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Comparison of Play Frequency in Four Sympatric Monkey Species in Kibale National Park,

Uganda

By

Sara Lucci

Submitted in partial fulfillment
of the requirements for the degree of
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Abstract

Play is thought to be a significant part of the early life history of primates, and different play behaviors could provide specific long-term benefits. Along with cataloging the types of play behaviors in primates, it is important to understand the adaptive significance not only of play in general but also specific types of play behavior. The Instinct-Practice Theory postulates that play allows an animal to practice instinctual behaviors necessary for survival in adulthood. Immature individuals of different species will therefore more often exhibit play behaviors that are relevant to the species-specific skills they will need as adults. An offshoot of Instinct-Practice Theory, known as the Fighting Skills Hypothesis, states that rough-and-tumble play is used to practice and develop fighting skills used in adulthood. It is predicted that within a species, rough-and-tumble play will be more common in males because they engage in aggressive competition for resources and/or mates in adulthood. This study describes a repertoire of play behaviors in the observed activity budgets of four monkey species in Kibale National Park, Uganda from June to December 2018: red colobus (*Procolobus rufomitratu*s), grey-cheeked mangabeys (*Lophocebus albigena*), black-and-white colobus (*Colobus guereza*), and redbtail monkeys (*Cercopithecus ascanius*). Rough-and-tumble play was compared between males and females of each species to test the Fighting Skills Hypothesis. Overall, the proportion of solitary locomotor play was highest in red colobus, followed by black-and-white colobus, and grey-cheeked mangabeys. Redtail monkey solitary locomotor play was lowest among the species. These findings partially support the Instinct-Practice Theory, as solitary locomotor play may be important for developing motor skills and reducing risk of injury due to locomotion in the highly arboreal red colobus. Contrary to the Fighting Skills Hypothesis, there were no differences between male and female rough-and-tumble play in any species except for the redbtail monkeys. The Fighting Skills

Hypothesis therefore needs to be reevaluated in how it explains sex differences in rough-and-tumble play, and how these differences are adaptive to adult behavior.

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Introduction

Play is a behavior that, while perhaps most recognizable in humans and other mammals, has eluded a systematic definition. Animals such as birds, rats, and even fish have shown behaviors that scientists argue are playful, although current research shows that it undoubtedly occurs most often in mammals and primates, in particular. Behavior must meet five criteria to be considered “play” (Burghardt, 2005). The behavior must first be nonfunctional in its present context, which means that it does not have any immediately apparent reward. The behavior must also be voluntary, modified from functional behavior, repeated by the same individual, and present in healthy animals (Burghardt, 2005). Play, in primates, is often seen during infant and juvenile development, a period that is greatly extended in primates when compared to other mammals (Western, 1979). A long developmental period may provide several benefits, including time to learn new skills and develop relationships that will be important for adult survival and reproduction (Lynch, et al., 2017; Perry, 2011). Therefore, play may provide valuable insight into what primates must learn and practice in order to grow into successful adults.

There are three main types of play: social play, object play, and solitary locomotor play (Pellis, et al., 2015). Social play involves play with conspecifics, and can be further divided into play-fighting, parental play, and sexual play (Graham & Burghardt, 2010). Object play is play with an inanimate object such as a stone, and locomotor play involves solo body movements without an object or play partners (Nahallage, Leca, & Huffman, 2016; Pellis, et al., 2015). Animal play has been studied for decades, and there are many hypotheses for the importance of the different types of play in both short- and long-term survival of individuals (Graham & Burghardt, 2010). Play behaviors may be costly as they consume energy and can increase the

risk of disease transmission between play partners (Kuehl et al., 2008; Nunes et al., 1999). Therefore, they should provide benefits to players that offset the costs.

There are arrays of behaviors in animal repertoires that follow Burghardt's five requirements for play (Graham & Burghardt, 2010). However, the majority of these play behaviors may be fit into a few major categories of play that have dominated animal research over the past several decades (Burghardt, 2005).

Types of Play

The most popular classification of play behavior in the literature is that of the three categories mentioned above: social, object, and solitary locomotor play (Fagen, 1981). However, these categories may be further divided into more refined play behaviors and can also be combined into more sophisticated types of play (Pellis, et al., 2015). There are even more play behaviors that have been observed in human children, partly because researchers can communicate with them about what they are doing. While these play types, such as "rule play" seen in games and "sociodramatic play" seen in roleplay, are important to the play literature, this review will keep with the play behaviors most closely related to those observed seen in the subjects of this study (Power, 2000).

Solitary Locomotor Play

Solitary locomotor play, also called locomotor-rotational play, is simply play that involves the sustained performance of often exaggerated movements of one's own body, and can include leaping, running, and body twisting (Wilson & Kleiman, 1974). Like the term "play" itself, solitary locomotor play is a bit of a catch-all term, in that it is meant to describe all play not directed towards an object or other individual (Pellis, et al., 2015). However, it is important because it is usually one of the first types of play seen in young individuals, and also thought to

be one of the least cognitively complex types of play (Fagen, 1995). In the South American fur seal (*Arctocephalus australis*), for example, solitary swimming play was observed during the first week of life in pups (Harcourt, 1991). The main theory behind solitary locomotor play is that it aids in development of motor skills, possibly for antipredator behaviors (Harcourt, 1991; Power, 2000). One recent study showed that in Assamese macaques (*Macaca assamensis*), social and solitary locomotor play is related to earlier competence in motor skills such as jumping between branches at the expense of body growth (Berghänel, Schülke, & Ostner, 2015).

