available partners, measured using a Shannon Diversity Index.

	Measures of partner preference					
Hypothesis	Number of play partners (Model 1)	Evenness of play* (Model 2)	Age Preference (Model 3)	Sex Preference (Model 3)	Preference stability (Model 4)	Correlation with proximity (Model 3 and 5)
Motor training	No sex difference in number of partners	**No sex difference in play evenness**	**Similar age partners**	**Males prefer males. Females no preference.**	Not stable over time	Not correlated
Social skill development	**Males more partners**	Males more even than females	No preference	***Social dominance*: Males prefer males. Females no preference.** *Social affiliation*: Males prefer females. Females prefer males	Not stable over time	Not correlated
Social bond formation	**Males more partners**	Males more even than females	No preference	Males prefer females. Females prefer males.	**Stable over time**	**Correlated with immature proximity in same time period but not mother proximity or immature proximity in subsequent time period**

4.2 Methods

Study population and subjects

Data were collected from five groups of mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park from Jan-2013 until Dec-2023, with a break in 2020 and early 2021 because of the Covid-19 pandemic (see Appendix C Table S4.1 for observation timelines of each group). A total of 32 individuals were included in the study between the ages of 0.59 to 8 years old. Specific data for this study were extracted from a general long-term behavioural database collected by several researchers (see Acknowledgments), trained according to the same protocol and supervised on a routine basis to ensure uniformity.

Data collection

Data collection occurred for up to 4 hours per day, in accordance with regulations from the Uganda Wildlife Authority. Focal sampling (Altmann, 1974) was performed with a minimum of 5 and maximum of 60 minutes, to ensure focal time was collected on multiple individuals throughout the day. The goal was 5 hours of focal time per month per individual, and total focal time was recorded throughout the month to maintain balanced sampling across individuals by selecting those with less overall focal time. When individuals were out of view for more than 60 seconds, focal animal sampling stopped. Social play behaviour was defined in the data collection protocol as: whenever two individuals interacted in a non-aggressive manner, usually in a form of wrestling, chasing, hitting, or tickling, which can be further identified as it its often accompanied by

a ‘play chuckle’ vocalisation, including all categories of play: rough-and-tumble, gentle, chase, sparring and rest (Eckardt, 2010; Fletcher, 1994; Heintz et al., 2017; Nowell, 2005; Winkler & Perry, 2022). Only play bouts of known duration, of a minimum of 5 seconds, that occurred during focal sampling were included in the analysis. We restricted our analysis to only dyadic play bouts because the networks were based on dyadic interactions and the majority of play only involved two individuals (91% of play bouts). For each play bout, the identity of both individuals was recorded (ID and Partner ID), and the length of the play bout was recorded to the nearest second by electronic tablet timer (nearest 5 second pre 2016 when data were collected on paper with a digital watch). Play bouts were considered finished when individuals engaged in another activity or stopped playing for more than 60 seconds, which accounted for a period of rest play which might occur before individuals reengage in active play (Fletcher, 1994).

Concurrent instantaneous scan sampling occurred at fixed time intervals (pre-May 2015: every 5 minutes, post-May 2015: every 10 minutes). During each scan, observers recorded all individuals in view, the activity they were engaged in (being carried, feeding, nursing, playing, resting, travelling), their height off the ground and the proximity of all individuals in view to the focal individual. Proximities were recorded in categories (0: physical contact, 1: 0-2 m, 2: 2-5 m, 3: 5-10 m, 4: 10-20 m, 5: > 20 m), which were used for measurements of immature proximity and mother proximity.

Dyadic association Scores

Association scores - were calculated to represent the strength of associations in social play and proximity at the dyad level. Dyadic association scores quantify the relative amount of interaction between each interacting dyads accounting for the amount of time

they were observed. Dyadic association scores were calculated using the netTS package (Bonnell & Vilette, 2021) in R (R Core Team, 2020). This package allows the user to determine the minimum reliable window that can be used for building networks, which in our dataset was 365 days. The window shift was set to 365 days, resulting in the next network being calculated for the next 365-day period with no overlap. Association scores were calculated for 365-day periods of continuous data collection before and after the pause in data collection because of Covid-19 (see Appendix C, Table S4.1). Networks were calculated for each group independently, as partner availability can vary per group which can influence partner preferences (Nowell, 2005). Dyadic interactions in play were treated as non-directional and therefore ID and Partner ID are considered interchangeable, and thus the age range of the focal and age range of the partner must be identical. Using this approach, we calculated association scores for all individuals between 0.59 and 8 years of age, during the same 365-day periods for 1) play behaviour (play association scores) and 2) immature proximity (immature-immature proximity association scores). We also calculated 3) mother-mother proximity association scores, that is proximity association scores between mothers of each individual in a dyad, from scans data during focal periods of the mothers. We calculated 24 networks for the 5 gorilla groups across 9 years, compromising of 91 unique immature dyad partnerships, totalling 216 data points.

1) Play association scores – were calculated from 9913 play bouts (351 hours of play) that included a focal animal as one of the play partners from a total of 8,598 hours of focal time. The dyadic association score was calculated based on the

duration, in seconds, that each unique dyad played (P_{ab}) over a 365-day period, controlled by the combined focal time of both individuals ($F_a + F_b$): play association = $P_{ab}/(F_a + F_b)$. Any dyad in the group which did not play together was assigned a 0 as their play association score. The play association score had a mean of $9.254e^{-05}$ (range 0 – $6.42e^{-04}$).

2) Immature-immature proximity association scores – were calculated from 85,772 scans in which one of the study subjects was the focal animal, excluding scans in which the activity was playing, to eliminate replication of considering play bouts as times of spatial proximity. To assess the strength of each dyadic association for proximity, a dyadic association score was calculated based on the number of scans in which dyads were within 5 m proximity ($S5_{ab}$) as in (Young & Robbins, 2022), controlled by the total number of scans that both individuals were present in ($S_a + S_b$): proximity association = $S5_{ab}/(S_a + S_b)$. Any dyad in the group which did not come within 5 m of one another was assigned a 0 as their proximity association score. The proximity association scores for immatures had a mean of 0.393 (range: 0-0.476).

3) Mother-mother proximity association scores – to account for the possibility that mother-mother proximity has an effect on offspring proximity, we also calculated proximity association scores for the mothers of each offspring dyad in the study using the same methods as above (immature-immature proximity association scores): mother-mother proximity association = $M5_{ab}/(M_a + M_b)$. If there was no proximity association for a particular mother dyad which matched the same period of the play association score for their offspring, the proximity association

was assigned as 0. The mother proximity association scores had a mean of 0.022 (range: 0 – 0.240).

Statistical Analyses

All statistical analysis were performed in R (R Core Team, 2020). To test our predictions we ran Mixed Models, using the glmmTMB package (Brooks et al., 2017). Where appropriate (when more than one predictor was present), we calculated Variance Inflation Factors (VIFs), using the performance package (Lüdecke et al., 2021) to verify that there was no collinearity between our fixed effects. We used the Dharma package (Hartig, 2020), to confirm that our models conformed to the model assumptions. We visually inspected Quantile-Quantile plots (QQ plot) to check for the assumption of normality in the dataset. We used testDispersion to check our models did not display under/over dispersion. We plotted the predicted vs. fitted residuals to confirm that there was not heteroscedasticity in the data. For each model we did a full-null comparison, with an ANOVA test, comparing the full model to a model with only the random effects to confirm that the full model had a higher predictive power, represented by having a lower AlC.

Analysis 1 – Number of play partners

We used focal data to assess if sex had an effect on the number of play partners a focal individual had as a percentage of available partners. We used 6,184 hours of focal animal sampling and excluded any months when an individual had less than 180 minutes of focal time (~20% of months), to limit months with small total amounts of observation

time which would not include as many play partners, giving a mean of 332 minutes of focal time per month (range 181 - 998 mins, 90% of data points had between 180-480 minutes). Using 319 hours of play, for every focal individual between 0.5 and 8 years old we calculated how many unique play partners they had for each month and each year. A play partner was any individual between the ages of 0.5 and 12 years that the focal played with. We included partners up to 12 years, in this analysis, to account for the possibility that some play partners are older than the focal animal and to not bias the number of partners for immatures that only had older partners to play with (this was not possible in the association scores as both partners were treated interchangeably so had to be the same age range). We expressed the number of play partners as a percentage of potential partners. Potential partners were the number of total individuals in the group between the ages of 0.5 and 12 years present during each month or year. We calculated 951 monthly data points, and 143 yearly data points of 31 individuals. We then calculated means, standard deviations, minimum and maximum values for focal males and females separately. Finally, we ran mixed models to examine if sex was a significant predictor of number of play partners per month and per year. The response variable was the number of unique play partners for each time period (month or year) for each individual, which was offset by the log transformation of the total number of potential partners, over that time period. The fixed effects were an interaction between sex and a quadratic term for age. Random effects were added for ID, group, and year. The models were run with a Gaussian error distribution (Zuur et al., 2009). Visual checks of quantile-quantile plots and statistical tests conformed to the assumptions of uniformity (monthly model KS test: $D = 0.0383$, p-value = 0.122; yearly model KS test $D = 0.0541$, p-value = 0.797) (see

Appendix C: Figure S4.1 & Figure S4.2). The models did not show overdispersion (monthly model dispersion = 1.01, p-value = 0.768; yearly model dispersion = 1.104, p-value = 0.56) and the frequency of outliers was lower than expected (monthly model p-value = 0.464; yearly model p-value = 0.316). Visual inspections of predicted residuals versus fitted residuals showed no heteroscedasticity.

Analysis 2 – Evenness of play

We used a Shannon Equitability Index to examine how an individual's time spent in play was distributed amongst available partners (Bitetti, 2000; Cheney, 1992; Shannon & Weaver, 1949). We calculated a Shannon-Wiener Diversity Index *(H)*, where $H = -\sum p_i * \ln p_i$, where *p* is the proportion of the focal individuals play time spent with each partner (*i*), e.g. the amount of time a focal individuals spend in play with a specific partner (*i*) divided by the total number of time playing for the focal with all partners. This was then converted to a Shannon Equitability Index (E_H) where $E_H = \frac{H}{\ln S}$, and S equals the total number of potential partners. This gives a value between 0 and 1, with 1 being even play with all available partners. We calculated a Shannon equitability index for males and females separately, to measure evenness of play on both a monthly and yearly scale.

Analysis 3 – Partner preference

To examine if individuals had preferred play partners we analysed if play association scores were correlated with the sex of the two partners, their age difference, their

immature-immature proximity association score, and the mother-mother proximity association scores during the same period. To assess if there was an age preference for play partners, for each network we assigned the age for each individual as their age at the middle of each yearly network constructed. Then to calculate an age difference for each dyad we subtracted the age of the individual from the age of the partner and converted it to an absolute age difference (abs age diff). Play rates change with age (see Chapter 3), therefore, we also calculated a mean age of the two individuals in the dyad (mean dyad age), to account for ontogenetic change in play.

A linear mixed model was run, with a gamma error distribution (Zuur et al., 2009). The square root transformation of the play association score was the response variable. This was further transformed by adding 0.00001 to all values, to remove any zero values but keep the association scores at the same magnitude (max play association score = 0.00064). The fixed effects were an interaction term between absolute age difference and mean dyad age. A preliminary analysis was run with mean dyad age as a quadratic effect, but model diagnostics were better with this as a linear effect. A fixed effect term was added for sex partnership (levels; female-female (control), female-male, or male-male). Fixed effects were added for immature proximity association and mother-mother proximity association, both of which were also square root transformed. Random effects were added for ID, partner ID and dyad ID, to account for variation amongst individuals and dyads. We also added random effects for group and network start date to account for the variation in the number of different potential age and sex partners that are available in different groups and during different periods. There was no collinearity between the fixed effects (all VIFs < 2), when checked on a model removing the interaction term. The QQ

plots showed a uniform distribution of the residuals (KS test: D = 0.0822, p-value = 0.108, see Appendix C Figure S4.3). There were no issues of dispersion (dispersion = 0.809, p-value = 0.736), and there were fewer outliers than expected (p-value = 0.426). Visual checks of predicted residuals against fitted residuals showed no presence of heteroscedasticity. To compare the 3 different levels of the sex partnership fixed effect we used a Tukey's post-hoc test using the lsmeans package (Lenth, 2016).

Analysis 4 – Stability of play partner relationships

To assess stability of play associations we examined if play association scores in one year were correlated with those in the next year. We ran a generalized linear mixed model, with a gamma error distribution (Zuur et al., 2009). The square root transformation of the play association score was the response variable. This was further transformed by adding 0.00001 to all values, to remove any zero values but to keep the association scores at the same magnitude (max play association score = 0.00064). Play association score for the previous network was the fixed effect, which was also square root transformed. Random effects were added for ID, partner ID, dyad ID, group, and network start date. Visual inspection of the QQ plot showed that model assumptions were not violated (see Appendix C Figure AS4.4) and the model residuals were uniform (KS test: D = 0.0.568, p-value = 0.766). The data were not overdispersed (dispersion = 1.128, p-value = 0.536), and there fewer less outliers than expected (p-value = 1). Visual checks of predicted residuals against fitted residuals showed no presence of heteroscedasticity.

Analysis 5 – play association and proximity association for subsequent year

To assess if play association and proximity association for the subsequent year were correlated, we ran a generalized mixed model with a gamma error distribution (Zuur et al., 2009). The square root transformation of the proximity association score was the response variable. This was further transformed by adding 0.01 to all values, to remove any zero values but keep the association scores at the same magnitude (max proximity association score = 0.476). The fixed effect was the square root transformation of the play association score in the previous network. Random effects were added for ID, partner ID, dyad ID, group, and network start date. Visual inspection of the QQ plot showed that models assumptions were not violated (see Appendix C Figure S4.5) and the model residuals were uniform (KS test: D = 0.0968, p-value = 0.1509). The data were not overdispersed (dispersion = 0.712, p-value = 0.28), and there were less outliers than expected (p-value = 0.301). Visual checks of predicted residuals against fitted residuals showed no presence of heteroscedasticity.

Ethical note

Data used as part of this study were collected non-invasively from nonhuman primates. Permission was granted for the study by Uganda Wildlife Authority and Uganda National Council of Science and Technology, and we adhered to all protocols and guidelines set by these institutions.

4.3 Results

Analysis 1 – Number of play partners

Females played with a monthly mean of 42.08% of available play partners (Table 4.2) and a yearly mean of 69.77% of available play partners (Table 4.3). Males played with a monthly mean of 48.18% of available partners (Table 4.2) and a yearly mean of 75.38% of available partners (Table 4.3).

Table 4.2: Percentage of available play partners that each sex plays with, on a monthly basis.

Sex	Mean (%)	SD	Min (%)	Max (%)	Number of focal individuals	Number of months
Female	42.08	19.61	10	100	12	431
Male	48.18	22.96	10	100	19	520

Table 4.3: Percentage of available play partners that each sex plays with, on a yearly basis.

Sex	Mean (%)	SD	Min (%)	Max (%)	Number of focal individuals	Number of years
Female	69.77	22.53	12.5	100	12	66
Male	75.38	23.52	12.5	100	19	77

For both the month-based and year-based number of play partner models, the full-null comparison indicated that the full and null models were significantly different (monthly model, $\chi 2$ =58.941, df = 5, p-value < 0.001; yearly model, $\chi 2$ =22.211, df = 5, p-value < 0.001). In the full model, the interaction between sex and age was significant for monthly number of play partners (Beta = -8.646, SE = 2.544 and, p-value < 0.001, Table 4.4, Figure 4.1), but showed only a trend towards significance for yearly number of

play partner (Beta = -4.568, SE = -1.812 and, p-value = 0.070, Table 4.5). In the month-based model, males had a quadratic relationship between age and number of play partners with individuals having the most play partners between 3 and 4 years old. Females showed a decrease in number of play partners with age.

Table 4.4: Results from the month-based number of play partners model, significant p-values at the 0.05 level are in bold, * = an interaction term.

Term	**Estimate**	**SE / SD**	**P**
ID	Random intercept	0.245	
Group	Random intercept	0.392	
Network start date	Random intercept	0.430	
Intercept	0.710	0.241	**<0.001**
Sex male	0.329	0.128	**0.010**
Age	-5.580	2.002	**0.005**
Age^2	-0.683	2.050	0.739
Sex (male)*age	-2.776	2.623	0.290
Sex (male)*age^2	-8.646	2.544	**<0.001**

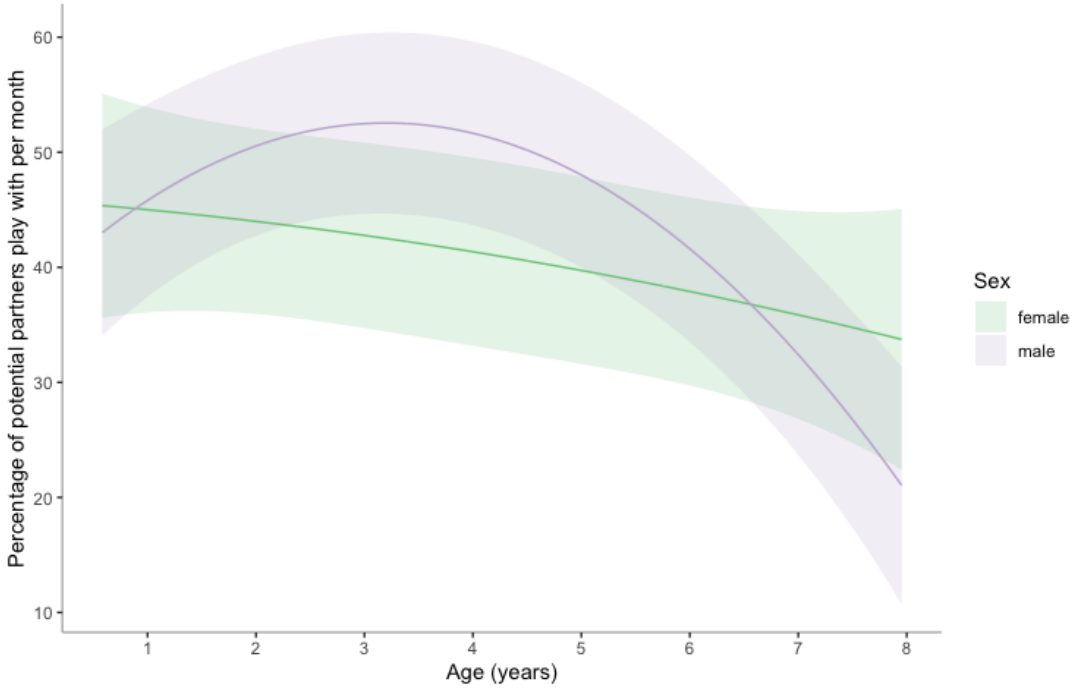

Figure 4.1: Model predictions for the effect of sex on month-based number of play partners. Variables have been back transformed for easier interpretation and displayed as percentage of total available partners.

Table 4.5: Results from the year-based number of play partners model, significant p-values at the 0.05 level are in bold, * = an interaction term.

Term	**Estimate**	**SE / SD**	**p**
ID	Random intercept	0.361	
Group	Random intercept	0.430	
Network start date	Random intercept	1.103	
Intercept	2.902	0.432	**<0.001**
Sex male	0.282	0.254	0.267
Age	-3.560	1.963	0.070
Age^2	-2.457	2.041	0.229
Sex male*age	1.474	2.589	0.569
Sex male*age^2	-4.568	2.521	0.070

Analysis 2 – Evenness of play

On a monthly basis, females had a Shannon Equitability Index of 0.322 (Table 4.6) and males had a Shannon Equitability Index of 0.373 (Table 4.6). On a yearly basis, females had a Shannon Equitability Index of 0.574 (Table 4.7) and males had a Shannon Equitability Index of 0.552 (See Table 4.7). The results suggest time spent in play was not evenly spread amongst an individual's play partners, but there was little difference in the level of evenness between females and males.

Table 4.6: Shannon Equitability Index for monthly time spent in social play by sex.

Sex	**Mean**	**SD**	**Min**	**Max**	**Number of individuals**	**Number of months**
Female	0.322	0.238	0	0.841	12	431
Male	0.373	0.245	0	0.979	19	520

Table 4.7: Shannon Equitability Index for yearly time spent in social play by sex.

Sex	**Mean**	**SD**	**Min**	**Max**	**Number of individuals**	**Number of years**
Female	0.574	0.216	0	0.939	12	66
Male	0.552	0.239	0	0.940	19	77

Analysis 3 – age preference, sex preference and preference stability.

The full-null comparison indicated that the full model had greater predictive power than the null model ($\chi 2$ =159.89, df = 8, p-value <0.001). The interaction between absolute age difference and mean age was significant correlated to play association scores (Beta = 0.030, SE = 0.01, p-value <0.001, Table 4.8), indicating that dyads with smaller age differences had higher play association scores (Figure 4.2). This effect was greater at lower ages (Figure 4.2). Male-male partnerships had significantly higher play association

scores (Beta = 0.451, SE = 0.088, p-value <0.001, Table 4.8, Figure 4.3), compared to female-female dyads. However female-male dyad association scores were not significantly different from female-female dyad association scores (Beta = 0.094, SE = 0.064, p-value = 0.146, Table 4.8, Figure 4.3). A post-hoc Tukey analysis demonstrated that male-male dyads also had higher play association scores than female-male dyads (Table 4.9). Proximity association scores displayed a significant positive correlation with play association scores (Beta = 1.943, SE = 0.336, p-value < 0.001, Table 4.8, Figure 4.4). There was no significant correlation between mother-mother proximity association scores and play association scores (Beta = 0.212, SE = 0.258, p-value = 0.41, Table 4.8).

Table 4.8: Model results of age preference, sex preference, preference stability, immature-immature proximity association scores and mother-mother proximity association scores, significant p-values at the 0.05 level are in bold, * = an interaction term.

Term	**Estimate**	**SE / SD**	**p**
ID	Random intercept	0.090	
Partner ID	Random intercept	0.0513	
Dyad ID	Random intercept	0.000113	
Group	Random intercept	0.207	
Network start date	Random intercept	0.158	
Intercept	-4.476	0.192	**<0.001**
Age gap diff	-0.209	0.049	**<0.001**
Mean dyad age	-0.177	0.030	**<0.001**
Sqrt(Immature proximity association score)	1.943	0.336	**<0.001**
Female-male dyads	0.094	0.064	0.146
Male-male dyads	0.451	0.088	**<0.001**
Sqrt(Mother-mother proximity association score)	0.212	0.258	0.410
Age_gap_diff*mean_dyad_age	0.030	0.011	**0.004**

Table 4.9: Post-hoc Tukey's tests for play association scores differences for each sex dyad composition; significant p-values at the 0.05 level are in bold.

Dyad comparison	**Estimate**	**SE**	**z-ratio**	**p-value**
FF – FM	-0.0936	0.0645	-1.452	0.314
FF – MM	-0.4515	0.0881	-5.126	**<0.001**
FM - MM	-0.3576	0.0612	-5.846	**<0.001**

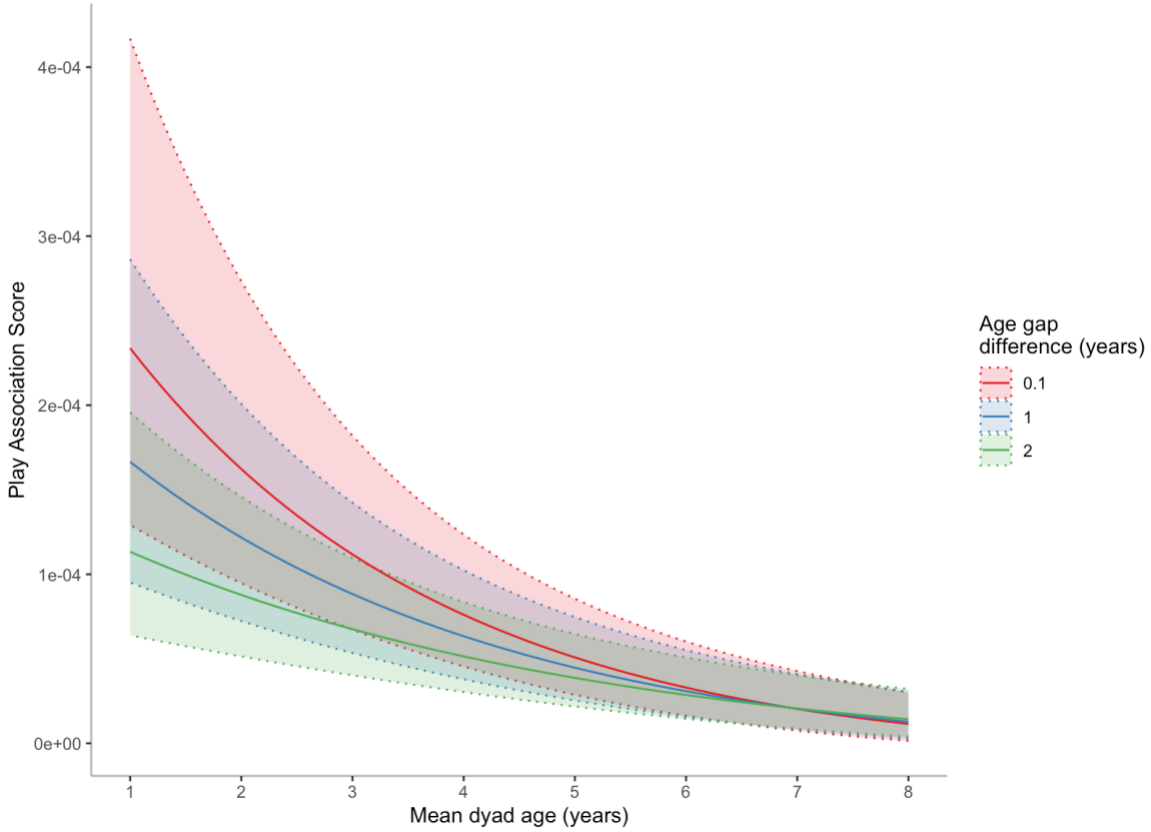

Figure 4.2: Model predictions of play association scores with different mean dyad ages and absolute age gap differences. Variables have been back transformed for easier interpretation.