Object Play

Object play is the manipulation of an object such as a stick or rock using the hands, feet, or mouth (Power, 2000). It can be seen in both social and solitary play bouts and has been observed in multiple animal taxa (Delfour & Aulagnier, 1997; Graham & Burghardt, 2010; McCowan, Marino, Vance, Walke, & Reiss, 2000). Although object play has the general definition given above, it has been tricky for scientists to define how object play relates to object exploration seen in young animals and tool use seen in various species. For example, it has been suggested that exploratory behavior should be defined as a young animal collecting information about an object, while object play appears in when animals play with objects with which they are already familiar (Bjorklund & Gardiner, 2012). However, these behaviors may be important to one another, as research has indicated that object play may be a precursor to tool use in cognitively competent animals (Graham & Burghardt, 2010). Chimpanzees (*Pan troglodytes*), for example, show some of the highest frequencies of object play, as well as some of the most extensive use of tools later in life (Bjorklund & Gardiner, 2012). Object play is also important to study because of its possible links behavioral traditions in certain primate lineages. The “stone handling” behaviors found in Japanese macaques (*Macaca fuscata*) meet the requirements to be

considered object play and are thought to help develop motor skills in immature individuals. They began in one group member and then picked up by close relatives and peers until it was also learned by younger individuals and is continued to be observed today (Nahallage, Leca, & Huffman, 2016).

Rough-and-Tumble Play

Rough-and-tumble play is one of the most intensely studied play behaviors across primates and other animals. It is observed as play-wrestling or play-chasing between conspecifics and includes such behaviors as grabbing, hitting, and biting (Pellis & Pellis, 1998). Rough-and-tumble play is thought to be more complex and difficult to perform than other types of play because it requires particular signals to communicate to play partners that the behaviors are playful and not meant to be aggressive. These behaviors are also important in helping researchers differentiate playful from aggressive interactions. They can include body postures, such as the “play bow” in dogs, vocalizations, and the facial expression known as the “play face,” which has been documented in several primate species (Palagi et al., 2016). There have been many theories on the specific benefits of rough-and-tumble play may have for present and future survival. Most have centered around social benefits, such as the finding that social play in Japanese macaques correlates with future social relationships, indicating that social play may help to reinforce social bonds (Shimada & Sueur, 2017). Rough-and-tumble play is also an important avenue for understanding differences in behavior between male and female conspecifics, and how it might relate to their fitness. In gelada monkeys (*Theropithecus gelada*) adult males must disperse from their natal groups and fight other males for mating opportunities with females, while adult females remain in their natal groups. It has been found that immature male geladas will play more frequently than females and with more play partners, while females

will stop playing earlier in their development to groom and maintain social relationships within their natal group. These behaviors would allow males to practice their fighting skills through rough-and-tumble play, while females are investing in social relationships that will continue to be valuable to them in the future (Barale, et al., 2015).

Sexual Play

Sexual play includes such precocial sexual behaviors as mounting, thrusting, and sniffing (Owens, 1976). It is because of this resemblance to actual sexual behavior that researchers have suggested that it is used by juvenile animals as a kind of substitute for sex since they are often unable to compete for fertile, adult females (Graham & Burghardt, 2010). This hypothesis has been somewhat confirmed by research on red deer calves (*Cervus elaphus*), but it was also shown to be present in other interactions, such as mounting the mother to gain her attention to nurse (Vaňková & Bartoš, 2002). In baboons (*Papio anubis*), researchers have observed that sexual play is closely associated with rough-and-tumble play and appears to serve other functions, such as greeting a conspecific, in addition to practicing successful mounting behaviors (Owens, 1976).

Parental Play

Parental play, or play-mothering, is observed when an immature individual holds or carries the infant of a conspecific mother (Lancaster, 1971). It is used synonymously with allomothering, although parental play appears to refer to when the caretaker is an immature individual (Kohda, 1985; Markus & Croft, 1995). It is thought that parental play, specifically for female juveniles, allows them to practice the parenting skills they will need when they have their own offspring (Lancaster, 1971). Evidence for this hypothesis was found in vervet monkeys (*Cercopithecus aethiops sabaesus*), where female juveniles that spent more time caring for the

infants of older females were more likely to successfully raise infants as adults (Fairbanks, 1990).

Play in Different Animal Clades

Primates show some of the most complex play behaviors in the animal kingdom. Although only five phyla of animals display play behaviors, it has been observed in a diverse array of species and studying it in these different species is important for understanding how it evolved and the conditions under which it is most likely to appear (Burghardt, 2005).

Reptiles, Birds, and Mammals

Although this paper focuses on play behaviors in primates, play in other animals such as birds, reptiles, and non-primate mammals is worth discussing because they can help demonstrate the base requirements for play. Unfortunately, of the relatively few observations of proposed play behaviors in reptiles such as lizards and snakes, most are anecdotal or involve a very limited sample size. However, there are a few studies on behaviors that may qualify as play (Dinets, 2015; Roggenbuck & Jenssen, 1985). The fence lizard (*Sceloporus undulates*) has well-documented head-bobbing patterns in adults that appear to be used in both courtship and aggressive territorial defense. In a study of hatchlings, young fence lizards were able to display these head-bobbing behaviors within their second day of life. However, the hatchlings do not appear to use these displays in the context of territorial defense or courtship, indicating that their head-bobbing in a social context is a form of social play (Roggenbuck & Jenssen, 1985).

Fortunately, there are far more documented examples of play behavior in birds. As endotherms with parental care and complex behavioral systems such as song-learning, birds show many different types of play including locomotor, object, and social play (Heinrich & Smolker, 1998; Kilham, 1974; Pandolfi, 1996). One of the most extensively studied bird species

in terms of play is the kea (*Nestor notabilis*). Keas display rough-and-tumble play bouts that often last several minutes. These play bouts display characteristic pushing with feet, locking bills, and rolling on top of one another, as well as vocalizations that are unique to these interactions. Keas will also display object play with various objects such as sticks and stones (Diamond & Bond, 1999).