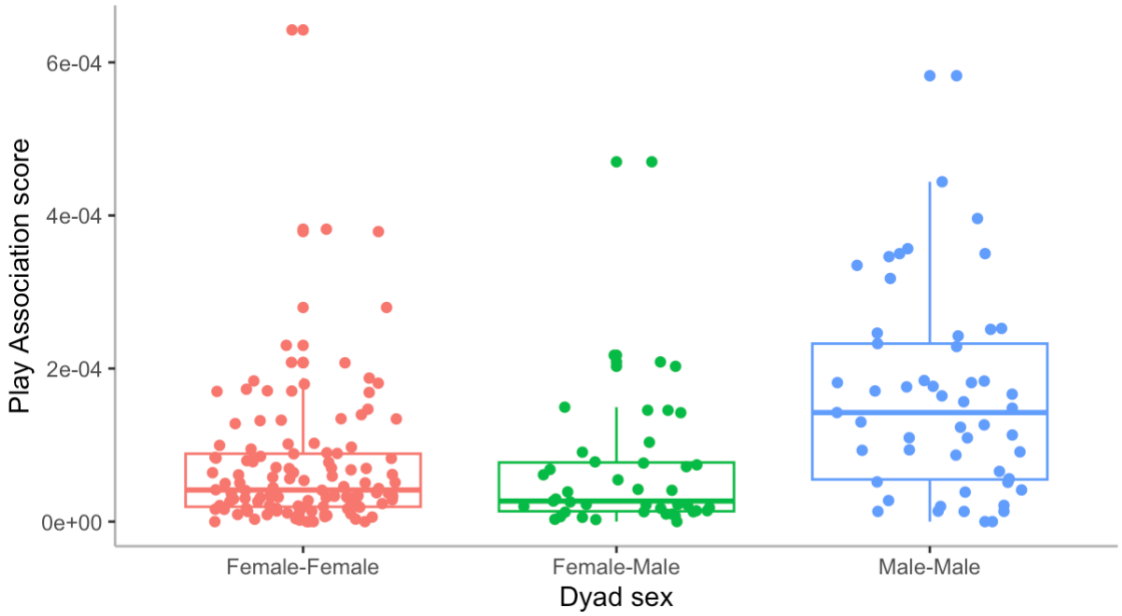

Figure 4.3: Raw data of play association scores with different sex partnerships. For graph of the model predictions see Appendix C Figure S4.6.

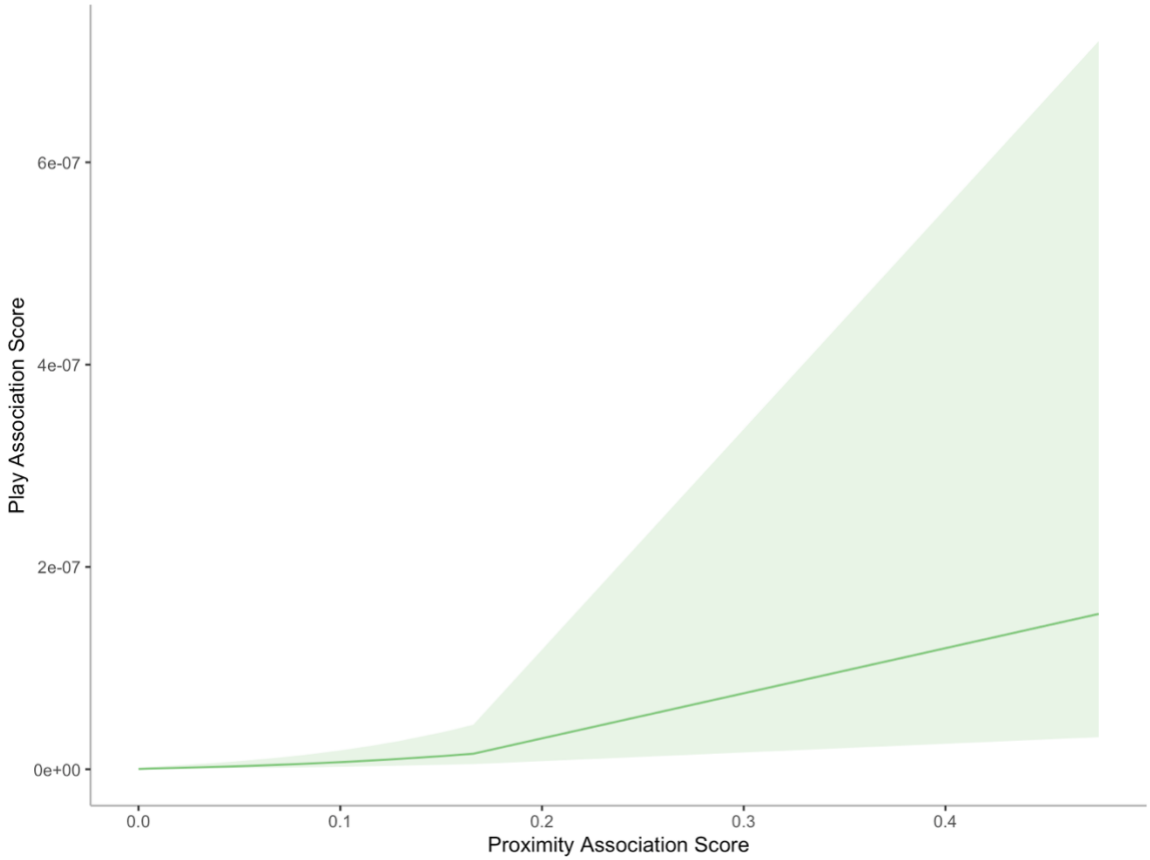

Figure 4.4: Play association scores correlated with immature-immature proximity association scores. Variables have been back transformed for easier interpretation.

Analysis 4 – play association stability

The full-null comparison indicated that the full model had greater predictive power than the null model ($\chi 2$ =14.862, df = 1, p-value <0.001). The play association score in each network period was significantly correlated to the play association score of the previous network period (Beta = 24.573, SE = 3.48, p-value <0.001, Table 4.10, Figure 4.5).

Table 4.10: Results from Model 4, play association score stability, significant p-values at the 0.05 level are in bold.

Term	Estimate	SE / SD	p
ID	Random intercept	0.080	
Partner ID	Random intercept	0.051	
Dyad ID	Random intercept	0.207	
Group	Random intercept	0.153	
Network start date	Random intercept	0.102	
Intercept	-4.972	0.0975	**<0.001**
Sqrt(play association score previous network)	24.573	3.48	**<0.001**

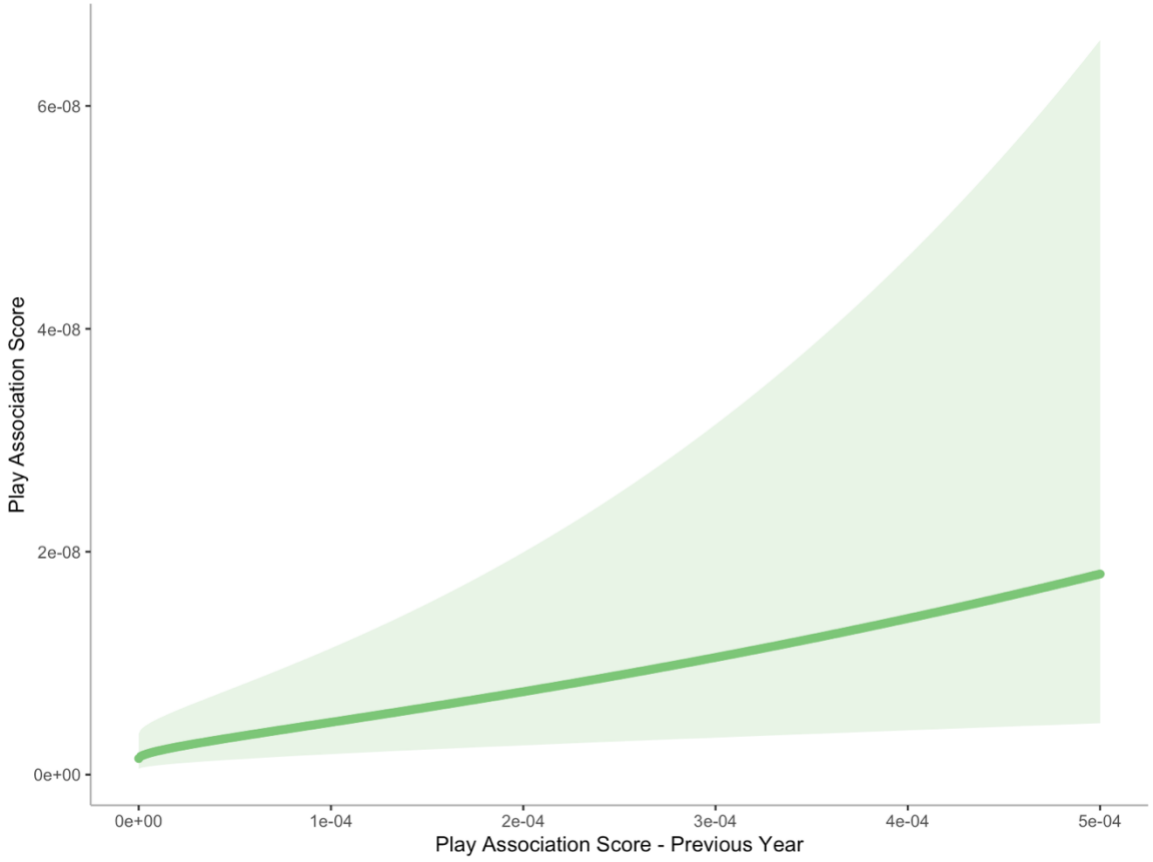

Figure 4.5: Play association scores from current year correlated with play association scores from previous year. Variables have been back transformed for easier interpretation.

Model 5 – play association and proximity association

The full-null comparison indicated that the full model did not have greater predictive power than the null model ($\chi 2$ =2.267, df = 1, p-value = 0.132). The play association score in each network period was not significantly correlated to the proximity association score of the subsequent network period (Beta = 4.724, SE = 3.132, p-value = 0.131, Table 4.11).

Table 4.11: Results from Model 5, play association scores and proximity association scores in the subsequent year, significant p-values at the 0.05 level are in bold.

Term	**Estimate**	**SE / SD**	**p**
ID	Random intercept	$1.07e^{-05}$	
Partner ID	Random intercept	$2.63e^{-06}$	
Dyad ID	Random intercept	0.203	
Group	Random intercept	$7.469\ e^{-06}$	
Network start date	Random intercept	0.209	
Intercept	-1.583	0.0666	**<0.001**
Play association score in previous network	4.724	3.132	0.131

4.4 Discussion

Our results demonstrate that immature Bwindi mountain gorillas have differentiated social relationships for both play and proximity, similar to differentiated affiliative relationships observed in adult gorillas (Morrison et al., 2019; Watts, 1992; Young & Robbins, 2022). Play behaviour in Bwindi gorillas was not correlated to mother proximity, suggesting partner preferences are driven by infant choice. We found support for a motor training function of play based on the results that we observed: a) higher play association scores between individuals of similar ages, b) male-male dyads had significantly higher play association scores than either female-male or female-female

dyads and c) sexes played equally unevenly with their available partners. In support of a social skills function of play, we found a) male-male dyads had stronger play associations in line with our prediction about social dominance interaction and b) males played with a higher proportion of available partners on a monthly basis, although this pattern was not significant on a yearly scale. However, contrary to our social affiliation predictions male-female dyads did not play more. In support of social bond formation, we found a) a correlation between play association scores from one network period to the next and b) play association scores were correlated to proximity association scores during the same network period, but they did not correlate to future proximity scores. Our results provide support for all three non-mutually exclusive hypothesis tested and suggest that motor training and social skills for dominance might be more important for male than female gorillas.

Motor training hypothesis

Our results were consistent with the prediction that motor training is more commonly developed through play with similar ability peers. We found that play association scores were higher for dyads which had smaller age differences, a relationship that was stronger at younger mean dyad ages. Given that play is risky and can result in injury (Symons, 1978), there may be advantages to age-related homophily in play partners (Fu et al., 2012), and thus similar size and ability. This may be more important at younger ages when ability, size and strength are likely to develop more rapidly (Galbany et al., 2017), creating a larger ability difference between individuals. While anecdotal observations suggest that Bwindi gorillas do exhibit self-handicapping (pers. obs.), in

which one individual tempers their ability and strength with younger individuals (Schank et al., 2018), this likely does not occur frequently enough to impact the overall pattern of preferring similar age partners in play. Self-handicapping by the older individual can reduce risk for the younger individual involved, yet it is unclear what the functional benefit is for the older individual; they may gain social skills rather than motor skills from the interaction (Carter et al., 2019; Fagen & Fagen, 2009).

As adults, gorillas exhibit high levels of male-male competition in the form of physical aggression, whereas female-female competition is weak (Doran & McNeilage, 1998; Robbins, 1996, 2008; Stoinski, Perdue, et al., 2009; Watts, 1994; Wright & Robbins, 2014). Our results showed that male-male immature gorilla dyads had higher play association scores than female-male or female-female dyads, consistent with partner predictions from the motor training hypothesis. These findings mirror patterns in baboons (Owens, 1975), Virunga mountain gorillas (Fletcher, 1994; Grebe et al., 2022) and Rhesus macaques (Kulik et al., 2015). Females did not play more with other females, suggesting that playing with the same sex is specific only to males, which could indicate that the benefits of play are different for males and females.

Social skills development

Gorillas live in male-led dominance hierarchies, driven by male-male competition (Robbins, 2010). Our findings that male-male dyads have higher play association scores than male-female or female-female dyads are consistent with the prediction that male Bwindi gorillas need competitive skills related to social dominance from play. It is yet to be explored if building skills related to dominance in play translate to dominance outside

of play in primates as it does in wolves (Cafazzo et al., 2018). Other primates which have both strong male and female hierarchies (Lutz et al., 2019; Palagi, 2018; Wright et al., 2018; Yanagi & Berman, 2017) showed preference for same sex dyads in play. Given female mountain gorillas have weak dominance hierarchies and very low rates of physical aggression, it may be less surprising that females did not have a same sex partner preference. This suggests that play interactions may not be necessary between females to build skills related to dominance.

Adult male-female dyads have the strongest affiliative relationships amongst adult gorillas (Harcourt, 1979; Watts, 1992), but male-female immature dyads did not have the highest play association scores, contrary to our social relationship hypothesis prediction about affiliation. In captive western lowland gorillas, males preferred male play partners, and female gorillas preferred male partners as well (Brown, 1988; Maestripieri & Ross, 2004). Female western lowland gorillas have weaker social relationships with one another than female mountain gorillas (Young & Robbins, 2022). Female mountain gorillas interact and groom one another more than western gorillas (Robbins et al., 2016), so they still need to develop affiliative social skills, and this could explain the differences observed between the two species. Furthermore, play behaviour may be a more suitable platform to develop competitive skills rather than skills relevant to adult affiliative social interactions, which are largely centred around close proximity and grooming. Grooming association scores among immature female gorillas may be a better indication of adult like social patterns.

Mountain gorilla groups typically have more adult females than males (Robbins, 2010). Therefore, adult males would be expected to maintain more social partnerships

than females. When comparing orangutan species, the more social Bornean orangutans had more play partners than Sumatran orangutans (Kunz et al., 2024). However, orangutans showed no age or sex difference in the number of play partners between these two species (Kunz et al., 2024). Bwindi gorilla males and females differed significantly in age-related variability in the number of monthly play partnerships. Males between 3-5 years played with a higher percentage of available partners than females of similar ages. This conformed to our prediction for a social development benefit of play, that males would play more, as they have to maintain more affiliative relationships as adults. However, males did not have a more even distribution of play amongst their partners than females. Furthermore, when the number of play partnership was assessed on a yearly basis, instead of monthly, this pattern was not as strong. We considered a play partner as any individual that the focal played with at a non-zero level. Therefore, over a long enough period individuals are likely reaching a maximum number of play partners that approximates the available number of partners, as even short one-off play bouts would result in counting that individual as a play partner. This could be tested by in future analysis by having a higher threshold for determining a play partner e.g. more than set percentage or duration of play per month.

Social bond formation

In some primate species, adults have strong social bonds that can last many years (Seyfarth & Cheney, 2012; Silk, Alberts, et al., 2006). Our study demonstrates that dyadic associations in play are stable from year to year, suggesting play relationships among immature individuals last for at least two years. Similar stable patterns in play

preferences have been reported in sable antelope (Thompson, 1996). Whilst play association scores and immature proximity association scores were correlated in the same network year, play association did not correlate with immature-immature proximity in subsequent year. Studies showing links between play and other affiliative activities have usually been conducted over the same time period (Cafazzo et al., 2018; Lutz et al., 2019) and not between sequential periods. Therefore, it is important to consider that that the non-linear ontogeny of play (Chapter 3) may not map on to the ontogeny of proximity associations. Specifically, play rates decline with age, whereas it is likely that rates of affiliative interactions, measured by proximity, may stay at a similar level between immaturity and adulthood and not show such a rapid decline as would be observed for play. Post-hoc analyses demonstrated that the reverse relationship, immature proximity association predicting play association in the subsequent year, was also not correlated (Beta = -0.0728, SE = 0.349, p-value = 0.835, see Appendix C Table S4.2, Figure S4.7). However, immature proximity scores were correlated from one year to the next (Beta = 0.709, SE = 0.209, p-value <0.001, Appendix C Table S4.3, Figure S4.8). This result supports the idea that although play associations and proximities are each stable over time, their ontogenies may not overlap. Furthermore, play could be having a different impact on dyadic social relationships beyond increased proximity. For instance, male prairie voles showed less aggression towards their play partners (Wilson, 1973).

Both male and female gorillas disperse from their natal groups (Robbins & Robbins, 2018). Therefore, social bonds built during immaturity are unlikely to be lifelong, which may impact the value of forming strong relationships as immatures. In particular, females emigrate at around 8 years of age (Robbins et al., 2023), so they may

not invest in play as a means to develop social relationships with peers. Females may develop relationships in ways other than play (e.g. grooming, proximity), or focus on building relationships with adults. Furthermore, our year-long metric may be too long to see correlations between affiliative activities. For instance, Japanese macaques showed links between play partners and proximity association (<3 meters) on a shorter time scale of 6 months later (Shimada & Sueur, 2018). However, forming social bonds during immaturity could still be beneficial, and adult female gorillas form associations that can last for 2 years or more with other females, despite the possibility of future dispersal to different groups (Young & Robbins, 2022).

Future Directions

The finding that immature Bwindi mountain gorillas exhibit differentiated social relationships in play poses many new questions for developmental and behavioural research. Furthermore, immatures appear to have differentiated social relationships with one another independently of their mothers. In chimpanzees, mothers may drive infant sociality, as suggested by the observation that mothers are more gregarious with male sons (Murray et al., 2014). This indicates how social structure can have a large impact on immature associations. In chimpanzee fission-fusion societies immature associations are more influenced by their mother's association patterns, whereas in gorilla social groups immature individuals are freer to associate independently from their mother. Gorilla infants spend their first years of life very close to their mother (Eckardt, 2010; Fletcher, 1994; Fossey, 1979), but as they gain independence and increase their play behaviour (Chapter 3), group living allows immature individuals access to enough individuals for infants to display more independent choice in social affiliation. The decreasing influence

of maternal behaviour on their offspring's movements as those offspring age may also demonstrate different levels of impact of mother-mother proximity on immature play association scores throughout ontogeny.

We observed that play relationships are stable from one year to the next, but it is unclear if these relationships last beyond this period. Adult female-female associations can last up to 3 years in Bwindi mountain gorillas (Young & Robbins, 2022). Therefore, immature play relationships could be lasting for longer periods since, given the dispersal of both males and female gorillas, the immature period could represent a long time period in which individuals co-reside.

Our analysis did not examine which specific dyads had association scores at the higher end of the population variation in scores (e.g. > 95% confidence interval from the mean), which is the common framework for defining social bonds (Silk et al., 2003, 2006). If top associates in play were the same from year to year, this would suggest that immature primates are developing stable long-lasting social bonds akin to adults. While play is an ideal behaviour to initially study social relationships in immatures, given that we find it is male-biased, determining whether other affiliative activities of immatures, such as grooming, show differentiated behavioural pattern according to sex would also be important to examine.

Our findings suggest males and females could be getting different benefits from play. Male gorilla patterns of play support the motor training hypothesis. This could be explored further in more detailed analysis of play types and what is happening during play bouts. Play is a structurally variable behaviour so it may be variable in its functions as well (Palagi, 2018). Given that there are many different types of social play (sparring,

rough-and-tumble, gently, chase), we may see changes in partner preference for different play types. For instance, having a partner of similar age may be more important in more vigorous play, which is riskier. Females western gorillas have higher rates of gentle play and a smaller age range of partners (Nowell, 2005) suggesting that their benefits from play may be more affiliative instead of learning dominance skills. Similarly, if male-male play is more focused on building motor skills, we would expect male-male play dyads to be structurally different, with more competitive behaviours compared to female-male or female-female dyads. Such studies would elucidate if play structure can be adjusted to perform multiple functions. Play partnerships give a greater indication of play function than play rates alone, especially potential social functions. Yet more direct measures of developmental benefits or trade-offs would be a productive step forward to examine functional benefits of play. Therefore, sex differences are important to consider when examining possible developmental changes or trade-offs related to time spent in play.

4.5 Conclusion

Our study demonstrates that immature Bwindi gorillas have differentiated social play relationships, independent of maternal affiliative relationships. Preferences for similar age partners and higher play association scores between male-male partners suggests that play may be a platform for developing motor skills or for learning about dominance. Refinement of motor skills may be more important to males given higher levels of physical competition among male gorillas. Furthermore, we provide evidence that immature Bwindi gorillas have differentiated dyadic relationships, in both play and spatial proximity, and that play relationships are stable for at least two years. This

demonstrates that stable preferential social relationships are being developed before adulthood and is consistent with the hypothesis that play may help in the formation of social bonds. Social play behaviour provides a context in which we can study the development of social bond in primates during immaturity.

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Chapter 5: Understanding the costs and benefits of social play in Bwindi mountain gorillas (*Gorilla beringei beringei*).

Keywords: social play, *Gorilla beringei beringei*, trade-offs, photogrammetry

Abstract

Play is highly conserved amongst mammals. It is the most common social activity of immature gorillas, and thus play should have a high benefit-to-cost ratio. Examining how play is prioritised amongst other life-history and behavioural activities can elucidate time and energetic demands, and benefits of this behaviour. Higher rates of play have been linked to increased fitness, driven by both decreased mortality and increased reproductive success, but showing linkages between behaviours of immature individuals and long-term fitness is difficult in long-living mammals. However, we can examine developmental trajectories to understand if there are short-term benefits to playing which align with proposed motor training and social skills development. Here, we pursue two strategies to test the costs and benefits of play. Using 11 years of behavioural data from 30 immature Bwindi mountain gorillas, *Gorilla beringei beringei* (0.5 – 8 years), we examined the trade-offs between time spent in different activities, body size and play. We also analysed the relationship between individual play rates and age of attainment of developmental milestones. We expected that an increase in time spent playing would reduce resting time, result in smaller body sizes-for-age (particularly for females who were expected to be more energetically constrained), and earlier attainment of developmental milestones. We found that increased time spent playing correlated with increased time spent suckling and locomoting. Increased time spent playing also correlated with decreased time spent feeding and resting. Females, but not males, showed a positive relationship between play rates and body size at low levels of fruit

consumption (<7%) and a negative relationship at high levels of fruit consumption (>7%). A greater play rate was correlated with earlier attainment of developmental milestones. This relationship was stronger in females than males and only specific to milestones related to agonistic behaviours and proximity to the mother. Periods of high fruit consumption may provide lower amounts of protein for growth, creating a larger trade-off between growth and play. However, more specific measures of both energy balance and growth would be needed to confirm this. Our results demonstrate that individuals that play more have faster behavioural developmental trajectories. In sum, we show that there are immediate costs of social play, which trade-off against growth and time spent in other activities, but these trade-offs and benefits of play appear to be different for females and males.

5.1 Introduction

Play behaviour is universally recognisable, yet the costs and benefits are poorly understood (Burghardt, 2005). Play has been highly conserved through evolution and is present in most Orders of mammals (Fagen, 1981), with its ubiquity implying that it has a high benefit-to-cost ratio. Play can be a vigorous and risky behaviour suggested to have high energetic costs (Miller & Byers, 1991). Since play behaviour is most prominent during immaturity, young individuals carry the costs of play. However, the benefits of play may be immediate or long-lasting and could provide ultimate fitness advantages such as reduced mortality (Théoret-Gosselin et al., 2015) and increased reproductive success (Dallaire & Mason, 2017; Heintz et al., 2017; Holmes et al., 2024). Linking immediate costs to long-term benefits, such as reproductive success, is impossible without long-term data, and very difficult in long-lived animals. However, using other

markers such as behavioural milestones can help us understand developmental mechanisms and test benefits proposed by evolutionary hypotheses of play, which may influence reproductive success in adulthood. Life-history milestones such as age at maturity, onset of reproduction, and dispersal, may be linked to attaining the physical skills of adults (Bray et al., 2017), socialisation of immatures (Fletcher, 1994), and achieving a minimum body size (Charnov & Berrigan, 1993). However, energetic and time constraints may lead to trade-offs among activities such as play and growth, to develop behavioural competences.

There has been little investigation of play's costs and short-term benefits (Caro, 1995) and how these trade-off with daily activities and life-history functions, such as growth (Berghänel et al., 2015). Young mammals can spend between 5-10% of their time in social play (Fagen, 1981), and Orders of mammals with bigger brains, such as primates, play more (Iwaniuk et al., 2001). Time spent in play is at the cost of time spent in other activities, given a finite daily time budget, but may confer advantages. For example, cheetah play bouts were observed to coincide with mother resting sessions (Caro, 1995) which suggests that time spent in play is more beneficial for immature individuals than resting. Re-allocating time spent resting to time playing allows immatures to maintain the same energy intake, through time spent in feeding. However, for immature individuals that are not yet weaned, feeding time can be offset by suckling. Similarly, immature individuals need to maintain a rate of travelling to keep up with their mothers or the group, though this may be less important in primates where immatures are carried for a significant amount of time (Nakamichi & Yamada, 2009).

Immature individuals devote both energy and time to play. Social play can be a vigorous activity, with estimates that the metabolic rate during play can be 1.5 - 2.5 times greater than resting metabolic rate (Martin, 1984) so this could potentially affect growth. Play in Assamese macaques was shown to account for 50% of the variation in growth, in which more time spent in play correlated with slower growth rates (Berghänel et al., 2015). Additionally, it has been estimated that pronghorn fawns that did not invest energy in play would have a 7% higher body mass (Miller & Byers, 1991). Energy being prioritised for play at the cost of growth contradicts the surplus energy theory (Spencer, 1872), which proposes that play only occurs during times of excess energy, and highlights how play may be prioritised over other functions so may be a key activity for development.

Social play shows the biggest sex differences of all types of play (Burghardt, 2005). Therefore, the costs of play are unlikely to be the same between the sexes. The energetic trade-offs between play and growth are prioritised differently for males and females in Assamese macaques (Berghänel et al., 2015), as males played more and grew less than females. Moreover, sex differences were more pronounced during periods of high food availability in which males increased play and females increased growth (Berghänel et al., 2015). Food availability in the Assamese macaques was a proxy for total energy intake (Heesen et al., 2013), and mirrors correlations found in other studies between increased play and other energy proxies, such as habitat quality, food availability, food supplementation and season (Asensio et al., 2022; Baldwin & Baldwin, 1974, 1976; Berghänel et al., 2015; Brownlee, 1954; Lee & Moss, 2014; Loy, 1970;

Moebius et al., 2019; Sommer & Mendoza-Granados, 1995; Wright et al., 2015, Chapter 3).