As mentioned above, various types of play behavior have been observed in non-primate mammals, such as solitary locomotor play in fur seals and sexual play in red deer (Harcourt, 1991; Vaňková & Bartoš, 2002). Sexual play and play wrestling have been examined in Richardson's ground squirrels (*Spermophilus richardsonii*), and object play with various types of objects has been observed in both captive and wild bottlenose dolphins (*Tursiops truncatus*) (Burghardt, 2005; McCowan, Marino, Vance, Walke, & Reiss, 2000). The rat (*Rattus norvegicus*), however, is the non-primate mammal with the most extensively studied play behaviors. Rats are an ideal model organism for play behavior because they naturally display multiple types of both simple and complex play, and they are able to be manipulated and experimentally observed in the lab (Pellis & Pellis, 2009). Locomotor-rotational movements have been meticulously described in rats, including forward jumping, and the "jerk" which is a jump with a rotation in body orientation. They occur in succession as solitary locomotor play, or as a response to conspecifics in social play (Pellis & Pellis, 1983). Their rough-and-tumble play is also well-described, which occurs early in life and continues into adulthood. The apparent "target" in play-wrestling is the nape of their opponent's neck, with role-reversals of attacker and defender within a play bout. Rats also show sex differences in play-wrestling, with the defensive tactics of females differentiating markedly from males near puberty. This type of social play also

appears to be important in rats, because elimination of social play in this early period has been correlated with social and behavioral issues later in life (Pellis & Pellis, 2009).

Primates

Primates are an ideal taxon to study comparative play behavior because play of some kind has been recorded in every species for which data are available (Burghardt, 2005). Despite this trove of data, there have been few systematic examinations of play types and frequencies as they are related to primate phylogeny. These studies often focus on adult play behavior, play in one or two species, and play in captive animals (Lewis, 2000; Nahallage & Huffman, 2008; O'Meara, Graham, Pellis, & Burghardt, 2015; Pellis & Iwaniuk, 2000). Through collecting and synthesizing existing data, we may begin to understand the life history traits in primates that correlate to certain play behaviors.

Strepsirrhines

The strepsirrhines are all species of lemurs in Madagascar, galagos, and lorises (Fleagle, 2013). There are few studies on play in lorises and galagos, and most of the studies that do exist are taken from individuals in captivity. However, lorises and galagos have been shown to engage in social play. Captive Malaysian slow lorises (*Nycticebus coucang*) have been shown to engage in social play in adults of both sexes and infants (Ehrlich & Musicant, 1977). In greater galagos (*Galago crassicaudatus*), infants engage in social play with the mother as early as 5 weeks old (Ehrlich, 1974). Wrestling and solitary locomotor play have also been documented in Senegal galagos (*Galago senegalensis braccatus*), where female immature galagos were observed performing more solitary locomotor play than males, but both sexes showed similar frequencies of play-wrestling (Nash, 2003).

There are data from captive lemurs available. Social play in immature ring-tailed lemurs (*Lemur catta*) is categorized by rough-and-tumble play. Interestingly, there was no difference found in either study in the frequency of social play between males and females. This lack of difference may be attributed to their female-dominated social structure, in which adult females must also act aggressively to defend territory, while adult males are aggressive to procure mates (Fagen, 2002; Gould, 1990). Black-and-white ruffed lemurs (*Varecia variegata variegata*) also engage in rough-and-tumble and solitary locomotor play, although rough-and-tumble play was observed in individuals of all ages, while only young individuals appeared to engage in solitary locomotor play (Pereira, Seeligson, & Macedonia, 1988). Rough-and-tumble play has also been examined in detail in gray mouse lemurs (*Microcebus murinus*) and appears to simulate aggressive adult behaviors as well as adult grooming and sexual behaviors. Therefore, it may serve as preparation for more than one type of adult behavior in these lemurs (Pellis & Pellis, 2018).

Platyrrhines

The platyrrhine clade is made up of all nonhuman primates within Central and South America, including howler monkeys, woolly monkeys, spider monkeys, marmosets, and tamarins (Fleagle, 2013). Play studies on the platyrrhines are far more common and include both wild and captive populations. Wild black and gold howler monkeys (*Alouatta caraya*) engage in rough-and-tumble play during intergroup encounters, and the most frequent participants in these play bouts were mixed-sex and male-only juveniles. The authors explain that these playful encounters may be important for gaining the social and motor skills needed to engage in these intergroup encounters as adults, particularly because males tend to play a more active role in these encounters as adults (Gennuso, Brividor, Pavé, Raño, & Kowalewski, 2018). Rough-and-

tumble play has been observed in all age and sex classes of woolly monkeys (*Lagothrix lagothricha*) except for newborns and adult males, while immature individuals have also been observed in solitary locomotor and object play (Kavanagh & Dresdale, 1975). In spider monkeys, juvenile black-handed spider monkeys (*Ateles geoffroyi*) exhibit an intriguing “head-shaking” behavior as a form solitary locomotor play, and brown spider monkeys (*Ateles hybridus*) have been recorded engaging in social play (Pellis & Pellis, 2011; Rimbach et al., 2015). Quite a few studies have also examined play in capuchins. Immature tufted capuchin monkeys (*Cebus apella*) display solitary locomotor, object, and rough-and-tumble play, but males engage in more rough-and-tumble play than females (Paukner & Suomi, 2008). White-faced capuchins (*Cebus capucinus*) also engage in rough-and-tumble play, as well as dyadic “games” that are gentler than rough-and-tumble play and appear to be learned traditions within certain groups (Perry et al., 2003).

Cercopithecines

The cercopithecines are a subfamily within the Old-World monkeys characterized by cheek pouches and low cusps on bilophodont molars (Fleagle, 2013). Studies on cercopithecines also make up a huge portion of the primate play literature. Play behavior in macaques in particular has been intensively studied. A review of play behavior in several species of macaques found important differences between different species, such as play existing between adult males and immatures in bonnet (*Macaca radiata*) and Japanese macaques (*Macaca fuscata*). Play between adults and immatures only happened rarely in the other macaque species. However, the authors state that across the studies, male macaques appeared to play more frequently than females (Caine & Mitchell, 1979). Since then, more direct comparisons between macaque species have been made, such as the finding that rough-and-tumble play in immature Tonkean

macaques (*Macaca tonkeana*) is more opportunistic, with a greater frequency of multiple partners playing at once in a cooperative manner. In contrast, Japanese macaques were found to engage in more directly competitive play between a pair of immatures. These differences are thought to reflect differences in their social organizations, where Japanese macaques form strict hierarchies and Tonkean macaques are more egalitarian (Reinhart et al., 2010).

Hamadryas baboons (*Papio hamadryas*), gelada monkeys (*Theropithecus gelada*), and olive baboons have all been observed in social play. In olive baboons, multiple studies have found a greater frequency of play-wrestling in immature males than females (Chalmers, 1980; Owens, 1975). This result was also found in geladas, where females tend to stop playing earlier in life and males were found to engage more frequently in rough-and-tumble play with a greater number of partners than females. These differences are thought to express different fitness strategies between males and females as adults, where males must leave their natal group and challenge other males for access to mates, while females remain in their natal group (Barale, Rubenstein, & Beehner, 2015)

Colobines

The colobines are the other subfamily within Old-World monkeys. They include colobus monkeys and langurs, and are characterized by their large, complex digestive systems (Fleagle, 2013). There are fewer studies for colobines than cercopithecines, but the studies available do cover a wide swath of the clade across its members in Africa and Asia. Male Hanuman langurs (*Semnopithecus entellus*) engage in more rough-and-tumble play than females (Meaney, Stewart, & Beatty, 1985). Black and white colobus (*Colobus guereza*) participate in both solitary and social play, where infants, juveniles, and subadults all participate in rough-and-tumble play. Non-sexual mounting, which appears to be sexual play, has also been recorded in adults,

subadults, and juveniles (Oates, 1977). Temminck's red colobus monkeys (*Procolobus badius temminckii*) engage in both social and solitary object play. Objects such as termite mound pieces, dead branches, and large leaves would be mouthed, rolled, swatted, or thrown. Interestingly, females showed a greater frequency of solitary object play than males. In social object play, objects would be incorporated into rough-and-tumble play to hit with or keep away from other players (Starin, 1990). Ugandan red colobus (*Procolobus rufomitratu*s) have also been observed engaging in solitary locomotor, object, and rough-and-tumble play. There did not appear to be a difference between immature males and females in frequency of rough-and-tumble play (Worch, 2010).

Non-human Apes

The non-human apes include both hylobatids, such as gibbons and siamangs, and the hominids, which include chimpanzees, bonobos, gorillas, and orangutans (Fleagle, 2013). Wild white-handed gibbons (*Hylobates lar*) have been observed engaging in social play, although adults only seemed to play when the partner was an immature individual (Brockelman, Reichard, Treesucon, & Raemaekers, 1998). Captive western lowland gorillas (*Gorilla gorilla gorilla*) engage in object and social play (Tanner & Byrne, 2010). Infant gorillas also choose play partners in ways that are consistent with adult social bonds, in that both males and females prefer to play with males (Maestriperi & Ross, 2004). Bornean orangutans (*Pongo pygmaeus wurmbii*) will engage in rough-and-tumble play in particular circumstances, such as in the offspring of related females when they occupy the same feeding patch. This type of social play has also been observed in unflanged Bornean orangutans, although it is rarer (van Noordwijk et al., 2012). Several studies have also investigated the differences in play between chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). Both members of the *Pan* genus engage in social,

solitary, and object play. However, key differences have been found in how these play behaviors are expressed. For example, it has been found that bonobos engage in object play well into adulthood, while adult chimpanzees do not display this type of play and reserve any interaction with objects for functional tool use. Interestingly, immature bonobo females also have a higher frequency of object play than males, although the evolutionary significance for this difference is not clear (Gruber, Clay, & Zuberbühler, 2010). This same pattern of differential age distribution of play behaviors has also been found in solitary play and social play. Other important differences have been found in social play behaviors of chimpanzees and bonobos, such as the rough-and-tumble play bouts of bonobos transitioning into aggressive fighting less frequently than chimpanzees, which highlights a greater tolerance to conspecifics in bonobos than chimpanzees (Palagi & Cordoni, 2012).

Evolutionary Theories for Play

Due to the relatively high frequency of play in infant and juvenile individuals, most of the earliest hypotheses dealt with the long-term benefits of play and its importance in development to survival as an adult (Graham & Burghardt, 2010). There are, however, quite a few other theories that have emerged in the literature, including those that only apply to certain types of play or play in certain animal species (Burghardt, 2005). This section will review major theories of play that have been suggested over the years, including the results of both primate and non-primate studies that have tested them.