The energetic trade-offs of play suggest its prioritisation over other activities and implies ultimate fitness benefits. Play rarely stops completely, even during lower energy periods (Baldwin & Baldwin, 1974, 1976), and mechanisms such as mother-infant play may continue to provide opportunities to immature individuals (Sabbi et al., 2024). However, studying ultimate fitness benefits can be difficult because this requires data on the full lifespans of individuals, and both reproduction and survival are dependent on an array of different skills (and a variety of ecological factors).

In lieu of data to study ultimate benefits of play we can concentrate on skill acquisition occurring during immaturity when play is at its highest rate. Improving skills in the short-term and reaching developmental milestones earlier (Bründl et al., 2020; Heintz et al., 2017) may lead to future improved fitness, if it leads to earlier attainment of reproductive maturity or enhanced skills needed for reproductive success. The 'motor training hypothesis' (Bekoff & Byers, 1981) (see Chapter 2, Table 2.2) posits that play is a platform to learn and hone motor skills that can be beneficial later in life. In support of motor training, the timing of peak play coincides with attaining adult-like numbers of cerebellar synapses and muscle fibre types, in cats, mice and rats (Byers & Walker, 1995). Furthermore, correlations between increased play and increased dendritic pruning (a sign of maturation and selection of the strongest neural pathways) in rats demonstrates a possible mechanism for how play behaviour may be improving motor performance (Ham & Pellis, 2023; Stark, 2021). Invasive studies of neural and muscular development cannot be performed on wild primates, but we can monitor immature development by

studying the appearance of specific behaviours. Motor milestones, such as dorsal riding in chimpanzees (Heintz et al., 2017) and leaping and climbing in macaques (Berghänel et al., 2015), were attained sooner for individuals with higher play rates (but see deer; Carter et al., 2019). Similarly, in humans increased physical activity correlated with improved motor proficiency (Wrotniak et al., 2006).

The 'social relationship hypothesis' (Baldwin & Baldwin, 1974) (see Chapter 2, Table 2.2) theorises that play assists in improving social integration and building a repertoire of social skills, which can be beneficial for long-term fitness (Feldblum et al., 2021; Ostner & Schülke, 2018; Silk, 2007). Social play is the only type of play that involves interaction between individuals, and thus is the only type of play that could have social benefits. Earlier attainment of social development milestones may lead to improved social skills as adults, and thus improve fitness. Play has also been shown to promote emotional regulation and social competence in children (Hamamcı & Dagal, 2021; Saad et al., 2022; Tastepe, 2021) and the links between play and social competence have been utilised in therapy for children with autism (O'Keeffe & McNally, 2021). Rats reared with a partner that played more, also demonstrated improved social skills (better able to differentiate between play and fighting) (Ham et al., 2024). Non-human primates have complex social structures and hierarchies which involve social communication and interaction, so learning better social skills and gaining those skills earlier should be advantageous for maturing individuals.

Among our closest living relatives (Ruvolo, 1997), gorillas have a slow life history and long developmental periods. Mountain gorillas, the subject of this study, exist in only two wild populations: Bwindi Impenetrable National Park, Uganda (extending into the

Sarambwe Forest in Democratic Republic of Congo [DRC]) and the Virunga Massif (in DRC, Rwanda and Uganda). Bwindi mountain gorillas spend over 50% of their time feeding, with females spending more time feeding and less time resting than males (Ostrofsky & Robbins, 2020). Fruit, which is more temporally and spatially variable than herbaceous vegetation, makes up on average 15% (ranging from 0-70%) of their feeding time each month (Ostrofsky & Robbins, 2020). During fruit feeding, energy intake is higher, and travel distances are longer (Nkurunungi et al., 2004; Wright et al., 2015). As gorillas are the most sexually dimorphic great ape, trade-offs between play and other developmental trajectories may be different for males and females (Leigh & Shea, 1995). Mountain gorilla females have their first offspring at around 10 years old, yet female Virunga mountain gorillas only reach 98% of their maximum body length at 11.7 years (Galbany et al., 2017; Robbins et al., 2023). This suggests that females may be more energetically constrained than males as they trade-off growth and reproduction. Conversely, males grow for longer periods, reaching 98% of their adult size by age 13.1 years (Galbany et al., 2017).

Gorillas live in socially cohesive groups and thus, immatures need to develop social skills to integrate into the group as they mature (Fletcher, 1994; Stewart, 2001). Gorilla groups have male-led dominance hierarchies in which male-male competition is stronger than female-female competition (Robbins, 2010). Therefore, skills related to physical competition may be more important for male gorillas. Conversely, male-female dyads have the strongest affiliative relationships (Harcourt, 1979; Watts, 1992, 2001), thus the development of affiliative skills may be equally important for both sexes.

Here we pursue three main objectives to analyse the costs and benefits of play in immature Bwindi mountain gorillas. 1) We examine trade-offs in time invested in play versus other activities (being carried, being nursed, feeding, fruit feeding, locomotion and resting) and predict that increased time spent in play will correlate with decreased time spent resting, and that all other activities will remain unchanged given their necessity to stay at a consistent level. 2) We test the energetic trade-off between play and body size and predict that individuals that play more will have smaller than average body size for their age. We expect this relationship to be stronger for females than males and to interact with fruit consumption, with periods of higher fruit consumption giving a weaker relationship as more energy will be available for both play and growth. 3) We test the developmental benefits of play and predict that higher play rates than average correlate with the earlier attainment of specific developmental milestones. We expect this relationship will be stronger for males than females for agonistic milestones, as agonistic behaviours are more important to male adults, but other milestone types (affiliative, carrying, mating, physical and proximity) will show no sex differences as they are equally important to both sexes

5.2 Methods

Study population and subjects

Data were collected on six habituated mountain gorilla groups in Bwindi Impenetrable National Park, Uganda from 2012 to 2023 (see Appendix D Table S5.1 for observation timelines per group). Data were collected by several researchers (see Acknowledgements), who were trained according to the same protocol and supervised on a routine basis to ensure uniformity. Specific data for this study were extracted from a

long-term behavioural database. Gorillas between 0.5 and 8 years and of known age (<+/- 15 days) were included in the study, totalling 30 individuals.

Data collection

Gorillas were observed for approximately 4 hours per day, according to guidelines set by Uganda Wildlife Authority. Focal sampling (Altmann, 1974) occurred in 5-60 minute intervals, with the goal of 5 hours of focal time per month. Focal periods were ended when individuals were out of view for more than 60 seconds. Focal subjects were chosen based on who was in view with an emphasis of securing equal focal time on every individual each month, and the maximum of 60 minutes ensured multiple individuals were focalled each day. Ad-libitum data were also recorded on all individuals in view, when possible, with particular emphasis on rare behaviours (displacements, drinking, aggression, mating, carrying). Scan sampling occurred concurrently with focal sampling at fixed intervals (pre-May 2015: every 5 mins, post-May 2015: every 10 mins). During each scan, observers recorded the activity of every individual in view (being carried, being nursed, feeding, fruit feeding, playing, locomotion and resting), their height off the ground, and their proximity to the focal individuals when focal sampling was occurring.

Social play was defined in the data collection protocol as: when two individuals wrestle, tickle, chase, hit, etc. in a non-aggressive manner, it is often accompanied by a 'play chuckle' vocalization by immatures (Heintz et al., 2017; Winkler & Perry, 2022). Durations of play were recorded at intervals of 5 seconds by digital watch (or 1 second by a tablet timer after 2016, when electronic data collection commenced), for any bouts of a minimum of 5 seconds.

Data Extraction

Activity budgets

Monthly activity budgets were calculated from the scan sampling for 30 individuals, from 201,529 scans. We calculated the total number of scans for all possible activities recorded (being carried = offspring being transported by the mother; being nursed = offspring suckling; feeding = consuming non-fruit plant parts; fruit feeding = consuming fruit; playing = social play with another individual, resting = sitting or lying down; independent locomotion = movement / travelling from one spot to the next). We also calculated the total number of scans that an individual was present conducting an activity, as an offset in the model to produce a proportion of each activity (see Figure 5.1). The focal individual's age for each month was calculated on the 15th day of each month.

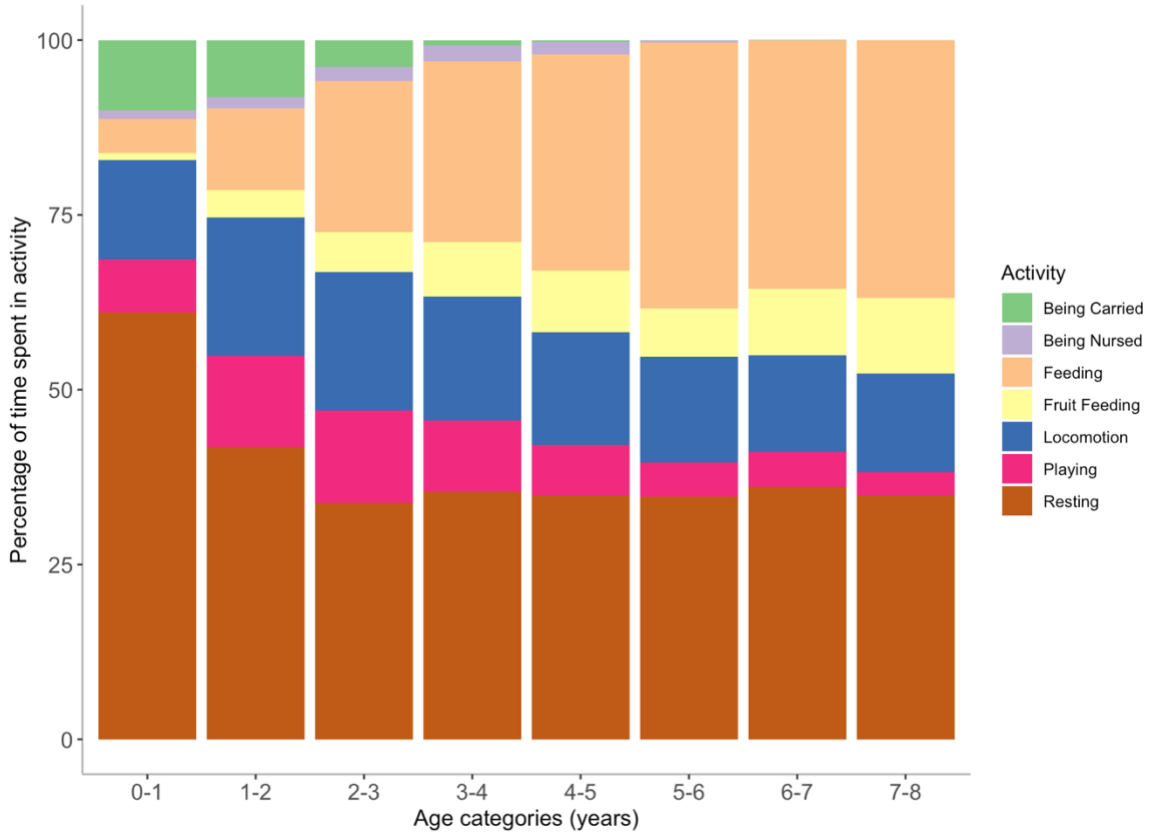

Figure 5.1: Activity budgets for immature Bwindi gorillas from 0-8 years in 1 year age categories. N.B the first age bin includes only individuals greater than 0.5 years.

Play rates

Play rates were calculated as a monthly duration of social play in seconds that occurred during focal time. We calculated an observed play rate for each individual for the 6-month period prior to each photogrammetry data point or developmental milestone, to account for a long enough period of time before the photogrammetry in which an individuals' play behaviour may impact growth or development. The play rate for each individual was calculated by totalling the number of seconds in play during focal time, divided by the number of seconds of focal time within that 6-month period. We calculated a population play rate based on a Generalized Linear Mixed Model with a negative binomial distribution of observed play rates of all individuals (see Chapter 3).

This population rate model was used to extract a predicted play rate for an individual of specific age and sex, at the centre of the 6-month period before each photogrammetry data point or age of attainment of a milestone. This allowed us to compare the observed play rate for each individual to the average play rate, controlling for age and sex.

Developmental milestones

Amongst humans developmental milestones are defined as "a set of behaviours, skills or abilities that are demonstrated by specified ages during infancy and early childhood in typical development" (Beighley & Matson, 2013; Bründl et al., 2020). A total of 31 developmental milestones were extracted from the behavioural data: 22 milestones from the focal and *ad lib* behavioural sampling (Table 5.1: Dataset = F/A) and 9 milestones from scan sampling (Table 5.1: Dataset = S). For each milestone, individuals were only included in the analysis if they met the following criteria: 1) they were born after the behaviour was introduced to the ethogram, 2) their age of attainment of the milestone did not occur within 4 months of the resumption of data collection after the pandemic (see Appendix D Table S5.1), to reduce uncertainty that the milestone may have occurred during the pause in data collection because of the pandemic, and 3) their age of first appearance in the behavioural data was less than 0.8 times the youngest age that any individual was observed to hit the milestone (calculated independently for each milestone). This reduced uncertainty that individuals reached milestones before they were incorporated into the data collection, and a proportion of minimum age (instead of a set time period e.g. 3 months) accounts for their being greater variation in age of attainment for milestones attained at later average ages (Figure 5.2).

All milestones were categorised according to six categories: Affiliative, Agonistic, Carry, Mating, Physical, and Proximity (see Table 5.1). For milestones in the affiliative, agonistic and physical categories, the age of attainment of the milestone was defined as the first time when a behaviour was observed twice within a 90-day period. Then the age of attaining the milestone was set as the age of the individual on the date the second observation of the behaviour. This measure was used to better ascertain when a specific behaviour or activity becomes a common occurrence in an individual's repertoire and reduces bias by not including very early one-off occurrences of behaviour. For milestones which included behaviours that were rare (mating, copulation play behaviour, denoted by * in Table 5.1), the age of attainment of the milestone was defined as the first occurrence of the behaviour. Milestones in the carry category, were based on the proportion of total carry behaviours (50%, 80%, 90% and 95%), by the mother of the individual, recorded in a month that were in the dorsal position. Months with less than 10 total recorded carries were excluded, to ensure that a small number of carries did not have large effects on monthly proportions. Milestones in the proximity category (those which measure proportion of time spent at different distances from the mother) were based on the proportion of total monthly scans in which mother and infant were within a minimum proximity category (physical contact, 2 m, 5 m, 10 m). Months in which there were less than 20 scans with both the mother and infant present were excluded. Thirty-one developmental milestones were described for 33 individuals (see Table 5.1, Figure 5.2). To analyse the relationship between developmental milestones and play rate, we only included individuals who were first focalled at least 6 months before their age of attaining

a milestone (calculated independently for each milestone), to evaluate their play rates in the previous 6 months.

Table 5.1: Milestones extracted from behavioural data. * = milestones that were calculated as first occurrence; other behavioural milestones were calculated at the age at which the behaviour was first observed twice within 90 days or as a proportion of total behaviours (carry and proximity categories). F/A = data using focal and adlib sampling, S = from scan sampling.

Category	**Milestone**	**Dataset**	**Definition**	**Number of individuals**
Affiliative	Copulation play actor*	F/A	Actor of non-reproductive sexual activity, including mounting and thrusting	19
Affiliative	Copulation play recipient*	F/A	Recipient of non-reproductive sexual activity	12
Affiliative	Grooming mother	F/A	Offspring runs their hands/fingers through the hairs of their mother	18
Affiliative	Social grooming	F/A	Individuals runs their hands/fingers through the hairs of another individual that is not the mother of the acting individual	19
Affiliative	Solicit play	F/A	Individual encourages another to play by chest beating, hitting, thumping the ground, running towards, or holding eye contact with the other individual	12
Agonistic	Agonistic mild	F/A	Mildly agonistic behaviour towards another group member (pig grunt)	13
Agonistic	Agonistic moderate	F/A	Moderate agonistic behaviour towards another group member (strut run, lunge)	8
Agonistic	Avoids	F/A	Submissive behaviour in the form of moving away/aside from another individual as they approach	20

Category	Milestone	Dataset	Definition	Number of individuals
Agonistic	Give supplant	F/A	The focal individual approaches another individual and causes them to move away and then the focal individual occupies the same spot where the other individual was	9
Agonistic	Receive supplant	F/A	The focal individual is approached by another individual which causes them to move away and then the approaching individual occupies the same spot where the focal individual previously was	18
Carry	Dorsal 50%	F/A	> 50% of monthly infant carries in which the offspring is carried on the back of the mother	3
Carry	Dorsal 80%	F/A	> 80% of monthly infant carries in which the offspring is carried on the back of the mother	5
Carry	Dorsal 90%	F/A	> 90% of monthly infant carries in which the offspring is carried on the back of the mother	8
Carry	Dorsal 95%	F/A	> 95% of monthly infant carries in which the offspring is carried on the back of the mother	11
Mating	Mating*	F/A	Male copulating (mounting and thrusting) with a mature female (>8 years)	4
Physical	Build nest	F/A	Individual bends branches and vegetation and places it underneath them to make a ‘bed’	6
Physical	Chest beat	F/A	Individuals is hitting upper body/ torso with both hands alternating between them	5
Physical	Climb tree using mouth	F/A	‘Biting’ into a tree while climbing	15

Category	Milestone	Dataset	Definition	Number of individuals
Physical	Drum	F/A	Individuals hitting another individual with palms of both hands, alternating between them	20
Physical	Drum object	F/A	Individual hitting an object with palms of both hands, alternating between them	11
Physical	Pull vegetation	F/A	An individual grabs a branch or plants and then runs bringing the branch along with them	17
Physical	Solitary play	F/A	Individual swings from branches, slaps vegetation, rolls around, pats objects, chest beat, with no other individual around or does not express interest to engage with another	2
Proximity	No contact with mother 50%	S	Individual not in physical contact with mother for more than 50% of scans in a month	6
Proximity	No contact with mother 70%	S	Individual not in physical contact with mother for more than 70% of monthly scans	6
Proximity	2 m distance from mother 50%	S	Individual more than 2 metres away from mother in 50% of monthly scans	15
Proximity	2 m distance from mother 70%	S	Individual more than 2 metres away from mother in 70% of monthly scans	15
Proximity	5 m distance from mother 10%	S	Individual more than 5 metres away from mother in 10% of monthly scans	15
Proximity	5 m distance from mother 20%	S	Individual more than 5 metres away from mother in 20% of monthly scans	14
Proximity	5 m distance from mother 50%	S	Individual more than 5 metres away from mother in 50% of monthly scans	12
Proximity	10 m distance from mother 5%	S	Individual more than 10 metres away from mother in 5% of monthly scans	15
Proximity	10 m distance from mother 10%	S	Individual more than 10 metres away from mother in 10% of monthly scans	16

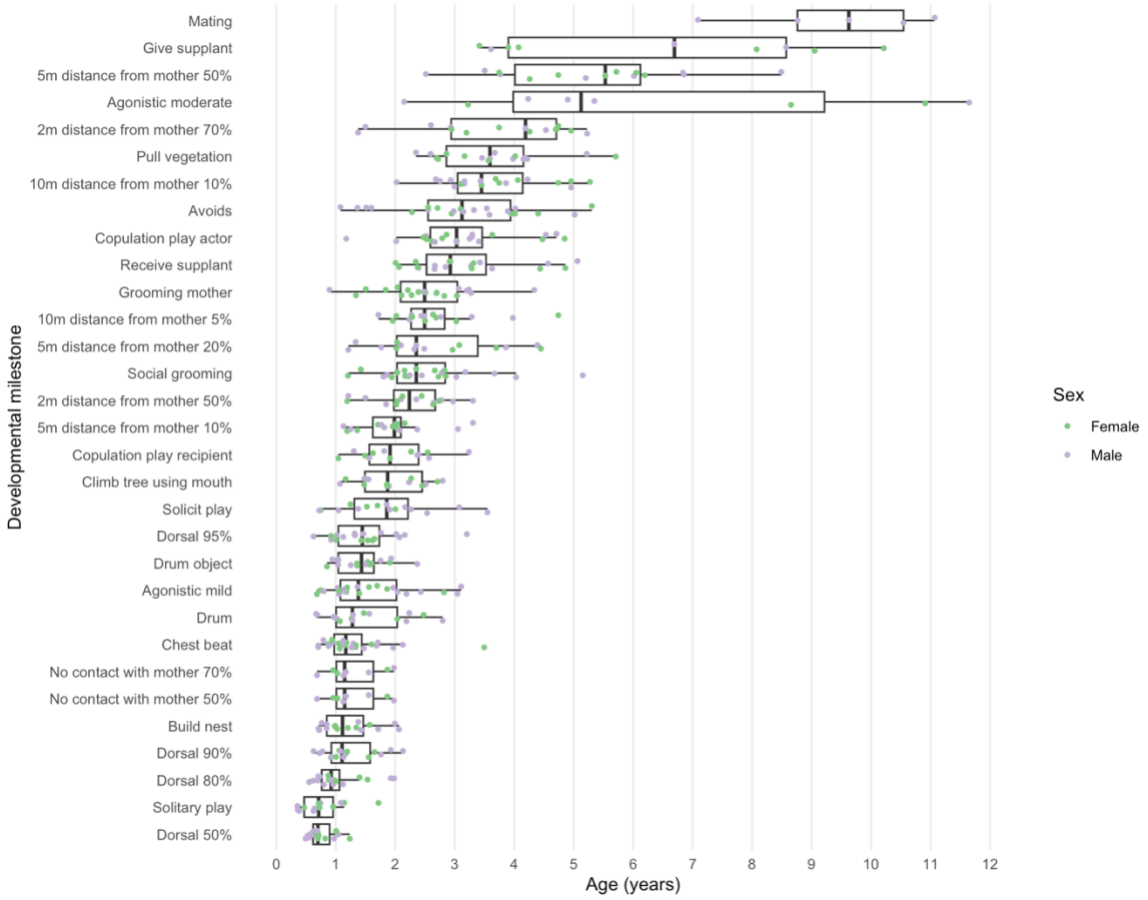

Figure 5.2: Age of attainment of all developmental milestones for all individuals.

Photogrammetry data collection

Body size measurements were collected using non-invasive parallel laser photogrammetry (Bergeron, 2007; Durban & Parsons, 2006). This method involves a digital camera mounted on a device which projects parallel lasers, set at a predetermined distance apart onto the back or side of the animal. The laser spots projected onto the animal provide a scale for measurements from the photograph. This method has been validated as precise compared to manually-collected measurements (Galbany et al., 2016) and has been implemented on wild mountain gorillas in previous studies (Galbany et al.,

2017; Wright et al., 2019, 2020). We collected 1804 photos and then measured two linear body dimensions, back breadth and body length as described in (Galbany et al., 2016, 2017; Wright et al., 2019). Both these dimensions were proxies for overall size, and are a composite measure of skeletal growth, muscular growth as well as skin and hair. Therefore, they may deviate from growth trajectories of body mass or skeletal length.

Body size measurements

Body dimension data points were created from a mean of 4 photos per sampling period (range: 3-16), collected for 85 individuals, totalling 437 data points (back = 217, body = 220). One sampling period consisted of at least 3 independent photos of the same individual and body part, which could be averaged to get one body size measurement for that sampling period. Photos for each sampling period were collected over a mean of 20 days (range: 0-68). Individuals ranged from 0.5 to 42.7 years of age and the photogrammetry dataset was approximately equal between females (216) and males (221). Only immature individuals with a birthdate known to within 15 days were included, because individuals were sampled every 4 months. All photos were measured by JR using an automated measurement program in a Python interface, which is an expansion of automated methods previously published (Richardson & Levy et al., 2022). The program automatically identified the laser spots and measured the distance between them. Laser spots are a pre-set distance (2 or 4 cm), thus a cm per pixel value for each photo is calculated. Back photos were taken in posterior view and the back breadth measurement was the maximum distance across the shoulders; the landmark points are identified as the bottom of the rounding contours of the upper arm on each shoulder

(Galbany et al., 2017). Body photos were taken in lateral view and the body length measurement was from the landmark of the anterior contour of the shoulder, to the landmark of the tangent of the rump of the animal (Galbany et al., 2017). In the measurement program, coloured spots were placed on the landmark of interest. The program measured the pixel-length between the two user-placed landmarks and automatically calculated an actual body size (in cm) based on the cm per pixel ratio calculated from the laser spots. For each data point a mean size was calculated and recorded along with a mean age based on age that each photo was taken. Measurements of different photos of the same individual and body part within each sampling period had low coefficient of variation (mean = 0.0203, range = 0.001 – 0.059).

Statistical analyses

We ran all statistical analyses in R (R Core Team, 2020). Mixed models were implemented using the glmmTMB package (Brooks et al., 2017) and model diagnostics were checked using the DHARMa package (Hartig, 2020). For models with multiple quantitative fixed effects, Variance Inflation Factors (VIFs) were calculated, using the performance package (Lüdecke et al., 2021), to check that there was no co-linearity amongst variables. Finally, we did full-null model comparison with an ANOVA test comparing the full models to a null-model with only the random effects. The full model is determined to fit the observed data better if it has a lower AIC.

Analysis 1 - Activity budgets

To assess how time spent in different activities changed with time spent in play, a mixed model was run with negative binomial distribution. The response variable was the

monthly number of play scans and fixed effects were added for the monthly number of scans of being carried, being nursed, feeding, fruit feeding, locomotion and resting. There was an offset term added for the total number of scans for each month to account for differences in the amount of observation. Random effect terms were added for age and individual ID. We ran models for each sex separately (female model and male model). VIFs showed that there were no issues of collinearity in the models (female model all VIFs <1.6; male model all VIFs <1.5). Visual checks of quantile-quantile plots and statistical tests conformed to the assumptions of uniformity (female model KS test D = 0.0583, p-value = 0.0669, see Appendix D: Figure S5.1; male model KS test D = 0.0484, p-value = 0.128, see Appendix D, Figure S5.2). The models did not show overdispersion (female model dispersion = 1.175, p-value = 0.496; male model dispersion = 0.921, p-value = 0.992) and the frequency of outliers was lower than expected (female model p-value = 0.92; male model p-value = 0.244). Visual inspections of predicted residuals versus fitted residuals showed no heteroscedasticity.