Surplus Energy Theory

Surplus Energy Theory, one of the earliest modern theories on the evolution of play behavior, suggests that play occurs in species with adequate food resources and a complex behavioral repertoire. The play behaviors that occur are also a reflection of the behaviors needed

in survival as adults and is therefore beneficial as a form of practice. This theory has been mainly examined in the context of habitat quality, because it stipulates that play is ultimately not a necessary behavior but appears given enough food (Spencer, 1872). Several studies have found that play frequency appears to decrease as habitat conditions worsen. Play frequency and play bout duration in Hanuman langurs were found to be significantly greater in a population with a greater proportion of fruit in its diet and better access to water than a population with a lower-quality habitat (Sommer & Mendoza-Granados, 1995). Similar results have been found in squirrel monkeys (*Saimiri oerstedii*) and Belding's ground squirrels (*Spermophilus beldingi*) (Baldwin & Baldwin, 1974; Nunes, Muecke, Anthony, & Batterbeet, 1999). Differential energy intake has also been suggested as an explanation for play frequency differences in male and female baboons, although there has been no supporting evidence based on empirical data (Altmann, 1991; Fagen, 2002). However, recent evidence indicates that play behavior occurs at the cost of physical development, so play behaviors are using up energy that could otherwise be allocated to growth, rather than surplus energy (Berghänel, Schülke, & Ostner, 2015). Therefore, there is evidence that play is important regardless of energy intake.

Instinct-Practice Theory

The Instinct-Practice Theory states clearly what had only been suggested in Surplus Energy Theory: that play originates in behaviors that are instinctual to an animal but is necessary to practice and refine these behaviors so that they may be used to their full effectiveness in adulthood. In this way, play is non-functional in the present but nevertheless important for future survival and reproduction (Groos, 1898). For this theory there can be found many supportive studies, including the above study that refutes the Surplus Energy Theory. Greater frequency of both social play and solitary locomotor play was found to correlate with an earlier acquisition of

motor skills such as jumping in between branches or running both on the ground and in trees (Berghänel, Schülke, & Ostner, 2015). This theory may also explain the presence of parental play in female vervet monkeys as well as stone-handling in young Japanese macaques (Fairbanks, 1990; Nahallage, Leca, & Huffman, 2016). This theory is reflected in the “Fighting Skills Hypothesis” which states that rough-and-tumble play may be used to practice fighting behaviors that will be necessary as an adult, so that an increased amount of rough-and-tumble play as an immature individual may be correlated with better fighting ability in adulthood (Smith, 1982). Conclusions for this hypothesis have been mixed, where it has been supported in some species (gelada baboons, Western lowland gorillas) but not others (red colobus monkeys, meerkats (*Suricata suricatta*)) (Barale, Rubenstein, & Beehner, 2015; Maestriperi & Ross, 2004; Sharpe, 2005; Worch, 2010). In addition, the Instinct-Practice theory is rather insufficient for all types of play behavior. For example, it cannot adequately explain play behavior in adults, which is extensive among primates and may have important immediate benefits (Pellis & Iwaniuk, 2000).

Socialization Theory

The Socialization Theory predicts that play may be used for learning proper social skills such as cooperation as well as navigating relationships within a hierarchy. In addition, play may be important at the group level in acting as a unifier (Carr, 1902). This theory obviously applies only to social play, but its implications for explaining both immediate and long-term benefits of play are worth discussing. Social play has been identified as an important component of maintaining affiliation networks in juvenile Japanese macaques (Shimada & Sueur, 2017). In addition, the outcomes of rough-and-tumble play bouts in immature yellow-bellied marmots (*Marmota flaviventris*) were found to correlate with later social hierarchy positions as adults

(Blumstein, Chung, & Smith, 2013). Although this study did not examine differences between males and females, it also supports the Fighting Skills Hypothesis, and thus Instinct-Practice Theory, since adult dominance hierarchies are decided in agonistic interactions, and the outcomes of these interactions are predicted by rough-and-tumble bout outcomes in younger individuals (Blumstein, Chung, & Smith, 2013). Therefore, social play may be beneficial in that it maintains social relationships and predicts social hierarchies. However, this theory may also explain observed short-term behaviors related to social play. In captive chimpanzees, it was found that the highest frequency of social play in adults and unrelated juveniles and infants occurred before the designated feeding time. It is suggested that social play, along with grooming, is used by this group as a means of decreasing tension and managing excitement before feeding (Palagi, Cordoni, & Tarli, 2004). Although it cannot account for other types of play such as solitary locomotor or solitary object play, the Socialization Theory may help explain both immediate and delayed benefits of social play.

Training for the Unexpected

The theory of Training for the Unexpected is the most recent of the theories in this review to be proposed. It states that play, like the Instinct-Practice theory, is used as training for future events. However, instead of directly training behaviors that will be useful in the future, the Training for the Unexpected theory hypothesizes that play allows the individual to purposefully put themselves in a sudden and stressful situation in order to learn how to cope both physically and mentally with unexpected situations in the future. Along with this theory are quite a few predictions for play that have mixed amounts of support from other studies. One prediction, for example, is that play should occur more frequently in juveniles than infants, because infants lack the capabilities to purposefully self-handicap themselves and place themselves in unexpected

situations (Špinka, Newberry, & Bekoff, 2001). However, Barale, Rubenstein, & Beehner, 2015 found that social play rate in geladas decreases from 0 to 6 years in males and females (Barale, Rubenstein, & Beehner, 2015). In addition, play-fighting rate has been found to negatively correlate with age in chimpanzees, but not bonobos (Palagi & Cordoni, 2012).

Despite these issues, Training for the Unexpected still appears to be the most well-supported theory on play behavior. It incorporates the more favorable features of other major play theories while still being flexible enough to avoid their pitfalls. Like the Surplus Energy Theory, it predicts that stress caused by environmental factors such as lack of food will result in a decrease in play. However, it does not stipulate that this is due to the use of only surplus energy for play, but rather indicates that suppression of play is caused by negative emotions (Spencer, 1872; Špinka, Newberry, & Bekoff, 2001). Like Instinct-Practice Theory, it provides an evolutionary explanation for certain types of play and their use for improving certain skills (Groos, 1898). However, it also explains the importance of play-specific behaviors not found in the adult counterparts. The evidence of self-handicapping is the main example, as it is used in play when an individual deliberately does not use their full strength or motor controls (Lutz & Judge, 2017). Self-handicapping allows the individual to purposefully put themselves in a physically awkward situation that allows them to develop coping mechanisms for future awkward situations, which is the main hypothesis of Training for the Unexpected (Lutz & Judge, 2017). The Fighting Skills Hypothesis cannot account for self-handicapping, because the immature individuals should be practicing their fighting skills as close to how they will use them in adulthood as possible (Smith, 1982). Therefore, Training for the Unexpected appears to be best supported by current evidence.

Diversity and Play Theories

Most of the studies cited in support of the above theories for play involve species with particular similarities: they are often group-living mammals (usually primates) with complex behavioral repertoires (Baldwin & Baldwin, 1974; Berghänel, Schülke, & Ostner, 2015; Blumstein, Chung, & Smith, 2013; Lutz & Judge, 2017; Palagi, Cordoni, & Tarli, 2004). However, studies on play in other animals, while less common, indicate that play may be found in species that do not fit this general pattern (Roggenbuck & Jenssen, 1985). Because these play theories attempt to explain the evolutionary value of play in animals, it is therefore important to evaluate them in the context of all animals, not just the ones in which play is most easily recognized.

In his explanation of the Surplus Energy Hypothesis, Herbert Spencer contends that play is present in “superior” animals, those that have an efficient digestive system and complex behavior repertoire that allow them to gain more energy from their diet than is needed to sustain necessary behaviors (Spencer, 1872). Thus, the excess energy is expended in play. These predictions may explain why play is seen more often in certain clades than others. Digestion is energetically costly in reptiles, for example, thus leaving little energy after feeding for extraneous activity (Wang, Busk, & Overgaard, 2001). Reptiles also have relatively smaller brains that do not allow for the complex behavioral repertoires found in mammals (Jerison, 1985). Therefore, Spencer’s prediction of play appearing in animals with efficient digestion and complex behaviors appears to be correct (Spencer, 1872). However, his theory begins to break down when examined within clades of playful animals in terms of play frequency and certain behaviors within play. A study on play in Kibale primates found that guenons with more energy-rich diets did not play more than colobus monkeys, which have relatively energy-poor diets

(Worch, 1998). In addition, Spencer's theory that play behaviors mimic adult behaviors as a means of practice does not explain self-handicapping (Lutz & Judge, 2017; Spencer, 1872).

The Instinct-Practice Theory does not examine play from the perspective of available energy, but rather from the perspective of life history. It points specifically to the period of infancy and adolescence, during which instinct compels an animal to play using behaviors they will require in adulthood (Groos, 1898). This theory also may explain why play is more present in certain clades than others. The theory assumes that an immature animal is not as proficient in survival behaviors as an adult, which is why this time period is required to learn and practice these behaviors (Groos, 1898). Many reptiles and fish are characterized as having little parental care and born already able to perform behaviors needed for adult survival, so they do not have the safety provided by parents in order to play, nor do they necessarily require it (Burghardt, 1988; Reynolds, Goodwin, & Freckleton, 2002). In contrast, parental care is more common in birds and mammals, which may explain why play is more prevalent in these clades (Farmer, 2000). Despite this support, the Instinct-Practice Theory, like the Surplus Energy Theory, fails to account for particular play phenomenon. It cannot account for play that occurs outside of immaturity, which is common among primates (Groos, 1898). It also does not explain how play may be immediately beneficial to immature animals (Groos, 1898). Socialization Theory is similarly constrictive, in that it cannot account for play in solitary animals, as well as non-social play behaviors in social species (Carr, 1902).

The Training for the Unexpected Theory is more flexible in its application among animal clades. The theory only makes one prediction regarding play among animal species, that play is related to higher encephalization quotients because of its complexity (Špinka, Newberry, & Bekoff, 2001). This prediction has been tested in mammals, where a study found that play

increases in frequency with increasing encephalization quotient (Iwaniuk, Nelson, & Pellis, 2001). However, this pattern only works when examining orders within mammals, and broke down when examining play within orders and families (Iwaniuk, Nelson, & Pellis, 2001). Although Training for the Unexpected cannot account for all phylogenetic patterns of play, it can help explain many more play behaviors than Surplus Energy or Instinct-Practice. Adult play does not refute the theory, because social play can help an adult continue to train for unexpected situations with another adults (Antonacci, Norscia, & Palagi, 2010; O'Meara et al., 2015; Špinka, Newberry, & Bekoff, 2001). It also accounts for immediate benefits of play, because increased motor skills are likely to be more immediately helpful as the body will continue to change as it grows (Špinka, Newberry, & Bekoff, 2001).

Ecology of the Four Study Species in Kibale, Uganda

Play behavior was examined in four monkey species in Kibale National Park, Uganda: the red colobus (*Procolobus rufomitratu*s), redbelt monkey (*Cercopithecus ascanius*), grey-cheeked mangabey (*Lophocebus albigena*), and black-and-white colobus (*Colobus guereza*). The red colobus monkeys are mainly folivorous primates, spending 75.5-86.9% of their feeding time consuming leaves, but they also eat fruit and flowers (Chapman & Chapman, 2000). Previous research on red colobus activity budgets found that they spend most of their time feeding (41.0%) and resting (32.4%), and also socialize through grooming (4.5%) (Struhsaker, 1980). They can live in groups with 3-85 individuals, with 50 being the average (Struhsaker, 1980). These groups are usually multi-male/multi-female with females dispersing from their natal group more often than males (Struhsaker, 2010). These red colobus groups are also known to have strict social hierarchies and particularly aggressive males (Struhsaker, 2010; Worch, 2010). In addition, males appear to be more involved in intergroup encounters, which usually involve