Analysis 2 - Play and body size

To assess if there was a trade-off between play rate and body size, we ran models to compare residual body size and residual play rate during the 6-month period prior to the body size measurement. We calculated separate growth curves for males and females given that gorilla sexes show different growth trajectories (Galbany et al., 2017). We calculated growth curves for back breadth and body length independently, using a non-linear mixed effect model with Gaussian error distribution and identity link using the package “brms” (Bürkner, 2017). We expected individuals to reach a maximum size and

then stop growing. Therefore, we used an exponential growth curve function (concave down, increasing) based on the equation: $y = a(b^{age}) + c$. Where a < 0 and a + c was the size at age = 0; b was between 0 and 1, and represented the growth factor; and c > 0 and was the asymptote, or point at which maximum size was reached (Bortz et al., 1990). To help with model convergence and to achieve the desired parameter space (a < 0, 0 < b < 1, c < 0), we transformed the variables as a' = -exp (a), b' = exp (b) / (1 + exp(b)) and c' = exp (c). Additionally, we included random intercepts for individual ID and group ID (group at the time the photo was taken). The model predictions were generated using Markov chain Monte Carlo methods, using four chains with 8,000 iterations and the argument thin was set to 10. To assess model convergence, we verified Rhat values were close to 1, and assessed that all chains mixed well, by visually assessing their overlap. We used the growth curves to calculate a predicted size for each age and sex corresponding to the age and sex for any individual below 8 years old for which we had a photogrammetry point (see Appendix D Figure S5.3: back breadth growth curves & Figure S5.4: body length growth curves).

We calculated a residual size value per individual by subtracting the predicted size at each age from the actual size (mean of photogrammetry measurements). We calculated a residual play rate by subtracting the predicted play rate, from the population play model Figure 3.1 (Chapter 3), 3 months before the age of attainment of the milestone (e.g. at the middle of the 6-month period of observed data), from the observed play rate for the 6-month period before the age of attainment of the milestone. We calculated proportion of fruit feeding for each individual for the 6-month period before

each photogrammetry data point as the number of scans feeding on fruit divided by total number of scans in which an individual was present (Chapter 3).

We ran mixed models with Gaussian error distribution to assess the relationships between residual play rate and residual size. The response variable was the residual size, and the fixed effect was an interaction term between residual play and proportion of fruit feeding. Random effects were added for individual ID, age and body part. We ran models for each sex separately (female model and male model). All models included back and body length data points. VIFs showed that there were no issues of collinearity in the models (female model VIFs <1.6; male model VIFs <1.5). Visual checks of quantile-quantile plots and statistical tests conformed to the assumptions of uniformity (female model KS test D = 0.0905, p-value = 0.497, see Appendix D Figure S5.5; male model KS test D = 0.0693, p-value = 0.752, see Appendix D Figure S5.6). The models did not show overdispersion (female model dispersion = 1.187, p-value = 0.496; male model dispersion = 1.098, p-value = 0.672) and the frequency of outliers was lower than expected (female model p-value = 0.489; male model p-value = 0.176). Visual inspections of predicted residuals versus fitted residuals showed no heteroscedasticity.

Analysis 3 - Play and milestones

For each of the milestones, we calculated a residual milestone age by subtracting the age that an individual reached a particular milestone from the mean age calculated from the ages that all individuals met each particular milestone. We calculated a residual play rate by subtracting the predicted play rate, from the population play model Figure 3.1 (Chapter 3), 3 months before the age of attainment of the milestone (e.g. at the middle

of the 6-month period of observed data), from the observed play rate for the 6-month period before the age of attainment of the milestone.

We ran a mixed model with Gaussian error distribution to assess the relationships between residual play rate and residual milestone age. The response variable was the residual milestone age, and the fixed effect was an interaction between residual play and sex. Random effects were added for individual ID and milestone. We ran a mixed model including data from all milestones (all-milestone model). Then we ran models only including milestones from each of the categories affiliative, agonistic, physical and proximity separately (excluding carrying and mating categories as the sample sizes were too small for model convergence). Visual checks of quantile-quantile plots conformed to the assumptions of uniformity (see Appendix D: Figure S5.7 – all milestones model, Figure S5.8 – physical model, Figure S5.9 – proximity model, Figure S5.10 – affiliative model & Figure S5.11 – agonistic model). The models did not show overdispersion (all milestone model: dispersion = 0.957, p-value = 0.728; physical model dispersion = 0.875, p-value = 0.672; proximity model dispersion = 1.014, p-value = 0.896; affiliative model dispersion = 1.010, p-value = 0.856; agonistic model dispersion = 1.023, p-value = 0.856) and the frequency of outliers was lower than expected (all milestone model: p-value = 0.218; physical model p-value = 1; proximity model p-value = 0.598; affiliative model p-value = 0.134; agonistic model p-value = 0.103). Visual inspections of predicted residuals versus fitted residuals showed no heteroscedasticity.

Ethical note

All data for this study were collected non-invasively, including body size measurements which used non-invasive parallel photogrammetry. Permission was

granted for the data collection from Uganda Wildlife Authority and Uganda National Council of Science and Technology, and research adhered to their protocols and guidelines.

5.3 Results

Analysis 1 – Activity budgets

The full-null comparison for both models indicated that the full model was significantly better at explaining the variation in the data than the null model (female model: $\chi 2$ =155.82, df = 6, p-value <0.001; male model: $\chi 2$ =175.17, df = 6, p-value <0.001).

In both female and male models there was no significant relationship between proportion of play scans and proportion of scans being carried (female model: Beta = -0.005, SE = 0.004, p-value = 0.289; male model: Beta = -0.00415, SE = 0.00400, p-value = 0.299, Table 5.2). In both models, an increased number of play scans was significantly correlated with a decreased number of scans for feeding (female model: Beta = -0.010, SE = 0.001, p-value <0.001; male model: Beta = -0.00446, SE = 0.00104, p-value <0.001, Table 5.2), and resting (female model: Beta = -0.004, SE = 0.001, p-value = 0.0017; male model: Beta = -0.00581, SE = 0.000905, p-value <0.001, Table 5.2), and an increased number of scans for being nursed (female model: Beta =0.044, SE = 0.008, p-value <0.001; male model: Beta = 0.0645, SE = 0.00568, p-value <0.001, Table 5.2) and locomotion (female model: Beta = 0.014, SE = 0.002, p-value <0.001; male model: Beta = 0.00566, SE = 0.00171, p-value <0.001, Table 5.2). An increased number of play scans was significantly correlated with a decreased number of scans for fruit feeding in the

male model (Beta = -0.00281, SE = 0.00132, p-value 0.033, Table 5.2), but not in the female model (Beta =-0.002, SE = 0.002, p-value = 0.312, Table 5.2).

Table 5.2: Model results of female and male activity budget models, significant p-values at the 0.05 level are in bold.

Term	**Model**	**Estimate**	**SE / SD**	**P**
Age	Female	Random intercept	0.2738	
	Male	Random intercept	0.0000826	
ID	Female	Random intercept	0.5875	
	Male	Random intercept	0.4303	
Intercept	Female	-2.923	0.222	**<0.001**
	Male	-1.984	0.133	**<0.001**
Being Carried	Female	-0.00507	0.00478	0.289
	Male	-0.00415	0.00400	0.299
Being Nursed	Female	0.0443	0.00846	**<0.001**
	Male	0.0645	0.00568	**<0.001**
Feeding	Female	-0.00962	0.00132	**<0.001**
	Male	-0.00446	0.00104	**<0.001**
Fruit Feeding	Female	-0.00182	0.00185	0.322
	Male	-0.00281	0.00132	**0.033**
Locomotion	Female	0.0139	0.00222	**<0.001**
	Male	0.00566	0.00171	**<0.001**
Resting	Female	-0.00411	0.00131	**0.0017**
	Male	-0.00581	0.000905	**<0.001**

Analysis 2 – Play and body size

The full-null comparison indicated that the full model was significantly better at explaining the variation in the data than the null model for the female model ($\chi 2$ = 14.67, df = 3, p-value = 0.00212) but not the male model ($\chi 2$ =2.034, df = 3, p-value = 0.565). Therefore, male model results are not shown.

For the female model, the interaction term between residual play and proportion of fruit feeding was significant (Beta = -0.0523, SE = 0.0133, p-value <0.001, Table 5.3, Figure 5.3). At high fruit consumption values (>7%), residual play and residual body size

were negatively correlated. At low fruit consumption values (<7%), residual play and residual size were positively correlated.

Table 5.3: Female model results of play and body size, significant p-values at the 0.05 level are in bold, * = an interaction term.

Term	**Model**	**Estimate**	**SE / SD**	**p**
ID	Female	Random intercept	2.57	
Age	Female	Random intercept	1.342	
Body part	Female	Random intercept	0.149	
Intercept	Female	0.613	0.816	0.453
Residual play	Female	0.364	0.104	**<0.001**
Proportion fruit feeding	Female	0.0274	0.0474	0.563
Residual play* Proportion fruit feeding	Female	-0.0523	0.0133	**<0.001**

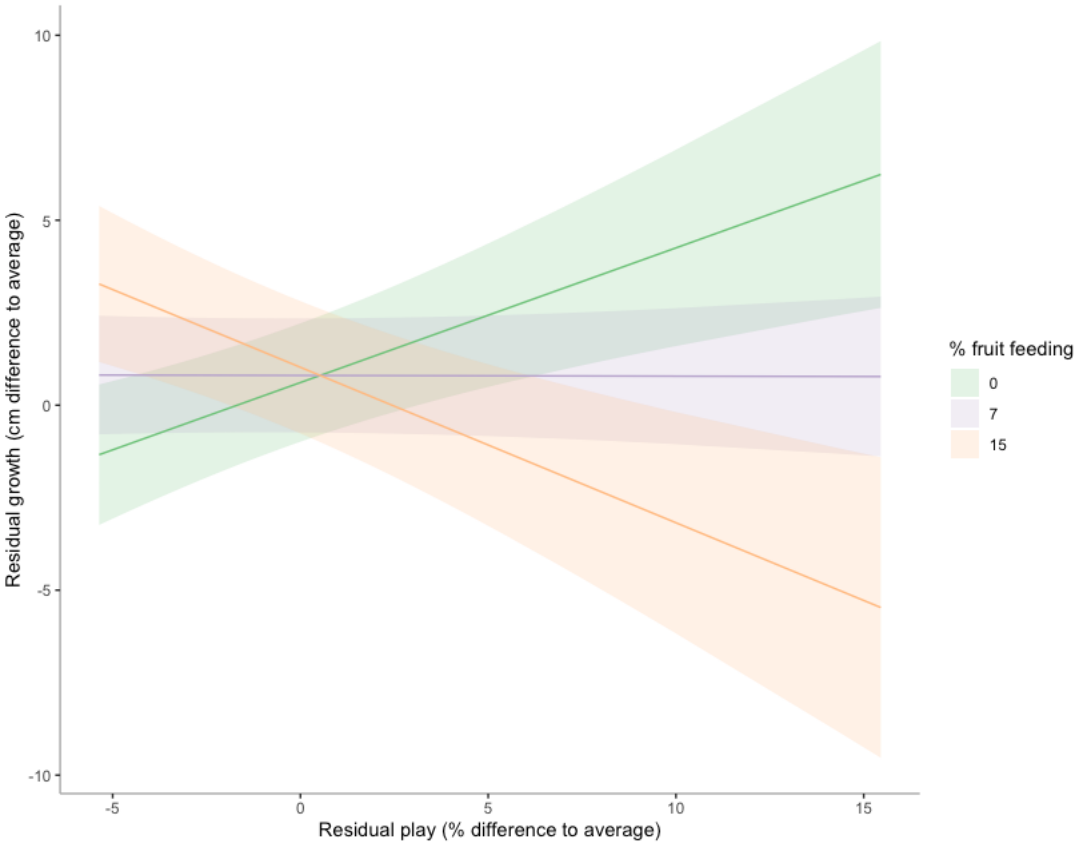

Figure 5.3: Female play and body size model predictions for the interaction term of residual play with proportion fruit feeding. Predicted at low (0%), mid (7%), and high (15%) levels of fruit feeding.

Analysis 3 – Play and milestones

The full-null comparison indicated that the full model was significantly better at explaining the variation in the data than the null model for the all-milestone model ($\chi 2$ =50.791, df = 3, p-value < 0.001), the proximity model ($\chi 2$ =20.387, df = 3, p-value < 0.001) and the agonistic model ($\chi 2$ = 24.153, df = 3, p-value < 0.001). The full model was not significantly better at explaining the variation in the data for than the null model for the physical model ($\chi 2$ = 3.738, df = 3, p-value = 0.291) or the affiliative model ($\chi 2$ = 5.972, df = 3, p-value = 0.113).

Residual play had a significant negative correlation with the interaction for residual milestone age and sex for the all-milestone model (Beta = 0.0829, SE = 0.0226, p-value <0.001, Table 5.4, Figure 5.4), and the agonistic model (Beta = 0.128, SE = 2.013, p-value = 0.0441, Table 5.4, Figure 5.5). Indicating that individuals that played at a higher rate than average had an earlier milestones attainment age than average, with females showing stronger negative correlation than males. The interaction between residual play and sex did not correlate in the proximity model (Beta = -0.0617, SE = 0.0374, p-value = 0.098, see Appendix D Table S5.2). However, when running the model without the interaction term (see Appendix D Figure S5.12 for diagnostics), there was a significant negative correlation between residual play and residual milestone age for proximity milestones (Beta = -0.084, SE = 0.0190, p-value <0.001, Table 5.4, Figure 5.6). Indicating that males and females that had higher play rates than average had earlier age of attainment of proximity milestones.

Table 5.4: Model results of play and milestone models, significant p-values at the 0.05 level are in bold, * = an interaction term. [+]Values for the proximity model are from the output of the model without the interaction.

Term	**Model**	**Estimate**	**SE / SD**	**p**
ID	All-milestone	Random intercept	0.486	
	Agonistic	Random intercept	0.0000112	
	Proximity[+]	Random intercept	0.671	
Milestone	All-milestone	Random intercept	0.0000217	
	Agonistic	Random intercept	0.0000913	
	Proximity[+]	Random intercept	0.0000117	
Intercept	All-milestone	0.233	0.161	0.147
	Agonistic	0.0833	0.269	0.757
	Proximity[+]	0.246	0.228	0.281
Residual play	All-milestone	-0.112	0.0156	**<0.001**
	Agonistic	-0.187	0.0359	**<0.001**
	Proximity[+]	-0.084	0.0190	**<0.001**
Sex	All-milestone	0.162	0.073	0.942
	Agonistic	0.240	0.490	0.624
	Proximity[+]	0.109	0.308	0.723
Residual play*sex	All-milestone	0.0829	0.0226	**<0.001**
	Agonistic	0.128	2.013	**0.0441**

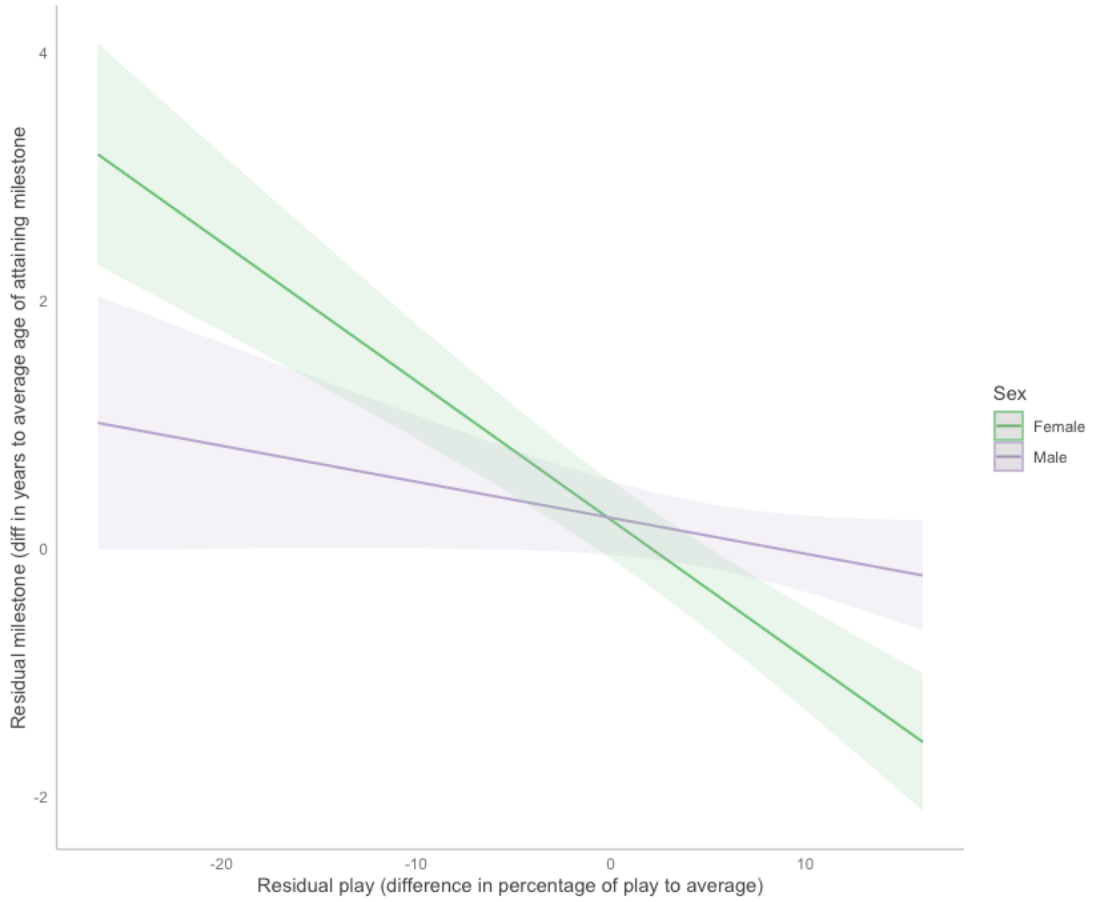

Figure 5.4: All-milestone model predictions for the interaction term of residual play and sex with residual milestone age.

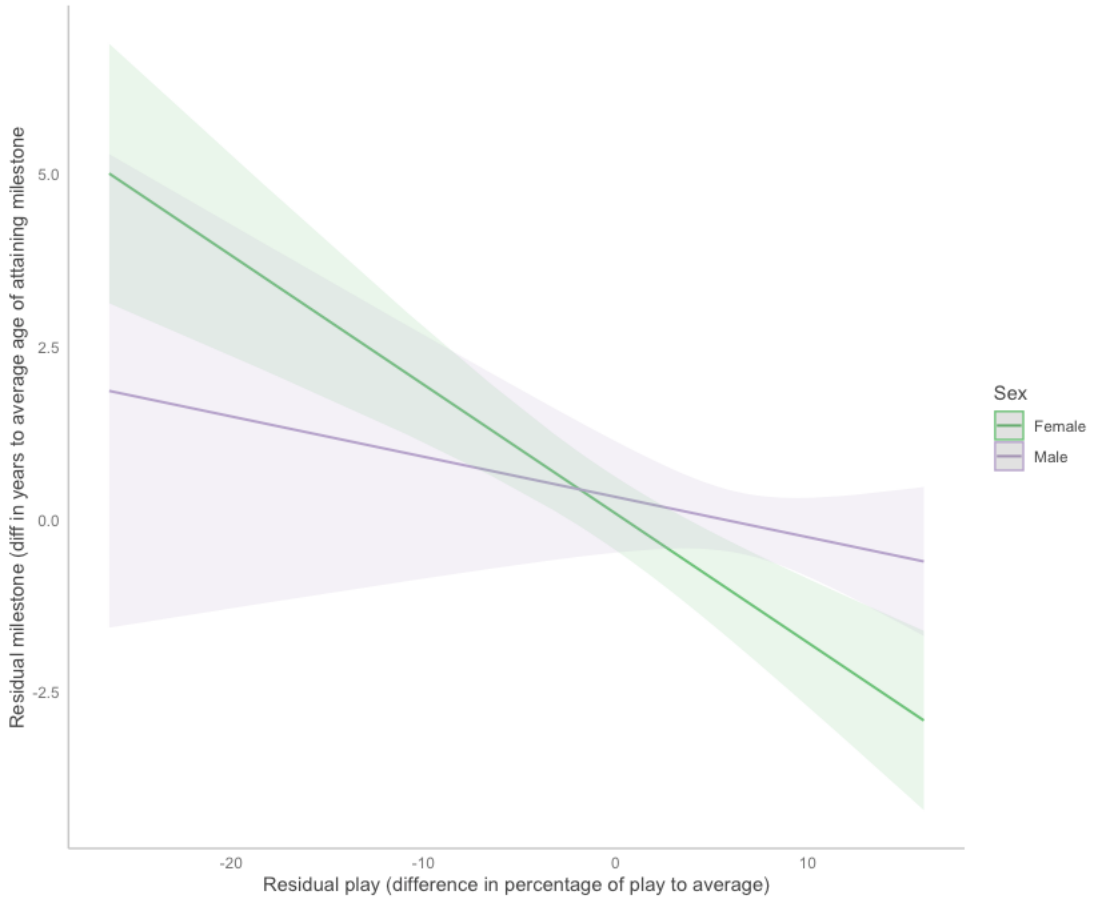

Figure 5.5: Agonistic milestone model predictions for the interaction term of residual play and sex with residual milestone age.

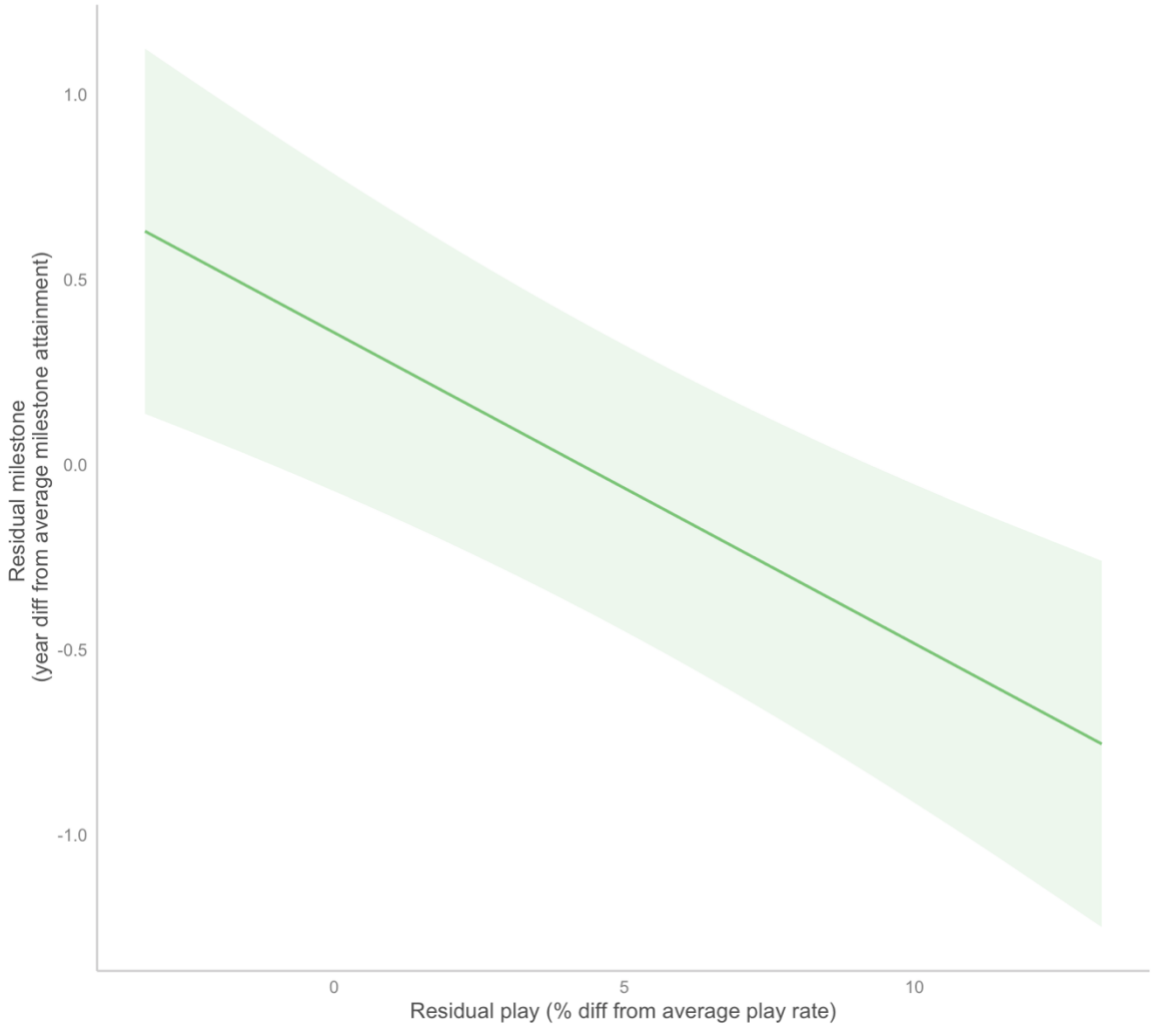

Figure 5.6: Proximity milestone model predictions for residual play with residual milestone age.

5.4 Discussion

We found evidence for both costs and benefits of play in immature Bwindi mountain gorillas. Time spent in play was traded off with time spent in other activities. Specifically, increased time spent in play correlated with decreased time spent being carried, feeding, and resting alongside increased time spent being nursed and in independent locomotion. The decrease in time spent resting conformed to our predictions, but we did not expect a reduction in time spent feeding. Additionally, there was a sex

difference, with males showing a decrease in proportion of time spent fruit feeding when play increased and females showed no effect of time spent in play on time spent fruit feeding. Our results indicated a relationship between residual play and residual size depending on fruit feeding for females, but not for males. During periods of low fruit feeding (<7% of activity), above average play rates for females correlated with above average body size. However, during periods of higher fruit feeding (>7% of activity), above average play rates correlated with below average body size. Our results show a complex interaction between play, fruit feeding and growth, but overall conform to the prediction that females are likely more energetically constrained than males. Finally, we found a relationship between increased play and earlier attainment of developmental milestones, consistent with our predictions. However, this relationship was stronger for females than males, contrary to our sex difference expectations. The relationship between play and attainment of milestones was only relevant for agonistic and proximity milestones, the latter of which showed no sex differences.

Trading off time spent in play and other activities

Gorillas live in cohesive social groups (Robbins, 2010) in which individuals must manage their time among activities. Whilst feeding would be expected to be the most important activity, our study showed that there can be a trade-off between feeding and resting versus social activities for immature individuals. For adult individuals, group resting sessions are often the time for affiliative social activities such as grooming (Fossey, 1979). During these periods, immature individuals may be spending more time playing as they are in close proximity with other play partners, reducing the amount of time they spend resting. Similar to other studies examining the effects of weaning on play

in gorillas, we found nursing and play to be positively correlated (Eckardt, 2010; Fletcher, 1994, Chapter 3). This supports the idea that milk provides additional energy that can be spent on play. Conversely, feeding declined when play time increased, which opposes predictions about energetic constraints of play. However, if play was increasing during times of nursing, it is possible that lower feeding proportions are offset by nursing. Females and males had the same time trade-off in all activities except for fruit feeding. Despite the change in fruit feeding not being significant for females, the effect sizes for males and females were of a similar magnitude, indicating little biological difference.