chasing and display behaviors (Struhsaker, 1980). Redtail monkeys, in contrast, spend most of their feeding time consuming insects, but also consume fruit and young leaves (Chapman & Chapman, 2000). Most of their activity budget is devoted to feeding (33.5%), with less time spent resting than red colobus (10.1%). However, they do spend a significant amount of time climbing (17.4%) and scanning their environment (20.5%). These behaviors are important for acquiring the arthropods and fruits on which they feed. Grooming is also present in their activity budget (5.6%) (Struhsaker, 1980). Redtail monkeys also tend to live in smaller groups of about 20-25 individuals, in one-male-units or multi-male/multi-female groups with a far less obvious hierarchy and less social cohesion than red colobus (Cords, 1984; Struhsaker, 1980; Worch, 2002). Males are generally not tolerant of one another, but females have also been observed chasing away males on the periphery of their groups, and both males and females will participate in the defense of their territory during intergroup encounters (Cords, 1984; Struhsaker, 1980).

Grey-cheeked mangabeys are mainly frugivorous and spend about 60% of their feeding time consuming fruit, which has been shown to produce contest competition, especially among females (Olupot, Chapman, Waser, & Isabirye-Basuta, 1997; Chancellor & Isbell, 2009). They spend approximately 40% of their day feeding on plants and about 13% searching for insects. They also spend about 27% of their day traveling, and only about 7% of their day in social behaviors (Poulsen, Clark, & Smith, 2001). Related females stay in their natal group and males disperse, with group sizes that can range from around 9 to 20 individuals (Arlet, Carey, & Molleman, 2009; Chancellor et al., 2011). Females have been shown to have clearly defined social hierarchies, but they appear to be mainly enforced by behaviors such as avoidance and supplants rather than physical aggression (Chancellor and Isbell, 2009). However, immigrant males are subjected to aggression by resident males when they attempt to transfer into a new

group (Olupot & Waser, 2001). Finally, black-and-white colobus mainly consume young leaves, but will also often consume mature leaves, fruits, and leaf buds (Oates, 1978). They spend between 22.9-28.3% of their time feeding, and about 63% of their time resting. They also spend between 5.6-6.7% of their time in social grooming (Fashing, 2001). They normally reside in smaller groups of 9 to 15 individuals, with an average of 11.4. These groups are highly cohesive and usually only contain one adult male, few subadults, and several adult females and their offspring. There are relatively few instances of aggression, and generally consist of supplanting behaviors. Ranges of different groups also commonly overlap, and these encounters may include aggressive behaviors. However, these behaviors are generally non-contact and include chasing or displays (Oates, 1977).

Play in Kibale Forest Monkeys

Play behaviors have been noted in each of the four species in this study, but the extent and detail to which they have been studied vary greatly among the species. An early study on red colobus showed that immature individuals spend 2.7% of their daily activity budget in play (Struhsaker, 1980). However, a later study found that immature red colobus spend almost one-third of their time playing, which is also significantly more time than has been recorded in other species (Worch, 2010). They engage in rough-and-tumble play, solitary locomotor play, and object play. However, males and females were found to engage in similar frequencies of rough-and-tumble play, which does not support the Fighting Skills hypothesis (Worch, 2010). Play behavior has also been examined in black-and-white colobus, where it has been observed in individuals as young as 5 weeks old. Immature individuals engage in rough-and-tumble play, usually during group rest periods (Oates, 1977). There are also no differences between immature males and females in frequencies of rough-and-tumble play, although this similarity has been

attributed to the stability of their social groups, rather than a refutation of the Fighting Skills hypothesis (Worch, 1998). Black-and-white colobus are also the only species in this study for which parental play has been noted and studied (Oates, 1977). There are considerably fewer studies on play in redbellied monkeys. It has been recorded to comprise 2.13 +/- 2.30% of the activity budget in immatures (Worch, 2004). However, details on types of play in this species have not yet been examined. Finally, there is virtually no previous research on play behaviors in immature grey-cheeked mangabeys. The only published data indicates that social play is present in adult members of this species (O'Meara et al., 2015).

Objective

The purpose of this study was to describe the play repertoires of immature individuals in four species of monkeys in Kibale National Park, Uganda. In addition, this study examined the differences in proportions of these play behaviors in the activity budgets of these species, and whether these differences might be attributed to the different sets of skills needed in adulthood for each species as part of the Instinct-Practice Theory. Finally, I investigated the difference between proportions of rough-and-tumble play between males and females within each species according to the Fighting Skills Hypothesis.

Hypotheses

According to the Instinct-Practice Theory, immature animals play to practice behaviors needed in adulthood. The four species in this study each have unique adult behavioral repertoires, therefore the following prediction can be made:

1. Different species will engage in different proportions of each play behavior: solitary locomotor play, object play, rough-and-tumble play, sexual play, and parental play.

The Fighting Skills Hypothesis states that animals use rough-and-tumble play as a means to practice the fighting behaviors that will be useful in adulthood. Depending on differences in physical aggression between sexes in a species, the following predictions may be made:

2. Red colobus and grey-cheeked mangabey males will engage in more rough-and-tumble play than females due to the greater amount of physical aggression observed in adult males than females of these species.
3. There will be no difference between males and females in rough-and-tumble play in black-and-white colobus and redbelt monkeys due to the similar amounts of physical aggression observed in adult males and females of these species.