Whilst we account for age in the model with a random effect, due to the linear nature of our predictions, there could be ontogenetic patterns that we did not account for in our analysis. Specifically, nursing is strongly affected by age (Robbins & Robbins, 2021). Immature great apes only reach adult-like feeding patterns around weaning (Bray et al., 2017; Schuppli et al., 2016) and play shows a quadratic relationship with age (for males only Chapter 3). So, it would be useful to examine using a quadratic term in the model in the future. These patterns could explain the positive relationship between play and nursing and negative relationship between play and feeding. Furthermore, our study employed scan sampling to look at activity budgets. Whilst this is commonplace (Masi et al., 2015; Mendonça et al., 2017; Ostrofsky & Robbins, 2020), the proportional nature of activity budgets means that there will always be an opposite and relative change in at least one other activity in response. However, when looking at multiple activities we can still make conclusions about which activities are being prioritised over others.

Trading off energy spent in play and body size

As gorillas are the most sexually dimorphic ape (Leigh & Shea, 1995), we expected energetic trade-offs between growth and other activities to exhibit differently between males and females. We found that the interaction between play rates and fruit feeding was significantly related to body size in females, but not males. During periods of lower fruit consumption (<7% of activity) females had a positive relationship between residual play and residual body size, indicating that individuals with higher-than-average play rates for their age were larger than average body size. However, during periods of higher fruit consumption (>7% of activity), female individuals with higher-than-average play rates were smaller than average in body size. Adult Bwindi mountain gorillas spend on average 15% (range = 0-70%) of their feeding time feeding on fruit, and about 40-50% of their daily activity feeding (Ostrofsky & Robbins, 2020). This equates to an average of 6-7.5% (range = 0-35%) of their total activity time spent fruit feeding per month, which is a similar percentage of fruit feeding at which female change from a positive to a negative correlation between play and body size. Therefore, during periods of higher fruit consumption, growth and play appear to be trading off more than during periods of lower fruit consumption.

Whilst we know that energy intake is higher when feeding on fruit than non-fruit (Wright et al., 2015), travelling distance is also higher during fruiting periods (Ganas & Robbins, 2005). Therefore, higher fruit feeding, if travel costs are substantial, could explain there being a greater trade-off during high fruit consumption periods. Furthermore, whilst energy intake is higher, fruits are lower in protein compared to herbaceous vegetation, which is the dominant part of mountain gorilla diet (Rothman et

al., 2011). Protein intake may be more important for growth, with higher protein intake rates suggested to drive higher growth rates (Janson & van Schaik, 1993; Leigh, 1994; but see Borries et al., 2022). Therefore, trade-offs between growth and play may only be relevant when gorillas are travelling further and prioritizing non-protein energy, such as fruit. During other periods of the year gorillas have a high protein diet, close to the maximum recommended for humans (Rothman et al., 2011). Moreover, the biological impact of this trade-off appears most relevant at very high or very low play rates, indicating gorillas are, for the most part, not energy or protein limited.

We found no significant correlation for males, which could indicate that females are more energetically constrained than males as they are subject to more trade-offs between energetically expensive activities, such as play and growth. Adult females spend more time feeding (and feeding on fruit) than adult males (Ostrofsky & Robbins, 2020), and female gorillas mature earlier than males (Robbins et al., 2019, 2023). Furthermore, reproductive skew in male gorillas is high (Bradley et al., 2005; Vigilant et al., 2015) with females having less variation in number of offspring and bearing larger energetic costs of reproduction than males. Immature females in this study were not investing energy in reproduction, but they may still prioritise growing faster than males because reaching maturity and full body size sooner could have larger reproductive benefits for females than males. Previous mountain gorilla studies have not found a relationship between female body size and reproductive success (Wright et al., 2020), but this does not exclude the possibility that reaching adult size sooner, even when your adult size is smaller, is linked to improved reproductive fitness (Charnov & Berrigan, 1993). Additionally, we did not measure growth in this study, but instead we compared body

size to average size-for-age to determine whether individual growth was faster or slower than expected for the population. However, this approach may not have adequately considered interindividual differences in body size growth trajectories over immaturity, which may also be influenced by genetic difference between individuals.

Benefits of play – developmental milestones

Our results indicated that individuals who spend more time in play for their age also reach developmental milestones sooner than average, consistent with other primate studies suggesting higher play rates are related to faster development (Berghänel et al., 2015; Heintz et al., 2017). Furthermore, we found differences between males and females. When analysing all 31 developmental milestones together we found that females have a stronger negative correlation between amount of play and age at attainment of milestones. Similar to previous studies, our methodology is based on correlational relationships between play rate and milestone age; it is not possible to determine the direction of causality in these relationships. Despite this, our results suggest that play and other developmental metrics are linked. This could be driven by a third factor that has not been accounted for in this analysis, such as body size.

To delineate motor training and social skill development hypotheses, we tested whether specific types of milestones were more related to play and whether there were sex differences in their development. In contrast to the motor training hypothesis (Bekoff & Byers, 1981), we did not observe any relationships between play and age of attainment of physical milestones. However, individuals that played more did attain proximity milestones earlier, with no sex differences apparent. It is likely that our results

demonstrate that individuals that move away from their mothers earlier are also those that play at higher rates, regardless of sex.

The social relationships hypothesis (Baldwin & Baldwin, 1974) posits that individuals learn social skills from play. Social behaviour involves both agonistic, competitive and affiliative behaviours. Here, attainment of social affiliative milestones was not correlated with amount of play. However, we did observe that agonistic milestones were attained earlier for individuals that played more. Contrary to our predictions, females had a stronger correlation between play rate and agonistic milestones. Females reach maturity and disperse sooner than males (Robbins et al., 2019, 2023). Therefore, they may need to develop agonistic and competitive skills related to social dominance sooner to be ready to manage a new social hierarchy, when they disperse from their natal group.

Future directions

Our results provide a step forward in understanding the costs and benefits of play in immature Bwindi mountain gorillas and pose many potential new avenues for study. We compared body size at specific ages to model predictions, as a proxy of energy invested in growth. However, individual growth curves could be calculated if studies had sufficient body size measurements of the same individuals across several years. This would be a more accurate measure of growth rates and provide a more exact measure of the energetic trade-off between play and growth.

Measuring energy balance directly would allow better understanding of when immature individuals have greater excess energy and how it is allocated. Gorillas are

unlikely to be highly constrained by food availability, because there is an abundance of terrestrial vegetation in the Bwindi mountain gorilla habitat (Ganas et al., 2009). Despite, energy intake being higher (Wright et al., 2015) when feeding on fruit, individuals also travel further. Therefore, they could be at an energetic loss, during high fruiting periods (Ganas & Robbins, 2005; Nkurunungi et al., 2004). Urinary C-peptide studies are an avenue that allows for the non-invasive estimation of energy balance, and could help ascertain if and when immature gorillas are more energetically constrained (Emery Thompson et al., 2009; Grueter et al., 2014).

We used developmental milestones to understand potential benefits of play in the framework of the motor training and social relationship hypothesis. However, most gorilla behaviours involve both motor and social skills. As such, measuring motor development may be more successfully quantified with kinematic data (Yaguramaki & Kimura, 2002; Young, 2009; Zeininger et al., 2017), which involves movements that are more independent from social behaviours.

Our results suggested that individuals playing more are on a faster developmental trajectory. This could be related to a possible third factor that was not measured in this study, such as maternal behaviour, maternal size or energy intake. It is also possible that individuals that play more and reach milestones sooner may also be larger for their age as they are on a faster developmental track, which would confound our results that examined body size. Other studies have linked body size with reaching specific life history milestones such as weaning (Altmann & Alberts, 2005; Lee et al., 1991), suggesting that attainment of developmental milestones may be more dependent on size than age (Harvey & Clutton-Brock, 1985).

5.5 Conclusion

Our results show costs and benefits of social play in immature Bwindi mountain gorillas. Our finding that time and energy spent in play trade-off with other activities and growth support the hypothesis that social play has ultimate fitness benefits. We found sex differences in the costs of play, suggesting that females are more energetically constrained, even before they reach reproduction. Finally, play appears to be correlated to other measures of development, and females have a stronger relationship between more play and earlier attainment of developmental milestones. Our study highlights the need for more studies of the trade-offs amongst play and other energetically costly activities and suggests future avenues to explore energetic costs and developmental trajectories more thoroughly.

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Chapter 6: Dissertation conclusion

This dissertation established a new methodological framework to study social play, in an attempt to distinguish between non-mutually exclusive hypotheses for its proposed costs and benefits, focusing on immature mountain gorillas located in Bwindi Impenetrable National Park, Uganda. The behaviour of wild primate populations is driven by socio-ecological variation, which needs to be considered in attempts to understand variation within immature development. Mountain gorillas, as one of our closest living relatives (Ruvolo, 1997), provide a suitable model to test this new framework. They display large levels of sexual dimorphism and sex-specific behavioural and reproductive strategies as adults (Leigh & Shea, 1995; Robbins, 2010), and thus we expect them to show differences between female and male immatures in social play. Previous studies have examined play behaviour in wild Virunga mountain gorillas (Eckardt, 2010; Fletcher, 1994; Grebe et al., 2022) and western lowland gorillas (Brown, 1988; Maestripieri & Ross, 2004; Nowell, 2005). This study is the first to provide data on social play in Bwindi mountain gorillas, with a focus on examining correlates of social play, play partnership patterns, and proposed costs and benefits of play, to link variation in play behaviour to competing functional hypotheses.

In Chapter 2, we reviewed prior studies of social play in mammals that tested four prominent, yet non-mutually exclusive, hypotheses: the motor training hypothesis (Bekoff & Byers, 1981), social relationships hypothesis (analysing the two component parts; social skills development and social bond formation)(Baldwin & Baldwin, 1974; Meaney et al., 1985; Poirier & Smith, 1974) and the energetic constraints hypothesis (based on the surplus energy theory)(Spencer, 1872). To address challenges of previous

work, we suggested a new framework for studying social play behaviour that attempts to more conclusively distinguish between these competing hypotheses, by incorporating multiple components: 1) understanding biological, ecological and social correlates of play variation, 2) linking structural variation in play (e.g. play partnerships) to specific behavioural and reproductive strategies, 3) measuring the costs of play in a trade-off framework with other activities and 4) measuring long-term fitness benefits and shorter-term developmental benefits of play.

In Chapter 3, we first described ontogenetic variation in rates of social play in Bwindi mountain gorillas, and its biological, ecological and social correlates. Using mixed effects models, the results indicated that females and males have very different ontogenies of play. Males play more than females, specifically between the ages of 2-6 years. This was consistent with our prediction that males would need to play more to develop motor and social skills, because they exhibit more physical competition and sustain more social affiliative relationships than females. Social play rates were higher in unweaned individuals, and during periods of higher fruit consumption, suggesting play rates increased during periods of reduced energetic constraints. However, we did not observe lower play rates for offspring of primiparous mothers. Social play rate had a positive and quadratic correlation with the number of other immature individuals (0-8 years) in the group. These results provide support for all three non-mutually exclusive hypotheses tested (motor training, social relationship and energetic constraints) and highlight how different biological, ecological and social measures can provide support for the different hypotheses. Whilst this was not sufficient to demonstrate conclusive support for any one hypothesis, this analysis provided an initial understanding of play ontogenies as a

foundation for subsequent investigations of play partnerships and proposed costs and benefits.

In Chapter 4, we examined structural variability in play, specifically play partnership patterns, to distinguish between the two components of the social relationship hypothesis (social skills development and social bond formation). We found that males had a higher number of play partners on a monthly but not yearly scale, and that play was not distributed evenly amongst partners for males or females. We then looked at the strength of dyadic play associations between different partners, in reference to mother-proximity, age, sex, infant proximity and previous years' associations. Results indicated that immature play associations were independent of their mother's proximity, suggesting play relationships are driven by the immature individuals themselves. Furthermore, dyads of similar age had higher play association scores, in line with predictions of the motor training hypothesis that play is less risky with same aged and sized peers. We found that male-male dyads had the highest play association scores, and there was no significant difference between female-male dyads and female-female dyads association scores. Male preference for same sex play partners supports that play is beneficial for the development of motor or social dominance skills, as males exhibit higher levels of social competition and more clearly differentiated dominance hierarchies than females, mediated through physical competition. Finally, we found that dyadic play relationships were correlated with proximity relationships, suggesting immature gorillas play with individuals they are spatially close too. Also, both play association scores and proximity association scores were stable from one year to the next, suggesting that immature individuals were exhibiting differentiated social relationships with available partners. However, strength of

play partnerships did not predict future strength of proximity relationships, likely because play partnership strengths decline over time as individuals play less whilst proximity relationships increase. The results supported motor training, social skill development (specifically for competitive behaviours) and social bond formation hypotheses. The sex differences in play partnership preference suggested that females and males are likely getting different benefits from play; specifically, competitive and motor skills patterns appeared more relevant for males, predicted by their male-male partnerships. Future studies should seek to understand how other affiliative interactions such as grooming may be avenues for immatures to form social bonds, and whether other non-play activities may be more important for affiliative social skills and/or social development in females.

In Chapter 5, we investigated proposed costs and benefits of social play. Results showed that play may be prioritised over other important daily activities. Increases in time spent playing are correlated with decreases in time spent feeding and resting and increases in time spent nursing and travelling. This was contrary to our predictions that only time spent resting would decrease, and implies that, during some periods, time spent in play could be more beneficial than time spent feeding. Secondly, play had a complex relationship with body size in females, but not in males. In females, higher play rates correlated with smaller than body size for age (predicted by growth curves) during times of increased fruit consumption (>7% of activity), and larger body size for age during decreased fruit consumption (<7% of activity). The relationship between body size and play for females, but not males, supported our prediction that females were more likely to be energetically constrained than males because they mature at younger ages and start reproducing before they reach full body size. Therefore, they may need to invest more

energy in growth to reach a larger proportion of their adult body size sooner. Additionally, the changing relationships between body size and play, dependent on fruit consumption patterns, may be in response to higher energy expenditure of travelling or lower protein availability for growth during periods of higher fruit consumption (Leigh, 1994; but see Borries et al., 2022). Future studies that take a more direct approach to measure energy balance (e.g., urinary C-peptides) (Emery Thompson et al., 2009; Grueter et al., 2014) or incorporate longitudinal observations of growth may be better prepared to uncover trade-offs between growth and play (Berghänel et al., 2015).

Lastly, in Chapter 5, we found support for the prediction that increased play rates would correlate with earlier attainment of developmental milestones. This relationship was stronger for females than for males. Additionally, when we analysed different types of developmental metrics separately (affiliative, agonistic, physical, proximity) the correlation between play and developmental measures was only significant for agonistic and proximity milestones. For agonistic milestones females had a stronger relationship between increased play and earlier age of attainment than males, but for proximity milestones there were no sex differences. Our analyses cannot suggest a direction of causation in our results and thus we interpreted our findings to mean that play rate ontogenies and other developmental metrics are likely linked, with individuals who play more than average for their age also reaching other developmental milestones at earlier ages. With long-term data it will be possible to test correlations between play and long-term fitness measures, such as mortality (Lee & Moss, 2014) and reproduction (Holmes et al., 2024), and investigate if lifetime fitness relates to metrics of faster development.

This hypothesis driven framework made progress towards delineating patterns of play that relate to different evolutionary hypotheses. Our use of a wild population with long-term data allowed a more accurate understanding of how socio-ecological variation in a primate's habitat can affect social play behaviour. We highlighted the need to go beyond play rate ontogenies and investigate more specific structural elements and trade-offs within play. Specifically, we found that analysis of play partnerships may facilitate distinguishing among predictions of the two components of the social relationship hypothesis: 1) social skill development and 2) social bond formation. We were less successful at differentiating between motor and social hypothesis of play. Predictions of these two hypotheses in gorillas were often overlapping given that their predictions were based on differences in dominance skills which rely on both motor and social development in gorillas. Using species in which dominance skills might be more strictly physical or social would be beneficial. Furthermore, along with more accurate measures of benefits and costs, the next steps would include focusing more on the connection between structural elements of play and the costs and benefits. For example, do specific partnerships in play lead to specific developmental benefits? Ground squirrels which play with more partners were observed to have greater motor skill improvement (Nunes et al., 2004). Additionally, by investigating other structural elements of play, such as play-type, asymmetry in play, behaviours within play, and initiation of play, and then connecting these with specific partnership and developmental benefits, would further improve our ability to translate what happens during play to both immediate and long-term fitness advantages.

Overall, we accomplished two major goals. 1) We created a new framework that can be used in different species to study rates, structure, costs and benefits of play and provided a better understanding of which patterns of variation support which hypothesis. 2) We tested this framework on Bwindi mountain gorillas, presenting data on social play for this population for the first time. Our study provided support for all four hypotheses tested in this dissertation (motor training, social skills development, social bond formation and energetic constraints). Therefore, we conclude that play can be a platform for the development of both motor and social skills (both skill development and bond formation), and it is under energetic constraints in Bwindi mountain gorillas. We found large sex differences in play rates, structures, costs and benefits in Bwindi mountain gorillas, confirming our prediction that social play behaviour among immatures may serve as a platform for the behavioural and morphological dimorphism present in adult gorillas. Whilst our framework can be used for other species, it should not be assumed that social play provides the same benefits and costs as we demonstrate in gorillas. It is necessary to contextualise predictions of this framework based on the behavioural and socio-ecological variation characteristics of each study population. As we study social play more comprehensively in a larger range of animal species, we may come closer to understanding the functional benefits of play and why it has been conserved across the tree of life.

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Appendices

Appendix A

Table S2.1: Classical theories of play, not discussed in this manuscript, as they do not present testable frameworks.

Hypothesis	Conceptualisation	Major Predictions
Surplus Energy Theory	Spencer 1872	Play occurs when individuals have excess energy.
Diversion Theory	Carr 1902	Play occurs to pass the time.
Autotelic Theory	Mitchell 1990	Play occurs for enjoyment.
Semblance Theory	Schillar 1967	Play occurs to mimic adult behaviours.
Reinforcement Theory	Baldwin & Baldwin 1977	Play occurs as a continuation of a behaviour enjoyed as immatures.
Recapitulation Theory	Hall 1904	Play occurs as an evolutionary remnant of an instinctive behaviour.

Table S2.2: Studies exploring correlates between social play and behavioural and developmental parameters.

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
African bush elephant	Lee & Moss	2014	Proboscidea	*Loxodonta africana*	W	% obs time in play	Age of death	Positive correlation
African bush elephant	Lee & Moss	2014	Proboscidea	*Loxodonta africana*	W	% obs time in play	Reproductive age	None
American fur seal	Harcourt	1991	Carnivora	*Arctocephalus australis*	W	% obs time in play	Risk of predation	Positive correlation
American mink	Dallaire & Mason	2017	Carnivora	*Neovison vison*	C	% obs time in rough and tumble play	Duration of copulation	Positive correlation
American mink	Dallaire & Mason	2018	Carnivora	*Neovison vison*	C	% obs time in rough and tumble play (males)	Copulation with females	None
American mink	Dallaire & Mason	2019	Carnivora	*Neovison vison*	C	% obs time in rough and tumble play (female)	Latency to start copulation	Positive correlation
Assamese macaque	Berghänel et al.	2015	Primates	*Macaca assamensis*	W	% obs time in play	Growth	Negative correlation
Assamese macaque	Berghänel et al.	2016	Primates	*Macaca assamensis*	W	% obs time in play * % rough and tumble play	Motor skills acquisition	Positive correlation
Belding's ground squirrel	Nunes et al.	2004	Rodentia	*Spermophilus beldingi*	W	% obs time in play	Motor skill improvement	Positive correlation
Belding's ground squirrel	Nunes et al.	2004	Rodentia	*Spermophilus beldingi*	W	Number of play partners	Motor skill improvement	Positive correlation
Bonobo	Palagi & Paoli	2007	Primates	*Pan paniscus*	C	Grooming partners	Play partner preference	Positive correlation

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Bottlenose dolphin	Holmes	2024	Cetacean	*Tursiops aduncus*	W	% obs time in actor role of play	Number of paternities	
Bottlenose dolphin	Matrai	2021	Cetacean	*Tursiops aduncus*	C	Cooperative play	Cooperative opening of enrichment task	Positive correlation
Brown bear	Fagen & Fagen	2009	Carnivora	*Ursus arctos*	W	% obs time in play	Survival to independence	Positive correlation
Brown capuchin	Lutz et al.	2019	Primates	*Cebus apella*	C	Affiliation partners	Play partner preference	Positive correlation
Brown rat	Byers & Walker	1995	Rodentia	*Rattus norvegicus domestica*	C	Time of peak play	Time of cerebellar synaptogenesis and muscle fibre type differentiation	Positive correlation
Cheetah	Caro	1995	Carnivora	*Acinonyx jubatus*	W	Predation behaviour within play	Predation behaviour outside play	Positive correlation
Chimpanzee	Heintz et al.	2017	Primates	*Pan troglodytes schweinfurthii*	W	% obs time in play	Riding dorsally milestone	Negative correlation
Chimpanzee	Heintz et al.	2017	Primates	*Pan troglodytes schweinfurthii*	W	% obs time in play	Independent travelling milestone	Negative correlation
Chimpanzee	Heintz et al.	2017	Primates	*Pan troglodytes schweinfurthii*	W	% obs time in play	Spatial independence	Negative correlation
Chimpanzee	Heintz et al.	2017	Primates	*Pan troglodytes schweinfurthii*	W	% obs time in play	Grooming non-kin	Negative correlation

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Chimpanzee	Heintz et al.	2017	Primates	*Pan troglodytes schweinfurthii*	W	% obs time in play	First mating attempt (males)	Negative correlation
Diademed sifaka	Lutz et al.	2019	Primates	*Propithecus diadema*	W	Affiliation partners	Play partner preference	Positive correlation
Domestic cat	Byers & Walker	1995	Carnivora	*Felis catus*	D	Time of peak play	Time of cerebellar synaptogenesis and muscle fibre type differentiation	Positive correlation
Domestic cat	Martin	1984	Carnivora	*Felis catus*	D	% obs time in play	% energy expenditure	Positive correlation
Gelada	Mancini et al.	2009	Primates	*Theropithecus gelada*	C	Grooming partners	% obs time in play	Positive correlation
Hamadryas baboon	Lutz et al.	2019	Primates	*Papio hamadryas*	C	Affiliation partners	Play partner preference	Positive correlation
Human	Saad et al.	2022	Primates	*Homo sapiens*	D	Play intervention	Aggression outside of play	Negative correlation
Human	Tastepe et al.	2021	Primates	*Homo sapiens*	D	% obs time in play	Social competence	Positive correlation
Human	Tastepe et al.	2021	Primates	*Homo sapiens*	D	% obs time in rough and tumble play	Social competence	Negative correlation
Human	Tastepe et al.	2021	Primates	*Homo sapiens*	D	% obs time in play	Anxiety-withdrawal	Negative correlation
Japanese macaque	Shimada & Sueur	2018	Primates	*Macaca fuscata*	W	Play partner	Association partners (<3m)	Positive correlation
Japanese macaque	Shimada & Sueur	2018	Primates	*Macaca fuscata*	W	Proximity <3m association	Play partner preference	Positive correlation
Long Evan rat	Ham & Pellis	2023	Rodentia	*Rattus norvegicus domestica*	C	% obs time in play	% time in non-play proximity	None

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Long Evan rat	Stark	2017	Rodentia	*Rattus norvegicus domestica*	C	Play amount	Dendritic pruning	Positive correlation
Marmoset	Chalmers & Locke-Haydon	1984	Primates	*Callithrix jacchus*	C	% obs time in play	Skill acquisition (1-3 weeks later)	Positive correlation
Marmoset	Chalmers & Locke-Haydon	1984	Primates	*Callithrix jacchus*	C	% obs time in play	Skill acquisition (10 weeks later)	None
Meerkat	Sharpe	2005b	Carnivora	*Suricata suricatta*	W	% obs time in play	Cooperative activity	None
Meerkat	Sharpe	2005c	Carnivora	*Suricata suricatta*	W	% obs time in play fighting	Fighting success	None
Mountain goat	Théoret-Gosselin et al.	2015	Artiodactyla	*Oreamnos americanus*	W	% obs time in play	Survival	Positive correlation
Mouse	Byers & Walker	1995	Rodentia	*Mus domesticus*	C	Time of peak play	Time of cerebellar synaptogenesis and muscle fibre type differentiation	Positive correlation
Pronghorn	Miller & Byers	1991	Artiodactyla	*Antilocapra americana*	W	% obs time in play	% energy expenditure	Positive correlation
Red necked wallabies	Watson	1993	Diprotodontia	*Macropus rufogriseus banksianus*	C	Play partner	Association partners (feeding and drinking)	None
Red necked wallabies	Watson	1993	Diprotodontia	*Macropus rufogriseus banksianus*	C	Play partner	Affiliation outside of play	None

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Squirrel monkey	Baldwin & Baldwin	1974	Primates	*Saimiri sp.*	W + C	% obs time in play	Proximity	Negative correlation
Squirrel monkey	Baldwin & Baldwin	1973	Primates	*Saimiri sp.*	W + C	Presence of play	Affiliation outside of play	Positive correlation
Squirrel monkey	Baldwin & Baldwin	1973	Primates	*Saimiri sp.*	W + C	Presence of play	Sexual behaviour repertoire	Positive correlation
Squirrel monkey	Biben	1986	Primates	*Saimiri sciureus*	C	Play partner	Partner in non-play affiliative behaviour	None
Syrian hamster	Kyle et al.	2020	Rodentia	*Mesocricetus auratus*	D	% obs time in play	Aggression outside of play	Negative correlation
White-faced capuchin monkeys	Perry et al.	2017	Primates	*Cebus capucinus*	W	% obs time in play	Male dispersal age	None
White-faced capuchin monkeys	Perry et al.	2017	Primates	*Cebus capucinus*	W	% obs time in play	Age at first alpha position	None
Wolf	Cafazzo et al.	2018	Carnivora	*Canis lupus*	C	% obs time in competitive play	Aggression outside of play	Negative correlation
Wolf	Cafazzo et al.	2018	Carnivora	*Canis lupus*	C	% obs time in relaxed play	Affiliation outside of play	Positive correlation
Wolf	Cafazzo et al.	2018	Carnivora	*Canis lupus*	C	Dominance in play	Dominance outside of play	Positive correlation
Yellow-bellied marmot	Blumstein et al.	2013	Rodentia	*Marmota flaviventris*	W	Rank in play	Rank in adulthood	Positive correlation

Table S2.3: Studies exploring factors predicting variation in social play.

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
African bush elephant	Freeman	2021	Proboscidea	*Loxodonta africana*	C	Age	Partner preference	Same age
African bush elephant	Lee & Moss	2014	Proboscidea	*Loxodonta africana*	W	Sex	% obs time in play	None
African bush elephant	Lee & Moss	2014	Proboscidea	*Loxodonta africana*	W	Drought	% obs time in play	Negative correlation
Assamese macaque	Berghänel et al.	2015	Primates	*Macaca assamensis*	W	Food availability	% obs time in play	Positive correlation
Assamese macaque	Berghänel et al.	2015	Primates	*Macaca assamensis*	W	Sex	% obs time in play	None
Beagle	Bekoff	1974	Carnivora	*Canis lupus familiaris*	D	Sex	Roughness of play	None
Belding's ground squirrel	Nunes et al.	2004	Rodentia	*Spermophilus beldingi*	W	Age gap	Partner preference	Same age
Bighorn sheep	Berger	1980	Artiodactyla	*Ovis canadensis*	W	Sex	% obs time in play	Males more
Bighorn sheep	Berger	1980	Artiodactyla	*Ovis canadensis*	W	Sex	Rough and tumble behaviour	Males more
Bighorn sheep	Berger	1980	Artiodactyla	*Ovis canadensis*	W	Temperature	No. of play bouts	Negative correlation
Bighorn sheep	Hass & Jenni	1993	Artiodactyla	*Ovis canadensis*	W	Age	Partner preference	Same age

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Bighorn sheep	Hass & Jenni	1993	Artiodactyla	*Ovis canadensis*	W	Sex	Partner preference	None
Bighorn sheep	Hass & Jenni	1993	Artiodactyla	*Ovis canadensis*	W	Sex	% obs time in play	Males
Blue monkey	Forster & Cords	2005	Primates	*Cercopithecus mitis stuhlmanni*	W	Sex	% obs time in play	Males more
Blue monkey	Forster & Cords	2005	Primates	*Cercopithecus mitis stuhlmanni*	W	Sex	% obs time in rough and tumble play	Males more
Blue monkey	Forster & Cords	2005	Primates	*Cercopithecus mitis stuhlmanni*	W	Sex	Play bout duration	Males more
Bonobo	Palagi	2006	Primates	*Pan paniscus*	C	Sex	Partner preference	Same sex
Bonobo	Palagi & Paoli	2007	Primates	*Pan paniscus*	C	Sex	% obs time in rough and tumble play	Positive correlation
Bonobo	Palagi & Paoli	2007	Primates	*Pan paniscus*	C	Age	Partner preference	None
Bonobo	Palagi & Paoli	2007	Primates	*Pan paniscus*	C	Contact partners	Partner preference	Positive correlation
Bonobo	Palagi & Paoli	2007	Primates	*Pan paniscus*	C	Sex	% obs time in contact play	Females more
Bornean orang-utan	Kunz	2024	Primates	*Pongo pygmaeus*	W	Fruit availability indices	Social play frequency	Positive correlation
Bornean orang-utan	Kunz	2024	Primates	*Pongo pygmaeus*	W	Matriline size	Social play frequency	None

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Bornean orangutan	Mendonça et al.	2017	Primates	*Pongo pygmaeus morio*	W	Age	% obs time in play	Positive correlation
Brown capuchin	Lutz et al.	2019	Primates	*Cebus apella*	C	Sex	Partner preference	Opposite sex
Brown capuchin	Lutz et al.	2019	Primates	*Cebus apella*	C	Age	Partner preference	None
Brown rat	Cuarenta et al.	2021	Rodentia	*Rattus norvegicus domestica*	C	Sex	% obs time in play	Males
Brown rat	Siviy & Panksepp	1985	Rodentia	*Rattus norvegicus domestica*	D	Food	% obs time in play	Positive correlation
Bush dog	Biben	1983	Carnivora	*Spethos venaticus*	W	Age	Partner preference	None
Bush dog	Biben	1983	Carnivora	*Spethos venaticus*	W	Sex	Partner preference	None
Cattle	Brownlee	1954	Artiodactyla	*Bos primigenius*	D	Food availability	% obs time in play	Positive correlation
Cattle	Brownlee	1954	Artiodactyla	*Bos primigenius*	D	Sex	% obs time in aggressive play	Males more
Chacma baboon	Cheney	1978	Primates	*Papio ursinus*	W	Sex	Partner preference	Same sex
Chacma baboon	Cheney	1978	Primates	*Papio ursinus*	W	Maternal rank	% obs time in play	Positive correlation (females only)
Chimpanzee	Heintz	2014	Primates	*Pan troglodytes schweinfurthii*	W	Sex	% obs time in play	None

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Chimpanzee	Heintz	2014	Primates	*Pan troglodytes schweinfurthii*	W	Age	Partner preference	Infants prefer same age
Chimpanzee	Lonsdorf et al.	2014	Primates	*Pan troglodytes schweinfurthii*	W	Sex	% obs time in play	Males more
Chimpanzee	Lonsdorf et al.	2018	Primates	*Pan troglodytes schweinfurthii*	W	Relation*sex	% obs time in play	Male sibling more
Chimpanzee	Lonsdorf et al.	2018	Primates	*Pan troglodytes schweinfurthii*	W	Relation*sex	Partner preference	Male/male siblings more play
Chimpanzee	Markus & Croft	1995	Primates	*Pan troglodytes*	C	Sex	Partner preference	None
Chimpanzee	Markus & Croft	1995	Primates	*Pan troglodytes*	C	Age	Partner preference	Different age
Chimpanzee	Moebius et al.	2019	Primates	*Pan troglodytes versus*	W	Sex	% obs time in play	Males more
Chimpanzee	Moebius et al.	2019	Primates	*Pan troglodytes versus*	W	Fruit availability	% obs time in play	Positive correlation
Chimpanzee	Moebius et al.	2019	Primates	*Pan troglodytes versus*	W	Partner availability* fruit availability	% obs time in play	Positive correlation (stronger when low fruit)
Chimpanzee	Moebius et al.	2019	Primates	*Pan troglodytes versus*	W	Maternal rank	% obs time in play	None
Chimpanzee	Sabbi et al.	2024	Primates	*Pan troglodytes schweinfurthii*	W	Diet quality (non-fig fruit consumption)	No. of days playing	Positive correlation

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Chimpanzee	Sabbi et al.	2024	Primates	*Pan troglodytes schweinfurthii*	W	Diet quality (non-fig fruit consumption)	No. of play bouts	Positive correlation
Coyote	Bekoff	1974	Carnivora	*Canis latrans*	C	Sex	Roughness of play	None
Crab-eating fox	Biben	1983	Carnivora	*Cerdocyon thous*	W	Age	Partner preference	None
Crab-eating fox	Biben	1983	Carnivora	*Cerdocyon thous*	W	Sex	Partner preference	None
Cuvier's gazelle	Gomendio	1988	Artiodactyla	*Gazella cuvieri*	C	Age	Partner preference	Same age
Diademed sifaka	Lutz et al.	2019	Primates	*Propithecus diadema*	W	Sex	Partner preference	Same sex
Diademed sifaka	Lutz et al.	2019	Primates	*Propithecus diadema*	W	Age	Partner preference	Same age
Domestic Goat	Toinon	2022	Artiodactyla	*Capra hircus*	D	Group size	% obs time play fighting	Positive correlation
Eurasian lynx	Antonevich et al.	2020	Carnivora	*Lynx lynx*	C	Age	Initiation	Inverted U-shape
Galápagos fur seal	Arnold & Trillmich	1985	Carnivora	*Arctocephalus galapagoensis*	W	Sex, age	% obs time in play	Males more
Gelada	Mancini et al.	2009	Primates	*Theropithecus gelada*	C	Sex	% obs time in play	None
Golden lion tamarin	De Oliveira et al.	2003	Primates	*Leontopithecus rosalia*	W	Substrate	% obs time in play	Branches preferred

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Golden lion tamarin	De Oliveira et al.	2003	Primates	*Leontopithecus rosalia*	W	Food supplementation	% obs time in play	None
Golden lion tamarin	De Oliveira et al.	2003	Primates	*Leontopithecus rosalia*	W	Age	Partner preference	Older partners
Hamadryas baboon	Abegglen	1984	Primates	*Papio hamadryas*	W	Sex	% obs time play fighting	Males more
Hamadryas baboon	Lutz et al.	2019	Primates	*Papio hamadryas*	C	Age	Partner preference	Same age
Horse	Cameron et al.	2008	Perissodaactyla	*Equus ferus*	W	Sex	% obs time in play	None
Horse	Cameron et al.	2008	Perissodaactyla	*Equus ferus*	W	Maternal condition	% obs time in play	Positive correlation (males only)
Howler monkey	Asensio et al.	2022	Primates	*Alouatta palliata*	W	Foraging on fruit	% obs time in play	Positive correlation
Howler monkey	Asensio et al.	2022	Primates	*Alouatta palliata*	W	Group size	% obs time in play	Positive correlation
Howler monkey	Baldwin & Baldwin	1978	Primates	*Alouatta palliata*	W	Age	Play frequency	Inverted U-shape
Human	DiPietro	1981	Primates	*Homo sapiens*	D	Sex	% obs time in rough and tumble play	Males more
Human	Hamamci & Dagal	2021	Primates	*Homo sapiens*	D	Sex	% obs time in rough and tumble play	Males more
Japanese macaque	Eaton et al.	1985	Primates	*Macaca fuscata*	C	Sex	% obs time in play	Males more

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Japanese macaque	French	1981	Primates	*Macaca fuscata*	C	Maternal rank	% obs time in play	Positive correlation
Japanese macaque	Shimada & Sueur	2018	Primates	*Macaca fuscata*	W	Sex	% obs time in play	None
Langur monkey	Sommer & Mendoza-Granados	1995	Primates	*Presbytis entellus*	W	Habitat quality	% obs time in play	Positive correlation
Maned wolf	Biben	1983	Carnivora	*Chrysocyon brachyurus*	W	Age	Partner preference	None
Maned wolf	Biben	1983	Carnivora	*Chrysocyon brachyurus*	W	Sex	Partner preference	None
Meerkat	Sharpe	2005b	Carnivora	*Suricata suricatta*	W	Sex	Partner preference	None
Meerkat	Sharpe	2005c	Carnivora	*Suricata suricatta*	W	Sex	% obs time play fighting	None
Mountain gorilla	Eckardt	2010	Primates	*Gorilla beringei beringei*	W	Weaning	% obs time in play	Negative correlation
Mountain gorilla	Eckardt	2010	Primates	*Gorilla beringei beringei*	W	Sex	% obs time in play	Males more
Mountain gorilla	Fletcher	1994	Primates	*Gorilla beringei beringei*	W	Sex	% obs time in play	None
Mountain gorilla	Fletcher	1994	Primates	*Gorilla beringei beringei*	W	Sex	% obs time in sparring play	Males more
Mountain gorilla	Fletcher	1994	Primates	*Gorilla beringei beringei*	W	Age	Partner preference	Same age

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Mountain gorilla	Fletcher	1994	Primates	*Gorilla beringei beringei*	W	Sex	Partner preference	Same sex
Mountain gorilla	Grebe et al.	2023	Primates	*Gorilla beringei beringei*	W	Age gap * relatedness	No. of play bouts	None
Mountain gorilla	Grebe et al.	2024	Primates	*Gorilla beringei beringei*	W	Age gap	No. of play bouts	Negative correlation
Mountain gorilla	Grebe et al.	2025	Primates	*Gorilla beringei beringei*	W	Male	Partner preference	Male
Mountain gorilla	Greuter et al.	2016	Primates	*Gorilla beringei beringei*	W	Bamboo availability	% obs time in play	Positive correlation
Olive baboon	Chalmers	1980	Primates	*Papio anubis*	W	Sex	% obs time play fighting	Males more
Olive baboon	Owens	1975	Primates	*Papio anubis*	W	Sex	% obs time in play	Males more
Olive baboon	Owens	1975	Primates	*Papio anubis*	W	Sex	Play bout duration	Males more
Olive baboon	Owens	1975	Primates	*Papio anubis*	W	Sex	% obs time in rough and tumble play	Males more
Olive baboon	Owens	1975	Primates	*Papio anubis*	W	Sex	% obs time in mauling play	Females more
Olive baboon	Owens	1975	Primates	*Papio anubis*	W	Sex	% obs time in sparring play	Males more
Olive baboon	Owens	1975	Primates	*Papio anubis*	W	Sex (males)	Partner preference (sparring)	Males

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Olive baboon	Owens	1975	Primates	*Papio anubis*	W	Sex (females)	Partner preference (sparring)	Males
Olive baboon	Owens	1975	Primates	*Papio anubis*	W	Sex (males)	Partner preference	Males
Olive baboon	Owens	1975	Primates	*Papio anubis*	W	Sex (females)	Partner preference	Males
Olive baboon	Owens	1975	Primates	*Papio anubis*	W	Age	Partner preference	Same age
Olive baboon	Owens	1975	Primates	*Papio anubis*	W	Age gap	Initiation	Positive correlation
Prairie vole	Chau et al.	2008	Rodentia	*Microtus ochrogaster*	C	Sex	Play bout duration	None
Prairie vole	Chau et al.	2008	Rodentia	*Microtus ochrogaster*	C	Sex	% obs time play fighting	None
Prairie vole	Chau et al.	2008	Rodentia	*Microtus ochrogaster*	C	Sex	Partner preference	None
Red necked wallaby	Watson	1993	Diprotodontia	*Macropus rufogriseus*	C	Sex (males)	Partner preference	Males
Red necked wallaby	Watson	1993	Diprotodontia	*Macropus rufogriseus*	C	Sex (females)	Partner preference	Males
Red necked wallaby	Watson	1993	Diprotodontia	*Macropus rufogriseus*	C	Age	Partner preference	Same age
Red necked wallaby	Watson	1993	Diprotodontia	*Macropus rufogriseus*	C	Age	Initiation	None

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Rhesus macaque	Gard & Meier	1977	Primates	*Macaca mulatta*	C	Maternal rank	% obs time in play	Positive correlation
Rhesus macaque	Gard & Meier	1977	Primates	*Macaca mulatta*	C	Maternal rank	% obs time in rough and tumble play	Positive correlation
Rhesus macaque	Gard & Meier	1977	Primates	*Macaca mulatta*	C	Sex	% obs time in rough and tumble play	Males more
Rhesus macaque	Gard & Meier	1977	Primates	*Macaca mulatta*	C	Cloud cover	% obs time in play	None
Rhesus macaque	Gard & Meier	1977	Primates	*Macaca mulatta*	C	Temperature	% obs time in play	Positive correlation
Rhesus macaque	Hinde & Spencer-Booth	1967	Primates	*Macaca mulatta*	C	Sex	% obs time in play	None
Rhesus macaque	Hinde & Spencer-Booth	1967	Primates	*Macaca mulatta*	C	Sex	% obs time in rough and tumble play	None
Rhesus macaque	Kulik et al.	2015	Primates	*Macaca mulatta*	W	Sex	% obs time in play	Males more
Rhesus macaque	Kulik et al.	2015	Primates	*Macaca mulatta*	W	Male	Partner preference	Male
Rhesus macaque	Kulik et al.	2015	Primates	*Macaca mulatta*	W	Age	Partner preference	Same age
Rhesus macaque	Loy	1970	Primates	*Macaca mulatta*	W (provisioned)	Food availability	% obs time in play	Positive correlation

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Rhesus macaque	Mitchell et al.	1966	Primates	*Macaca mulatta*	C	Mother parity	Play frequency	Multiparous more
Rhesus macaque	Tartabini & Dienske	1979	Primates	*Macaca mulatta*	C	Maternal rank	% obs time in play	Positive correlation
Rhesus macaque	Tartabini & Dienske	1979	Primates	*Macaca mulatta*	C	Maternal rank	Partner preference	Same rank
Rhesus macaque	Yanagi & Berman	2017	Primates	*Macaca mulatta*	W	Sex	No. of play bouts	Males more
Rhesus macaque	Yanagi & Berman	2017	Primates	*Macaca mulatta*	W	Sex	Partner preference	Same sex
Richardson's ground squirrel	Pasztor	2001	Rodentia	*Urocitellus richardsonii*	C	Sex	% obs time in rough and tumble play	None
Sable antelope	Thompson	1996	Artiodactyla	*Hippotragus niger*	W	Age	Initiation	None
Sable antelope	Thompson	1996	Artiodactyla	*Hippotragus niger*	W	Age	Partner preference	Same age
Sable antelope	Thompson	1996	Artiodactyla	*Hippotragus niger*	W	Size	Partner preference	Same size
Sable antelope	Thompson	1996	Artiodactyla	*Hippotragus niger*	W	Sex	Partner preference	None
Scimitar oryx	Pfeifer	1985	Artiodactyla	*Oryx dammah*	C	Sex	Aggression during play	Males more
Scimitar oryx	Pfeifer	1985	Artiodactyla	*Oryx dammah*	C	Age	Partner preference	Same age

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Scimitar oryx	Pfeifer	1985	Artiodactyla	*Oryx dammah*	C	Sex	Partner preference	None
Scimitar oryx	Pfeifer	1985	Artiodactyla	*Oryx dammah*	C	Suckling	% obs time in play	None
Siberian ibex	Byers	1980	Artiodactyla	*Capra ibex sibirica*	C	Sex (males)	Partner preference	Males
Siberian ibex	Byers	1980	Artiodactyla	*Capra ibex sibirica*	C	Sex (females)	Partner preference	None
Siberian ibex	Byers	1980	Artiodactyla	*Capra ibex sibirica*	C	Age	Partner preference	Same age
Siberian ibex	Byers	1977	Artiodactyla	*Capra ibex sibirica*	C	Slope of terrain	% obs time in play	Positive correlation
Slow loris	Barrett et al.	2021	Primates	*Nycticebus javanicus*	W	Age	Partner preference	Older partners
Slow loris	Barrett et al.	2021	Primates	*Nycticebus javanicus*	W	Aggressive posture style	Aggressive postures in play	Similar
Slow loris	Barrett et al.	2021	Primates	*Nycticebus javanicus*	W	Rain	% obs time in play	Positive correlation
Slow loris	Barrett et al.	2021	Primates	*Nycticebus javanicus*	W	Moonlight	% obs time in play	Positive correlation
Spotted hyena	Holekamp & Smale	1998	Carnivora	*Crocuta crocuta*	W	Maternal rank	% obs time in play	Positive correlation
Spotted hyena	Pederson et al.	1990	Carnivora	*Crocuta crocuta*	W (provisioned)	Sex	% obs time in rough and tumble play	Females more

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Spotted hyena	Pederson et al.	1990	Carnivora	*Crocuta crocuta*	W (provisioned)	Sex	% obs time in play	Females more
Squirrel monkey	Aghababian et al.	2021	Primates	*Saimiri collinsi*	W	Age, sex	No. of play bouts	Males more
Squirrel monkey	Aghababian et al.	2021	Primates	*Saimiri collinsi*	W	Age	No. of initiations	Positive correlation
Squirrel monkey	Aghababian et al.	2021	Primates	*Saimiri collinsi*	W	Age	No. of rough and tumble behaviours	Positive correlation
Squirrel monkey	Aghababian et al.	2021	Primates	*Saimiri collinsi*	W	Sex	No. of rough and tumble behaviours	Males more
Squirrel monkey	Aghababian et al.	2021	Primates	*Saimiri collinsi*	W	Age gap	Partner sex preference	Larger age gap = opposite sex partner
Squirrel monkey	Baldwin & Baldwin	1971	Primates	*Saimiri sp.*	W	Social group size	% obs time in play	Positive correlation
Squirrel monkey	Baldwin & Baldwin	1971	Primates	*Saimiri sp.*	W	Social group size	Play group size	Positive correlation
Squirrel monkey	Baldwin & Baldwin	1976	Primates	*Saimiri sp.*	C	Food allocation	% obs time in play	Positive correlation
Squirrel monkey	Baldwin & Baldwin	1974	Primates	*Saimiri sp.*	W & C	Sex	% obs time in play	Males more
Squirrel monkey	Biben	1986	Primates	*Saimiri sciureus*	C	Sex	No. of play bouts	Males more
Squirrel monkey	Biben	1989	Primates	*Saimiri sciureus*	C	Sex	Partner preference	None

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Squirrel monkey	Biben	1989	Primates	*Saimiri sciureus*	C	Age	Partner preference	None
Squirrel monkey	Stone	2008	Primates	*Saimiri sciureus*	W	Season	% obs time in play	Wet season more
Sumatran orang-utan	Kunz	2024	Primates	*Pongo abelii*	W	Fruit availability indices	Social play frequency	None
Sumatran orang-utan	Kunz	2024	Primates	*Pongo abelii*	W	Matriline size	Social play frequency	None
Tibetan Macaque	Mayhew et al.	2020	Primates	*Macaca thibetana*	W (provisioned)	Age gap	Partner preference	Same age
Tibetan Macaque	Mayhew et al.	2020	Primates	*Macaca thibetana*	W (provisioned)	Maternal rank	% obs time in play	None
Tibetan macaque	Wang et al.	2021	Primates	*Macaca thibetana*	W	Sex	% obs time in play	Males more
Tibetan macaque	Wang et al.	2021	Primates	*Macaca thibetana*	W	Sex	% obs time in aggressive play	Males more
Tibetan macaque	Wang et al.	2021	Primates	*Macaca thibetana*	W	Sex	% obs time in affiliative play	Females more
Tibetan macaque	Wang et al.	2021	Primates	*Macaca thibetana*	W	Maternal rank (infant)	% obs time in play	None
Tibetan macaque	Wang et al.	2021	Primates	*Macaca thibetana*	W	Matriline rank (infant)	% obs time in play	None
Tibetan macaque	Wang et al.	2021	Primates	*Macaca thibetana*	W	Maternal rank (juvenile)	% obs time in play	Positive correlation

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Tibetan macaque	Wang et al.	2021	Primates	*Macaca thibetana*	W	Matriline rank (juvenile)	% obs time in play	None
Tibetan macaque	Wright et al.	2018	Primates	*Macaca thibetana*	W	Sex	Partner preference	Same sex
Titi monkey	Chau et al.	2008	Primates	*Callicebus cupreus*	C	Sex	Play bout duration	None
Titi monkey	Chau et al.	2008	Primates	*Callicebus cupreus*	C	Sex	% obs time play fighting	None
Titi monkey	Chau et al.	2008	Primates	*Callicebus cupreus*	C	Sex (males)	Partner preference	None
Titi monkey	Chau et al.	2008	Primates	*Callicebus cupreus*	C	Sex (females)	Partner preference	Males
Vervet monkey	Fairbanks	1993	Primates	*Cercopithecus aethiops*	W	Age	Partner preference	Same age
Vervet monkey	Fedigan	1972	Primates	*Cercopithecus aethiops*	C	Sex	% obs time in play	Males more
Western lowland gorilla	Brown	1988	Primates	*Gorilla gorilla gorilla*	C	Sex	% obs time in play	None
Western lowland gorilla	Brown	1988	Primates	*Gorilla gorilla gorilla*	C	Sex (males)	Partner preference	Males
Western lowland gorilla	Brown	1988	Primates	*Gorilla gorilla gorilla*	C	Sex (females)	Partner preference	Males

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Western lowland gorilla	Hoff et al.	1981	Primates	*Gorilla gorilla gorilla*	C	Sex	% obs time in rough and tumble play	Males more
Western lowland gorilla	Maestripieri & Ross	2004	Primates	*Gorilla gorilla gorilla*	C	Sex	% obs time in play	Males more
Western lowland gorilla	Maestripieri & Ross	2004	Primates	*Gorilla gorilla gorilla*	C	Sex (males)	Partner preference	Males
Western lowland gorilla	Maestripieri & Ross	2004	Primates	*Gorilla gorilla gorilla*	C	Sex (females)	Partner preference	Males
Western lowland gorilla	Meder	1990	Primates	*Gorilla gorilla gorilla*	C	Sex	% obs time in play	Males more
Western lowland gorilla	Nowell	2005	Primates	*Gorilla gorilla gorilla*	W	Sex	% obs time in rough and tumble play	None
Western lowland gorilla	Nowell	2005	Primates	*Gorilla gorilla gorilla*	W	Sex	Partner preference	None
Western lowland gorilla	Palagi et al.	2007	Primates	*Gorilla gorilla gorilla*	C	Age	Partner preference	Same age
Western lowland gorilla	Palagi et al.	2007	Primates	*Gorilla gorilla gorilla*	C	Age	Initiation	Same age

Common Name	Author	Year	Order	Species	Wild/ Captive/ Domesticated	Explanatory Variable	Response Variable	Relationship
Western lowland gorilla	Palagi et al.	2007	Primates	*Gorilla gorilla gorilla*	C	Sex	% obs time in rough and tumble play	Males more
White headed langur	Yang et al.	2022	Primates	*Trachypithecus leucocephalus*	W	Sex	Partner preference	Same sex
White-faced capuchin	Winkler & Perry	2022	Primates	*Cebus capucinus*	W	Sex	% obs time in play	Males more, males peak later
Wolf	Bekoff	1974	Carnivora	*Canis lupus*	C	Sex	Roughness of play	None

Appendix B

Table S3.1: Observation periods for each group in the study, including months in which data collection was paused because of the Covid-19 pandemic.

Group	**Start of observations**	**Start full data collection**	**End of data collection for this study**	**Covid-19 pandemic gap**
Kyagurilo (KYA)	Aug-1998	Jun-2000	Feb 2016 (fission)	-
Oruzogo (ORU)	Dec-2013	May-2014	Sep-2023	Apr-Oct 2020, Jan-2021, Jul-Oct 2021
Bitukura (BIT)	Aug-2014	Sep-2014	Sep-2023	Apr-Oct 2020, Jan-2021,
Mukiza (MUK)	Mar-2016	Mar-2016	Sep-2023	Apr-Oct 2020, Jan-2021,
Rukara (RUK) / Kyagurilo A (KYA A)	Mar-2016	Mar-2016	Sep-2023	Apr-Jan 2021,

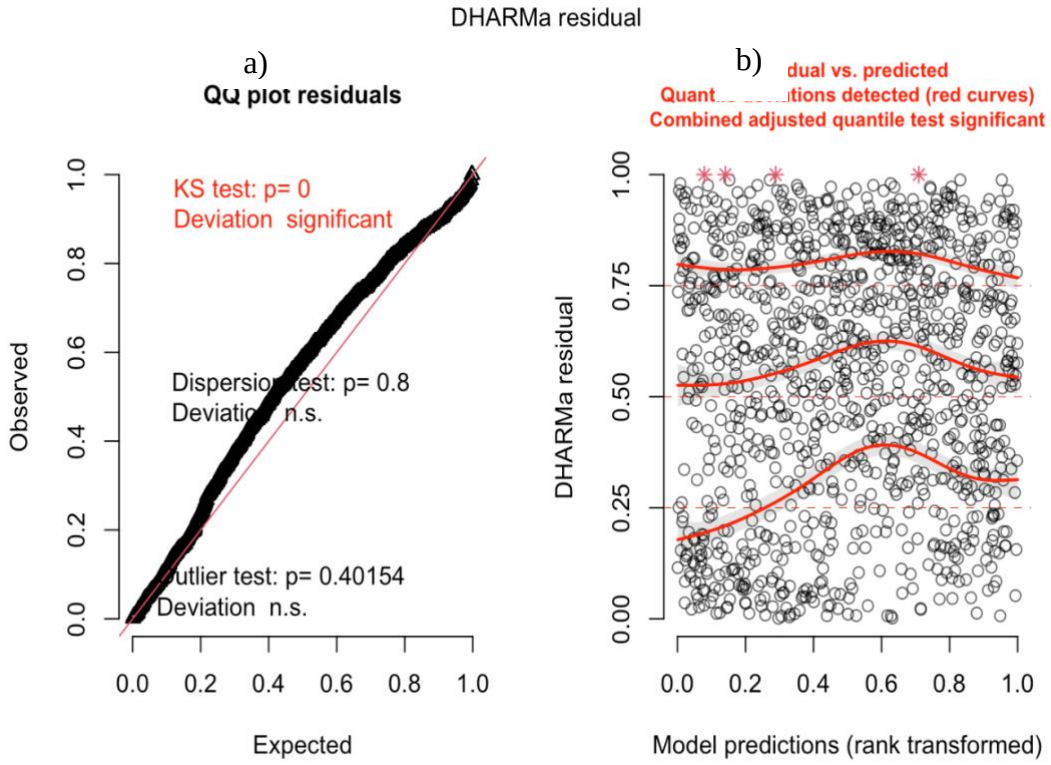

Figure S3.1: DHARMa package model diagnostics for the play rate model with group as a random intercept, a) quantile-quantile plots of the expected vs observed residuals, red line indicates ideal relationship. Overlayed with statistical tests for uniformity (KS test), dispersion and outliers. b) Predicted values plotted against fitted values to assess the assumption of homoscedasticity, red solid lines indicate that each quartile fitted values were significantly different from predicted (red dotted lines).

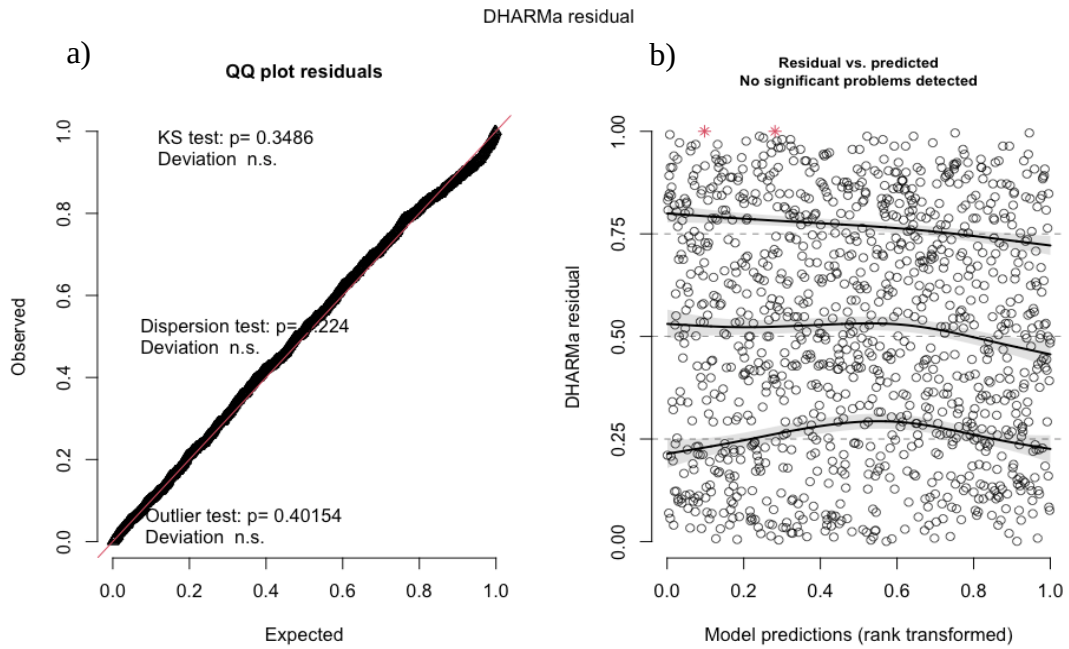

Figure S3.2: DHARMa package model diagnostics for the play rate model without group as a random intercept, presented in this manuscript, a) quantile-quantile plots of the expected vs observed residuals, red line indicates ideal relationship. Overlayed with statistical tests for uniformity (KS test), dispersion and outliers. b) Predicted values plotted against fitted values to assess the assumption of homoscedasticity, black lines indicate at each quartile that fitted values were not significantly different from predicted (dotted lines).

Appendix C

Table S4.1: Observation timelines for each gorilla group, including the pause in observation because of the Covid-19 pandemic.

Group	Start of observations	Start of data collection for this study	End of data collection for this study	Covid-19 pandemic gap
Kyagurilo (KYA)	Aug-1998	Jan-2013	Feb 2016 (fission)	-
Oruzogo (ORU)	Dec-2013	May-2014	Dec-2023	Apr-Oct 2020,
Bitukura (BIT)	Aug-2014	Sep-2014	Dec-2023	Apr-Oct 2020,
Mukiza (MUK)	Mar-2016	Mar-2016	Dec-2023	Apr-Oct 2020,
Rukara (RUK) / Kyagurilo A (KYA A)	Mar-2016	Mar-2016	Dec-2023	Apr-Jan 2021,

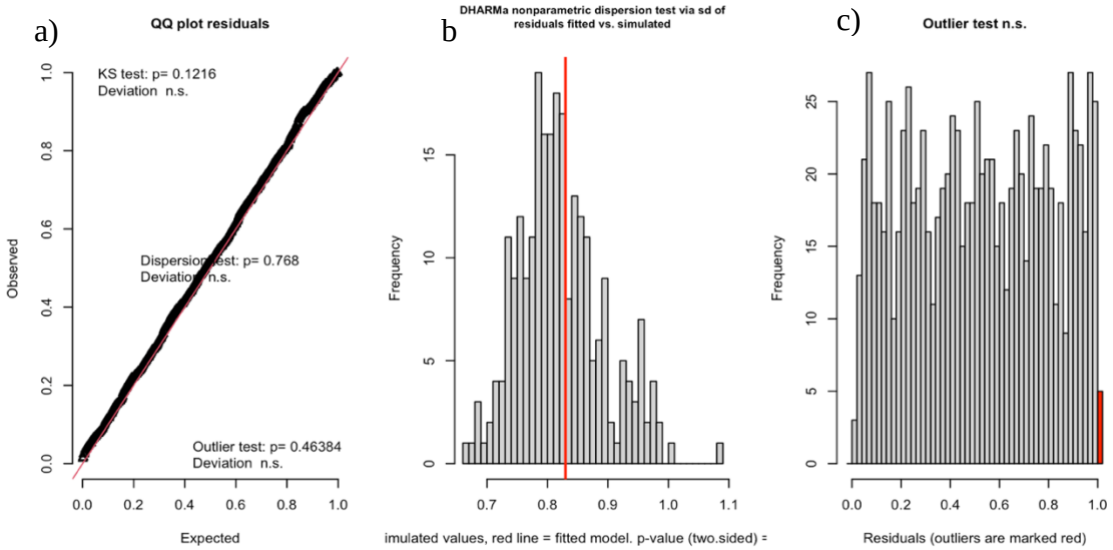

Figure S4.1: DHARMa package model diagnostics for analysis 1, month-based number of available partners, a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

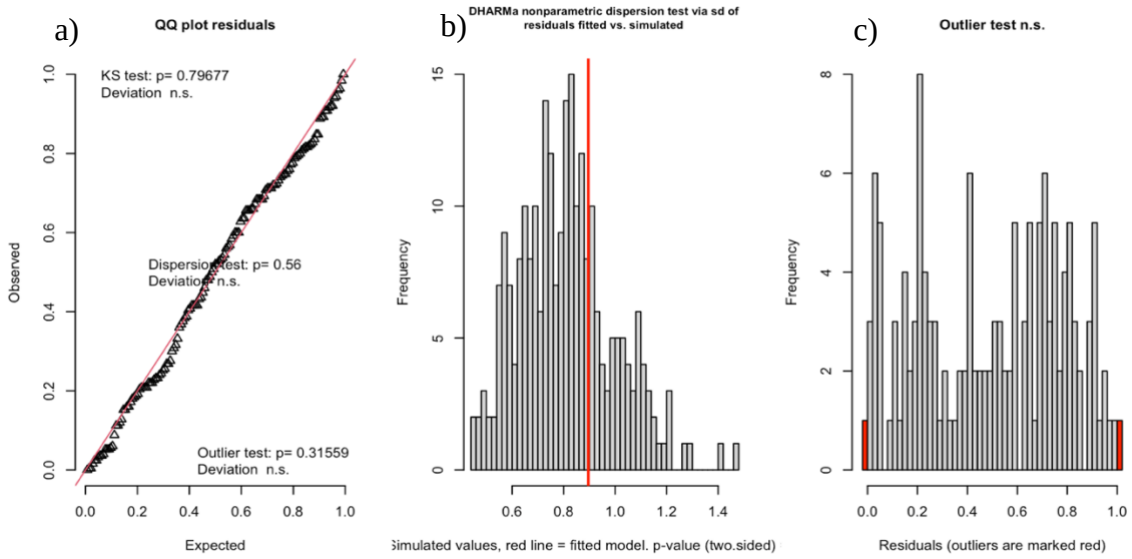

Figure S4.2: DHARMa package model diagnostics for analysis 2, year-based number of available partners, a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

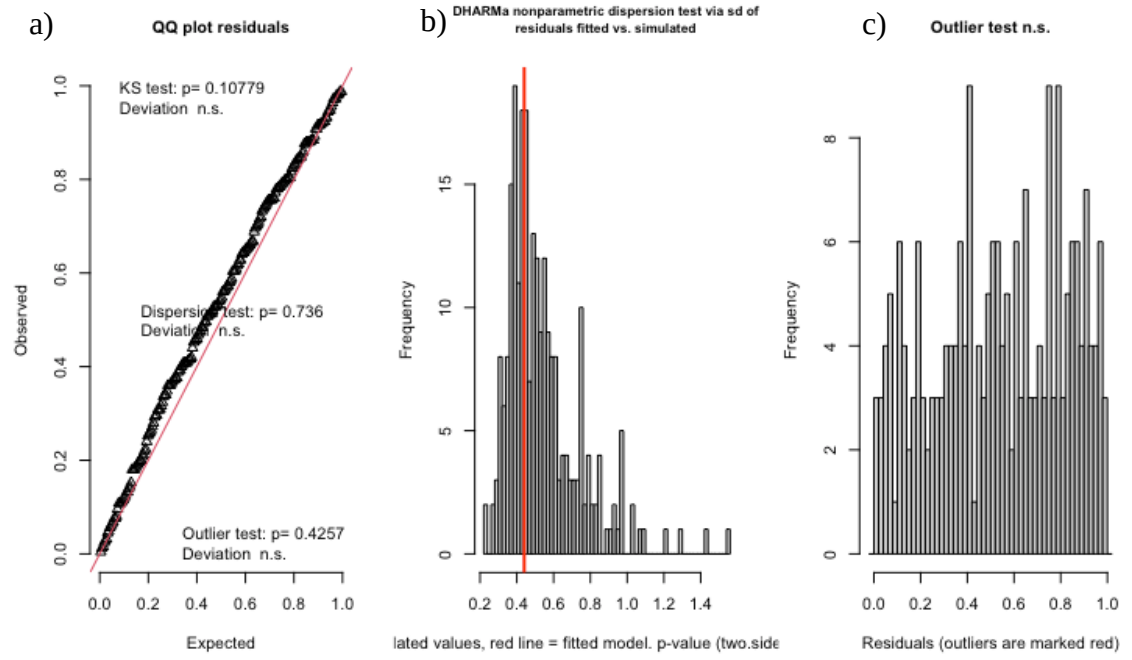

Figure S4.3: DHARMa package model diagnostics for analysis 3, partner preference in age, sex, immature proximity and mother proximity, a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

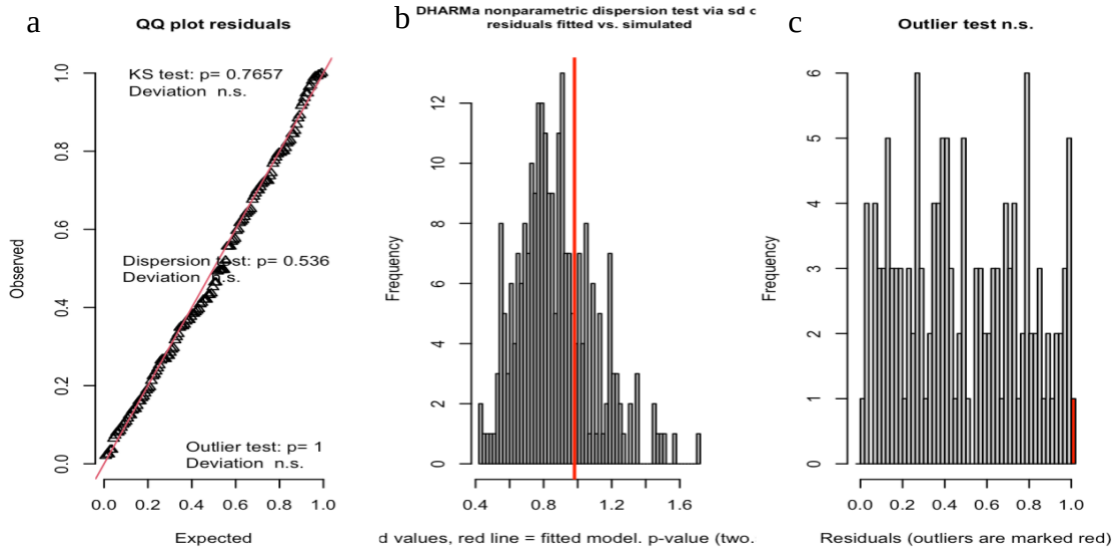

Figure S4.4: DHARMa package model diagnostics for analysis 4, stability of play partner relationships, a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

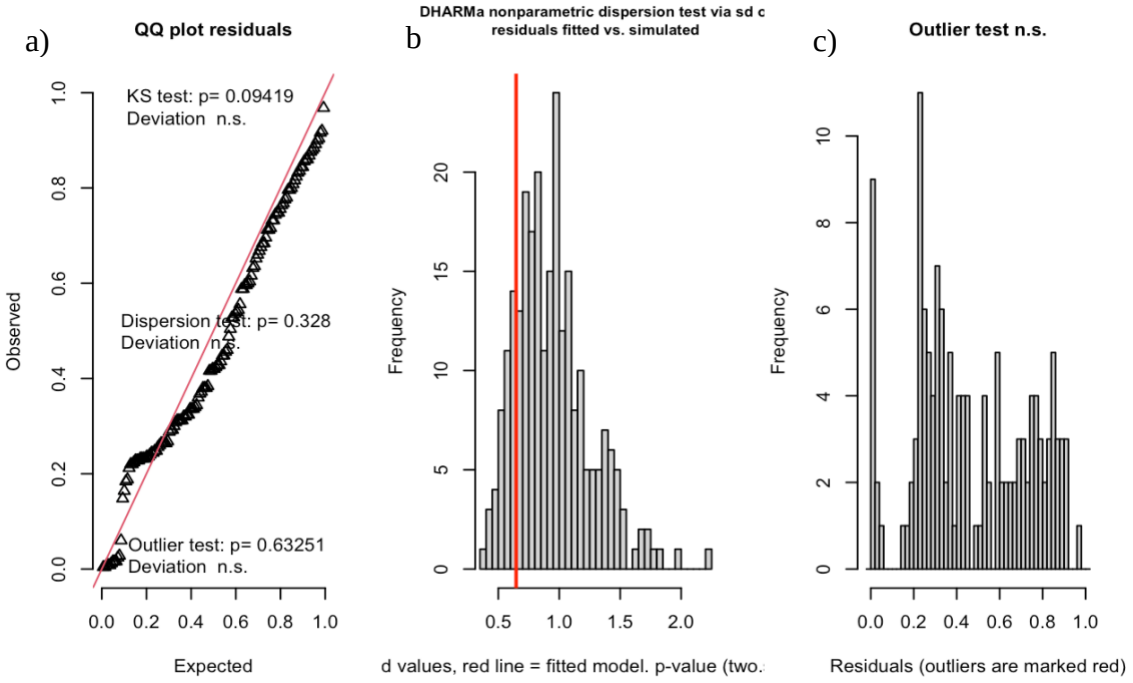

Figure S4.5: DHARMa package model diagnostics for analysis 5, play association scores and proximity association scores for subsequent year, a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

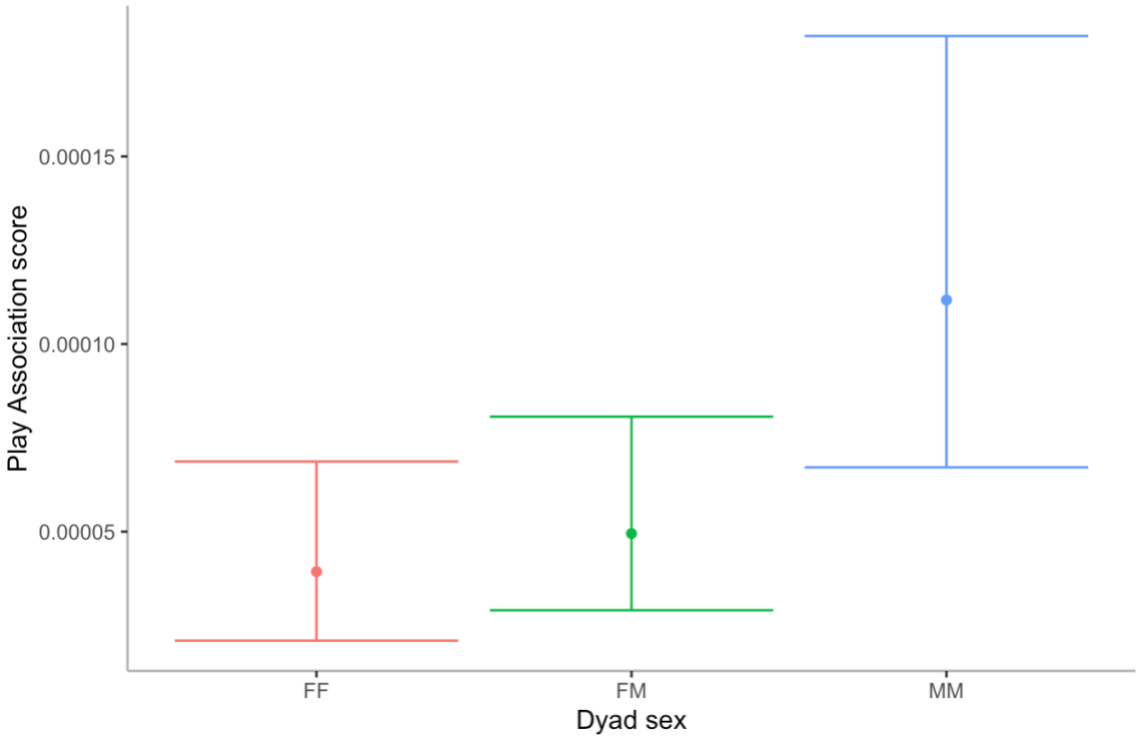

Figure S4.6: Model predictions for the effect of different sex partnerships on play association scores. Variables have been back transformed for easier interpretation.

Analysis 6 - Post-hoc analysis of immature proximity association score and subsequent play association score.

Methods

To assess if play association and proximity association for the previous year were correlated, we ran a generalized mixed model with a gamma error distribution. The square root transformation of the play association score was the response variable. This was further transformed by adding 0.00001 to all values, to remove any zero values but

keep the association scores at the same magnitude. The fixed effect was the square root transformation of the proximity association score in the previous network. Random effects were added for ID, partner ID, dyad ID, group, and network start date. Visual inspection of the QQ plot showed that models assumptions were not violated (see Appendix C Figure S4.77) and the model residuals were uniform (KS test: D = 0.0433, p-value = 0.9657). The data were not overdispersed (dispersion = 1.0564, p-value = 0.736), and there were less outliers than expected (p-value = 0.632). Visual checks of predicted residuals against fitted residuals showed no presence of heteroscedasticity.

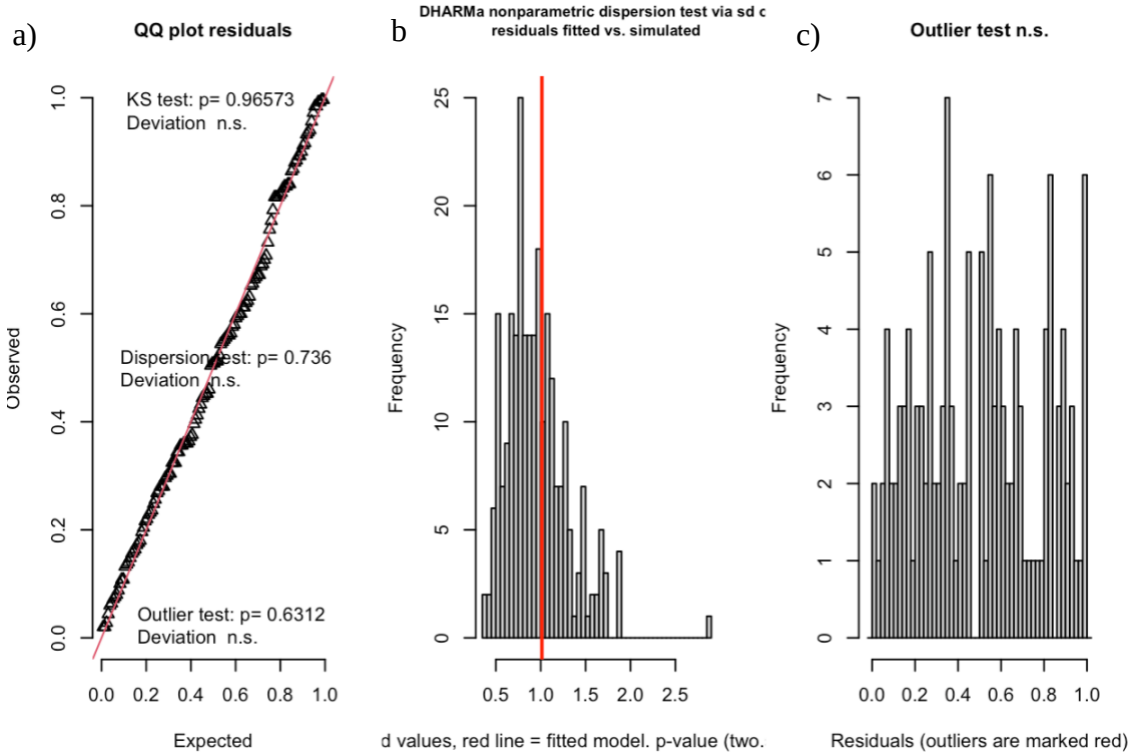

Figure S4.7: DHARMa package model diagnostics for post-hoc analysis 6, proximity association scores and subsequent play association scores, a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

Results

The full-null comparison indicated that the full model did not have greater predictive power than the null model ($\chi 2$ =2.267, df = 1, p-value = 0.132). The immature proximity association score in each network period was not significantly correlated to the play association score of the previous network period (Beta = -0.0180, SE = 0.354, p-value = 0.96, Table S4.2).

Table S4.2: Model results for post-hoc analysis 6, immature proximity association scores and subsequent play association scores, significant p-values at the 0.05 level are in bold.

Term	**Estimate**	**SE / SD**	**p**
ID	Random intercept	0.637	
Partner ID	Random intercept	0.0000466	
Dyad ID	Random intercept	0.295	
Group	Random intercept	0.1292	
Network start date	Random intercept	0.0834	
Intercept	-4.818	0.122	**<0.001**
Play association score in previous network	-0.018	0.354	0.96

Analysis 7 - Post-hoc analysis of immature proximity association score stability

Methods

To assess if immature proximity association was correlated from year to year, we ran a generalized mixed model with a gamma error distribution. The square root transformation of the immature proximity association score was the response variable. This was further transformed by adding 0.01 to all values, to remove any zero values but keep the association scores at the same magnitude. The fixed effect was the square root transformation of the proximity association score in the previous network. Random effects were added for ID, partner ID, dyad ID, group, and network start date. Visual

inspection of the QQ plot showed that models assumptions were not violated (see Appendix C Figure S4.8) and the model residuals were uniform (KS test: D = 0.109, p-value = 0.085). The data were not overdispersed (dispersion = 0.706, p-value = 0.28), and there were less outliers than expected (p-value = 0.0893). Visual checks of predicted residuals against fitted residuals showed no presence of heteroscedasticity.

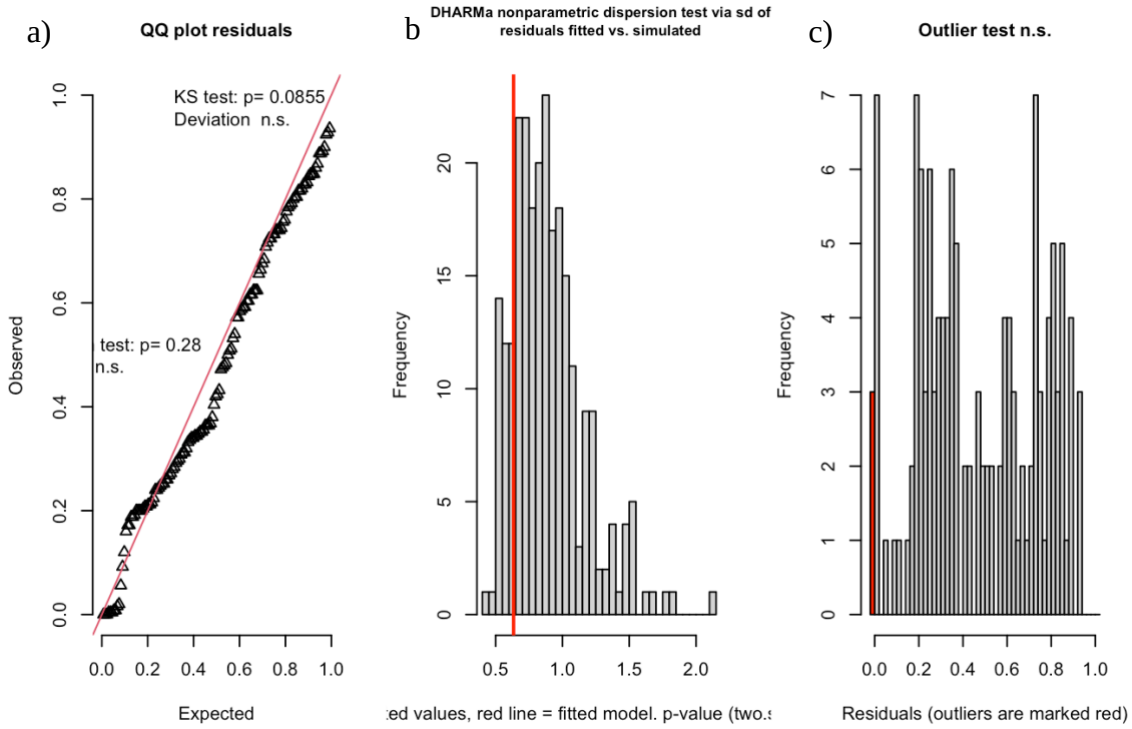

Figure S4.8: DHARMa package model diagnostics for post-hoc analysis 7, proximity association scores and subsequent proximity association scores, a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

Results

The full-null comparison indicated that the full model did have greater predictive power than the null model ($\chi 2$ =12.798, df = 1, p-value <0.001). The immature proximity association score in each network period was significantly correlated to the immature

proximity association score of the previous network period (Beta = 0.709, SE = 0.209, p-value <0.001, Table S4.3).

Table S4.3: Model results for post-hoc analysis 7, immature proximity association scores and subsequent immature proximity association scores, significant p-values at the 0.05 level are in bold.

Term	**Estimate**	**SE / SD**	**p**
ID	Random intercept	$3.82e^{-06}$	
Partner ID	Random intercept	$7.62e^{-06}$	
Dyad ID	Random intercept	0.165	
Group	Random intercept	$3.61e^{-07}$	
Network start date	Random intercept	0.192	
Intercept	-1.668	0.0687	**<0.001**
Play association score in previous network	0.709	0.209	**<0.001**

Appendix D

Table S5.1: Observation timelines for each gorilla group, including the pause in the observation because of the Covid-19 pandemic.

Group	Start of observations	Beginning of data collection for this study	Beginning of data collection	Covid-19 pandemic gap
Kyagurilo (KYA)	Aug-1998	Jan-2013	Feb 2016 (fission)	-
Oruzogo (ORU)	Dec-2013	May-2014	Dec-2023	Apr-Oct 2020, Jan-2021, Jul-Oct 2021
Bitukura (BIT)	Aug-2014	Sep-2014	Dec-2023	Apr-Oct 2020, Jan-2021,
Mukiza (MUK)	Mar-2016	Mar-2016	Dec-2023	Apr-Oct 2020, Jan-2021,
Rukara (RUK) / Kyagurilo A (KYA A)	Mar-2016	Mar-2016	Dec-2023	Apr-Jan 2021,
Kyagurilo B (KYA B)	Apr-2022	Apr-2022	Dec-2023	-

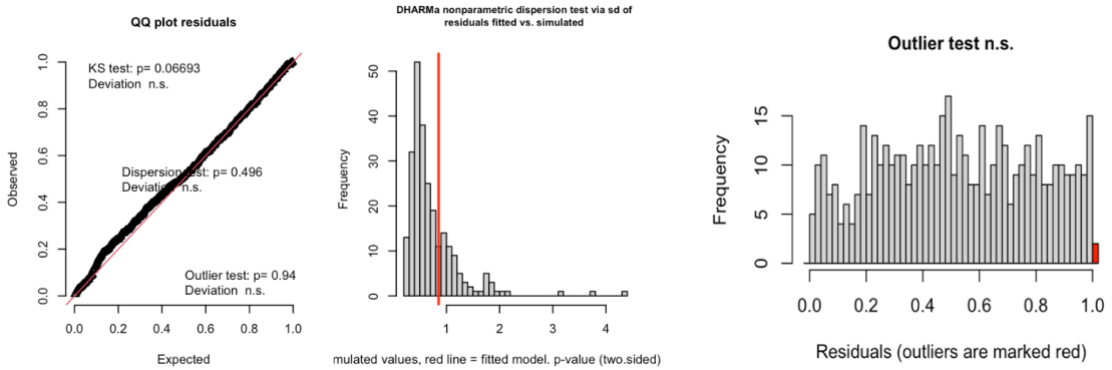

Figure S5.1: DHARMa package model diagnostics for model of female activity budgets, from left to right: a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

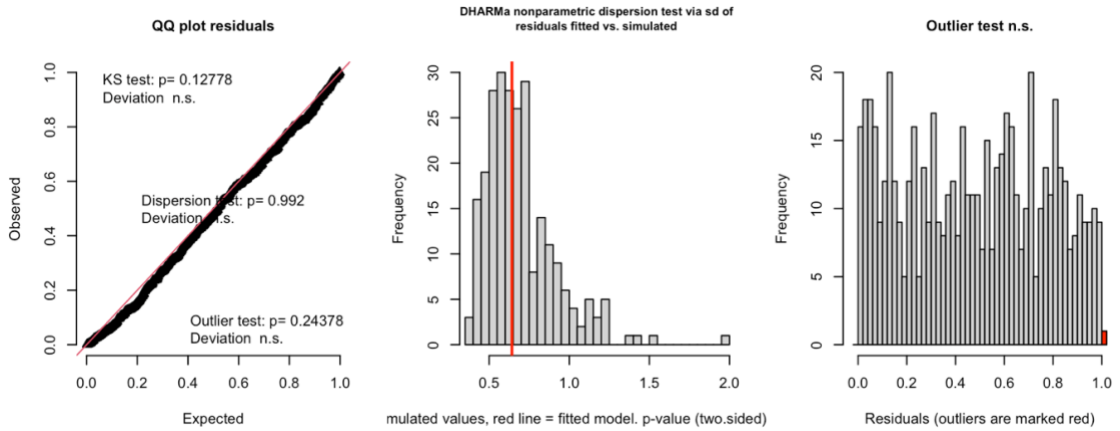

Figure S5.2: DHARMa package model diagnostics for male activity budget model, from left to right: a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

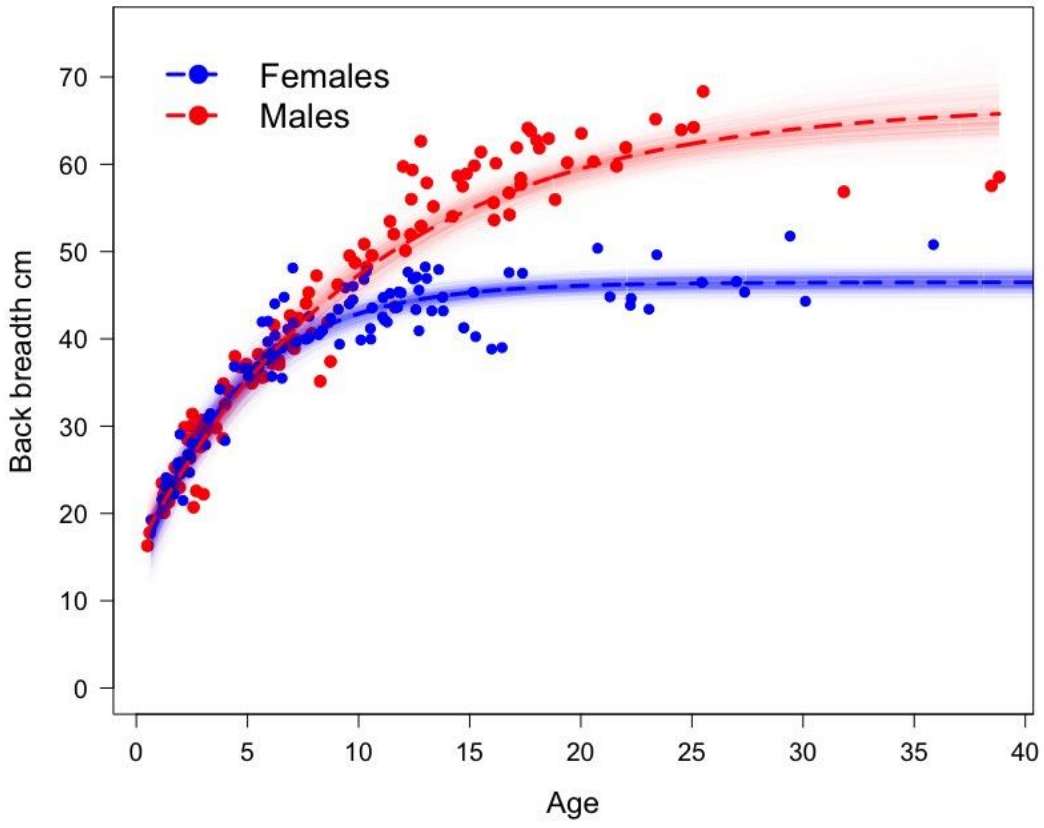

Figure S5.3: Growth curves for Bwindi gorilla back breadth. Curves represent predicted growth trajectories; points are photogrammetry data points for female (blue) and male (red) gorillas, with between 1 and 7 data points per individual.

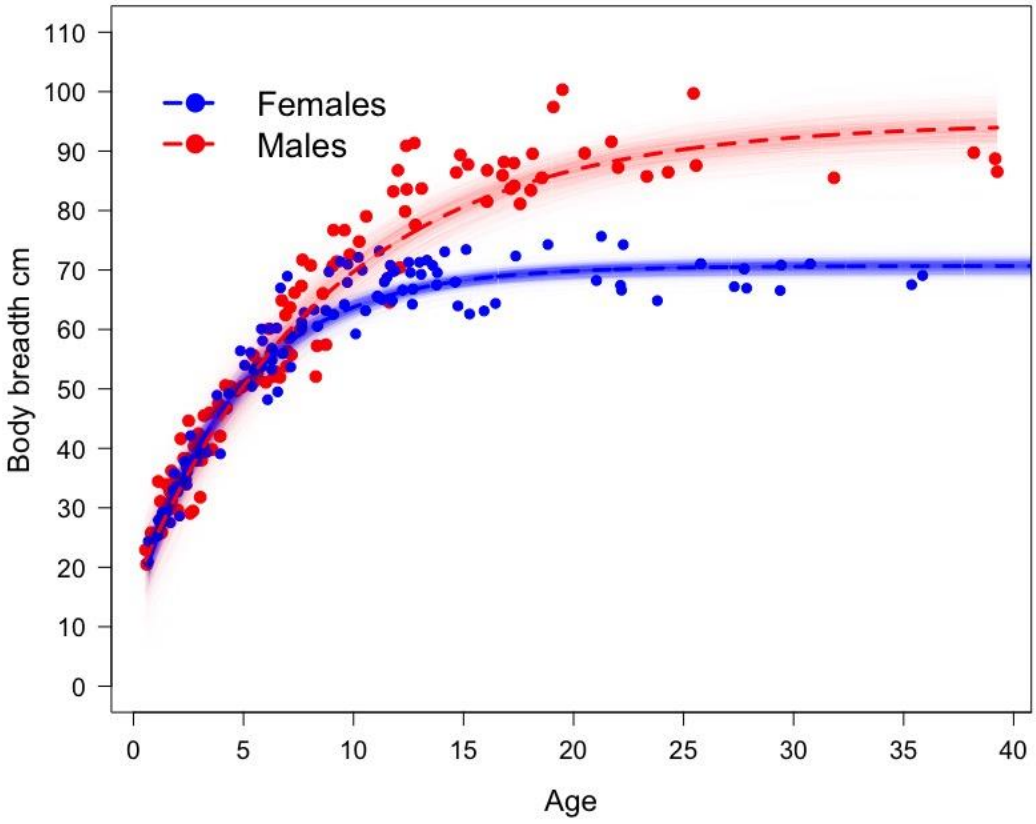

Figure S5.4: Growth curves for Bwindi gorilla body length. Curves represent predicted growth trajectories; points are photogrammetry data points for female (blue) and male (red) gorillas, with between 1 and 8 data points per individual.

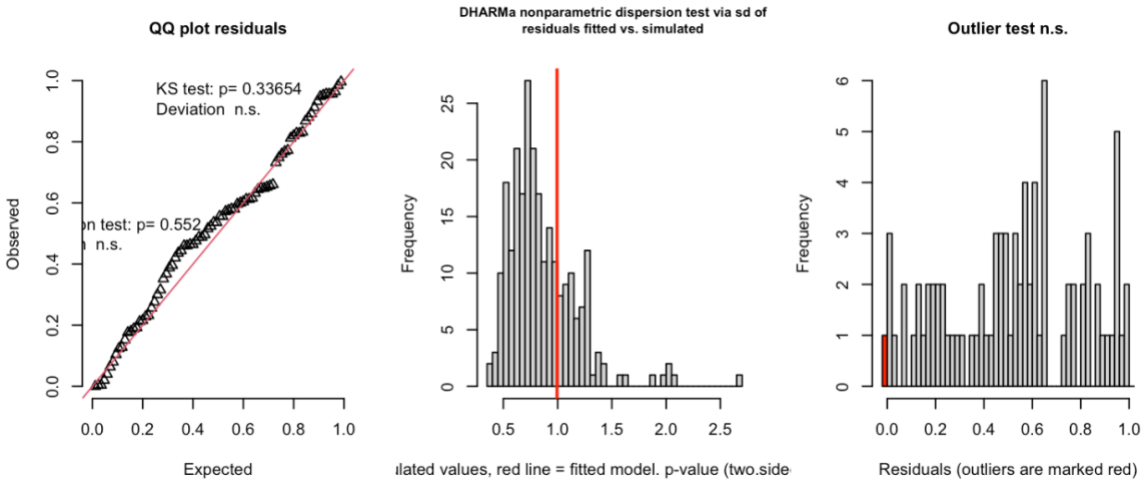

Figure S5.5: DHARMa package model diagnostics for female body size model, from left to right: a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

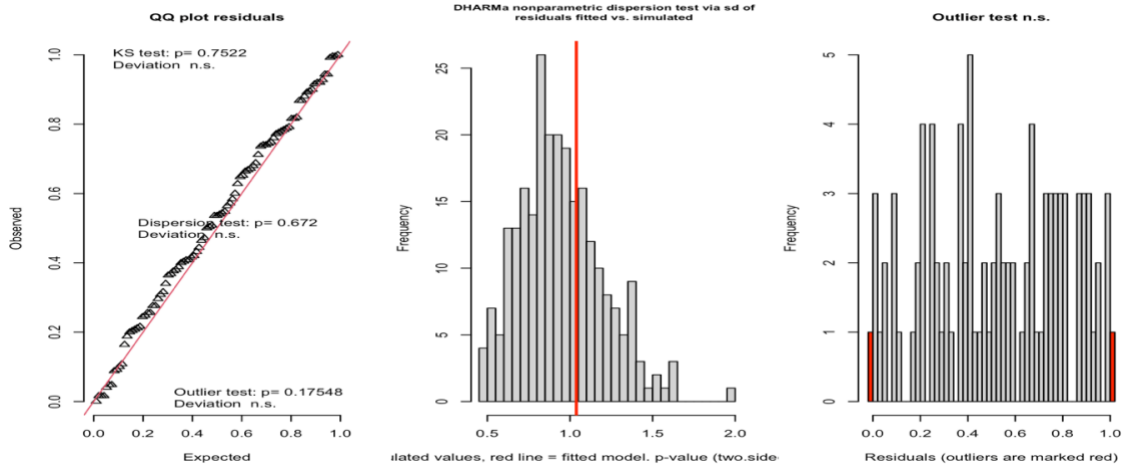

Figure S5.6: DHARMa package model diagnostics for male body size model, from left to right: a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

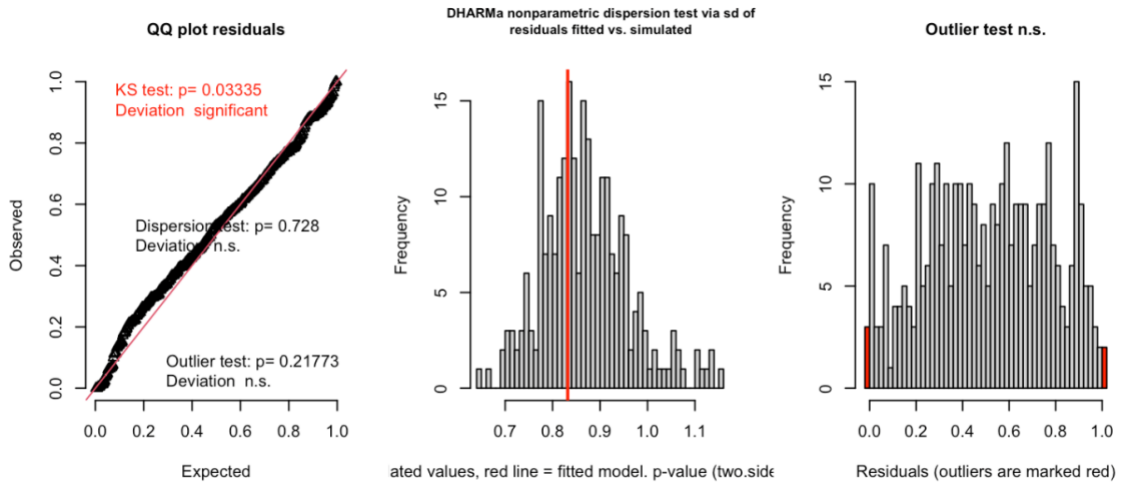

Figure S5.7: DHARMa package model diagnostics for all milestone model, from left to right: a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

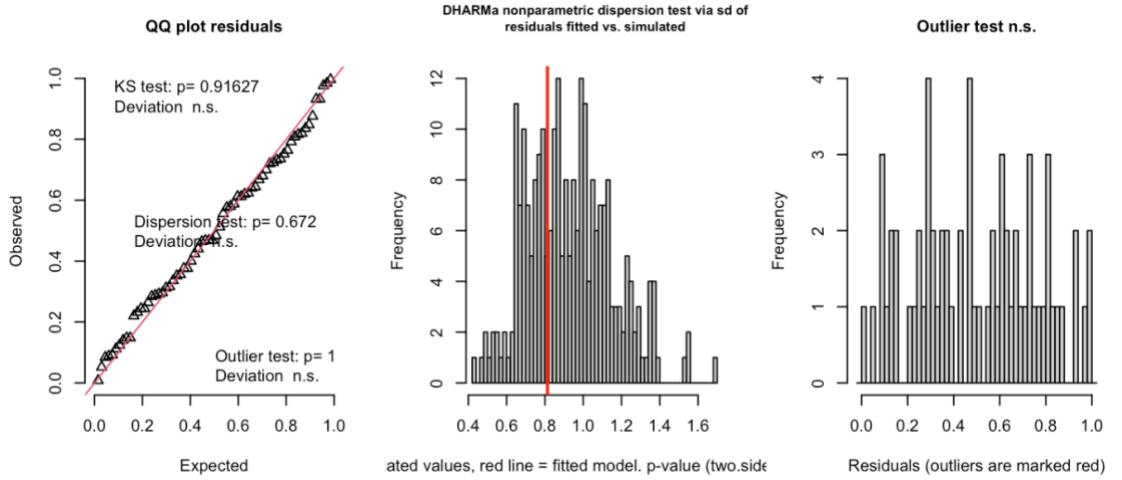

Figure S5.8: DHARMa package model diagnostics for physical milestone model, from left to right: a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

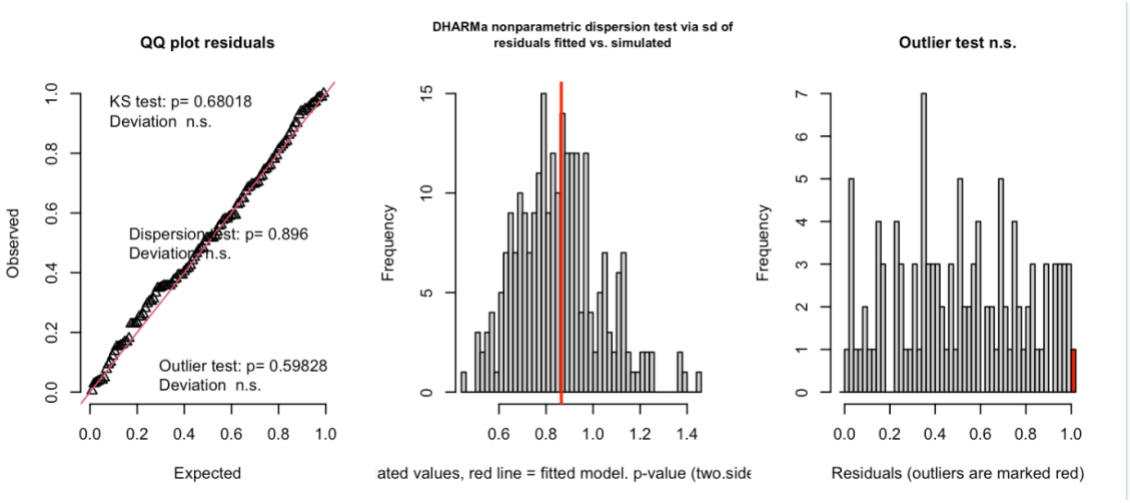

Figure S5.9: DHARMa package model diagnostics for proximity milestone model, from left to right: a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

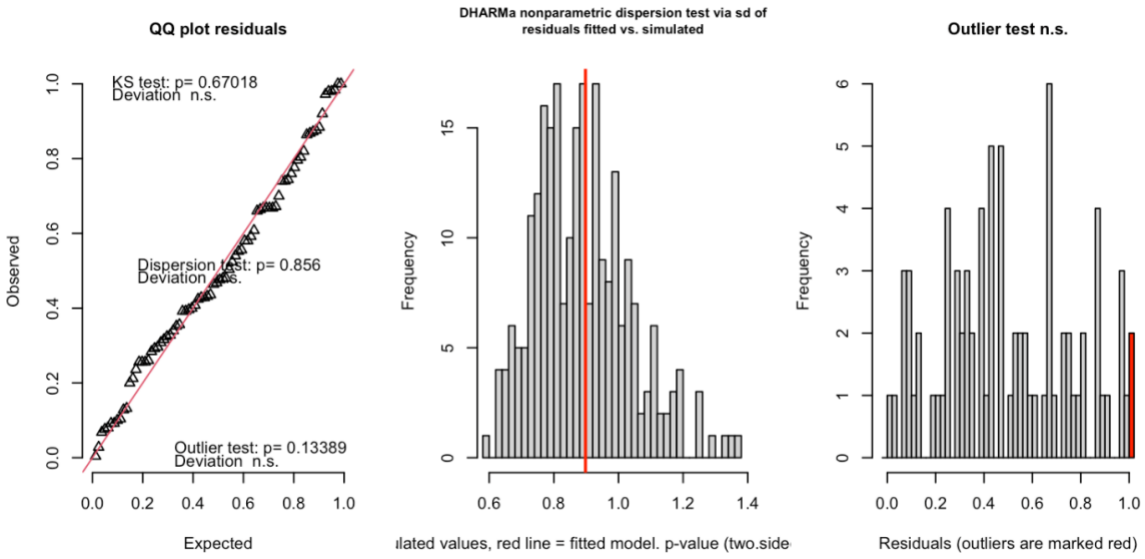

Figure S5.10: DHARMa package model diagnostics for affiliative milestone model, from left to right: a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

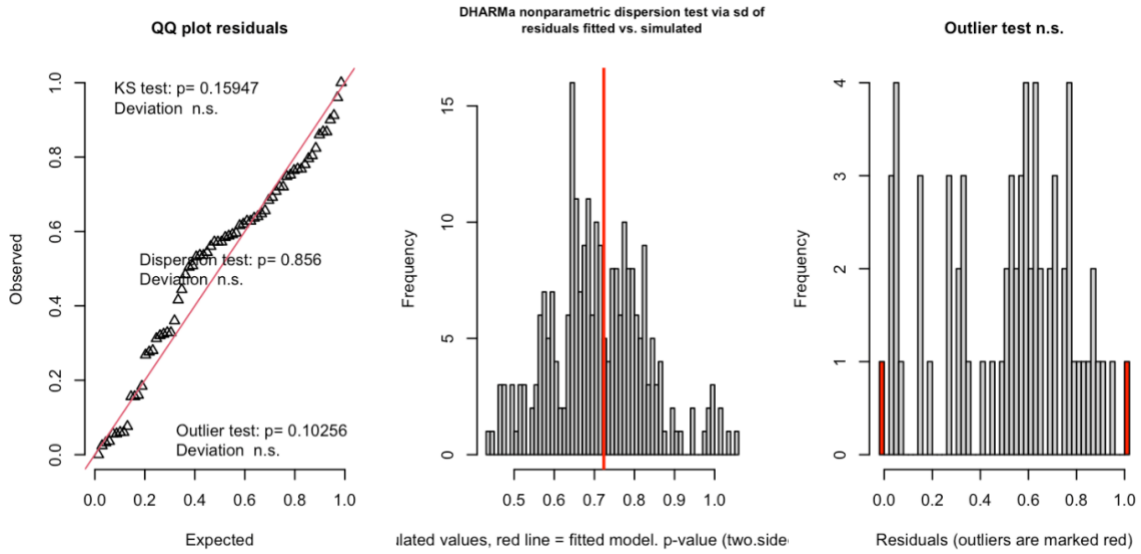

Figure S5.11: DHARMa package model diagnostics for agonistic milestone model, from left to right: a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.

Table S5.2: Model output for proximity model including the interaction between sex and residual play, * = an interaction term.

Term	**Estimate**	**SE / SD**	**p**
ID	Random intercept	0.693	
Milestone	Random intercept	0.0000136	
Intercept	0.207	0.235	0.378
Residual play	-0.0581	0.0245	**0.0176**
Sex	0.326	0.340	0.339
Residual play*sex	-0.0617	0.0374	0.098

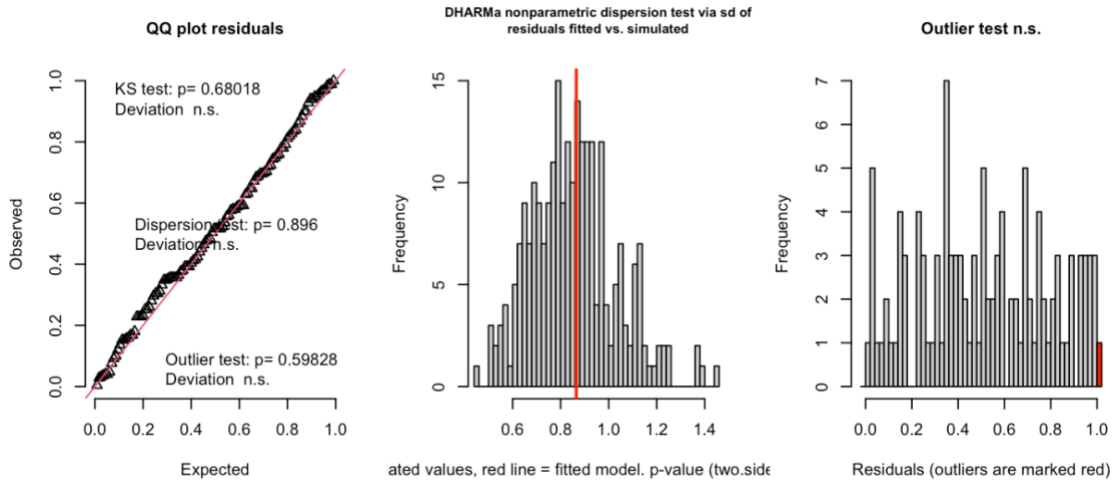

Figure S5.12: DHARMa package model diagnostics for proximity milestone model, without interaction between sex and play, from left to right: a) Quantile-Quantile plot b) plot of model dispersion, c) plot of model outliers.