Methods

Study Site

The study took place from June 2018 to December 2018 at Kibale National Park in Uganda near the Kanyawara Field Station. Kibale is 766 km,² located 0°13' to 0°41' N and 30°19' to 30°32' E and was formally established as a national park by the Ugandan government in 1993. It includes areas that were once heavily logged, lightly logged, and untouched by commercial logging (Chapman, Chapman, Wrangham, Isabirye-Bausta, & Ben-David, 1997; Chapman & Lambert, 2000). Kibale is characterized as a moist evergreen forest and shifts between montane forest and lowland rain forest (Chapman et al., 1997). It also has an average annual rainfall of 1778 mm, and an average temperature range of 15.5°C-23.7°C (Chapman & Chapman, 2000). The dry season in Kibale generally occurs in July-August and December-February, while the wet season occurs in March-June and September-November (Olupot, Chapman, Waser, & Isabirye-Basuta, 1997).

Study Groups

Immature monkeys from two groups of each species were studied. The groups under observation were the red colobus groups K14 and Mikana, the redbelt monkey groups Kyomuhendo and Sukaali, the grey-cheeked mangabey groups Lower Camp 1 and Lower Camp 2, and the black-and-white colobus groups Bwango and Batekaine.

Table 1: Demographic data for study groups of red colobus, grey-cheeked mangabeys, black-and-white colobus, and redbelt monkeys.

| Species | Group | Number of Infants | Number of Juveniles |
|---|--------------|-------------------|---------------------|
| Red Colobus (<i>Procolobus rufomitratus</i>) | K14 | 5 | 14 |
| | Mikana | 23 | |
| Grey-Cheeked Mangabey (<i>Lophocebus albigena</i>) | Lower Camp 1 | 7 | 3 |
| | Lower Camp 2 | 4 | 2 |
| Black-and-White Colobus (<i>Colobus guereza</i>) | Bwango | 3 | 2 |
| | Batekaine | 1 | 2 |
| Redbelt Monkey (<i>Cercopithecus ascanius</i>) | Kyomuhendo | 6 | 2 |
| | Sukaali | 4 | 7 |

Observation Days

Over the course of the study, focal follows were conducted for 100 days to collect behavioral data, including 24 days of observations for red colobus, 28 days for grey-cheeked mangabeys, 26 days for black-and-white colobus observations, and 22 days of observations for redbelt monkeys.

Data Collection

Each group was followed for a maximum of 18 days over the six-month period. The author and two experienced field assistants were involved in data collection during the first two months, after which the field assistants collected the data. Data were collected from approximately 8 am to 4 pm and taken using data sheets and pen. The data sheets were then transferred to an Excel spreadsheet. Focal observations were limited to older infants and juveniles that were distinguished from adults and each other based on relative body size and appearance of primary and secondary sexual characteristics (Deputte, 1992; Worch, 2002). Due

to the large number of individuals across the four species and eight groups, it was impossible to recognize individuals throughout the study. However, the field assistants used certain physical attributes in each species to distinguish infants from juveniles and males from females. Newborn and very young infants that were not observed engaging in independent locomotion were eliminated from analyses, as it was unknown if they were yet capable of the full range of play behaviors in the study, but older infants that were capable of independent locomotion were included. Individuals underwent a 20-minute continuous focal observation, and at the start, the individual's age and sex class, species and group were recorded (Altman, 1974). Sex was not identified for individuals during the first month of study, therefore the sample sizes examining differences in rough-and-tumble play between sexes are smaller than those of play behaviors among species. The main observer that day chose the individuals to follow, in order to prevent repeat sampling. In addition, the observer tried to choose an individual in a different age or sex class from the previous one. This also prevented repeat sampling and bias for a particular age or sex class at a particular time during the day.

Recorded play behaviors were divided into six major types: solitary locomotor play, object play, wrestling, chasing, sexual play, and parental play. Solitary locomotor play was defined as swinging, bouncing, or jumping on a branch repetitively. Object play was defined as manipulating an object while remaining seated or standing, and included tugging, waving, or mouthing an object (Starin, 1990). Wrestling was considered physical engagement with another individual, and included grabbing, hitting, biting, pushing, tumbling, and other movement patterns that are usually observed in aggressive fights (Barale et al., 2015; Palagi & Cordoni, 2012; Palagi et al., 2016). Play chasing was the quick and excited movement to follow another individual. Play wrestling and play chasing were differentiated from actual chasing and fighting

by a lack of observable aggression or fear behavior (Barale et al., 2015; Palagi & Cordoni, 2012). Sexual play was the engagement of sexual behavior with another individual, such as mounting, but not copulation. Finally, parental play was when an immature individual took an infant from its mother and held, cuddled, or carried it, behaviors that are usually only performed by the mother (Graham & Burghardt, 2010; Lancaster, 1971).

Table 2: Play behaviors and their definitions as used in the ethogram for red colobus, grey-cheeked mangabeys, black-and-white colobus, and redtail monkeys.

| Behavior | Definition |
|-------------------------|---|
| Solitary locomotor play | Swinging, jumping, or bounding on a branch by ones' self. |
| Object Play | Manipulating an object, such as tugging, mouthing, or picking it up. Can include branches or leaves still attached to the tree. |
| Play-wrestling | Physical engagement with another, such as grabbling, hitting, or tumbling in the trees or on the ground. |
| Play-chasing | Following or being followed at a fast pace by another individual, different from aggressive chasing. |
| Sexual Play | Mounting, sniffing, or other sexual behaviors without copulation. |
| Parental Play | Taking and carrying, cuddling, or holding an infant. The focal may be the actor or the (older) infant being taken. |

Analyses

Species Differences in Play

I first calculated descriptive statistics for each species for the proportion of each play behavior in the activity budget. To better interpret results, play-wrestling and play-chasing were combined into “rough-and-tumble play” in the following analyses. Activity budgets were calculated by dividing the amount of time a particular behavior was observed in the individuals of a species in one day by the amount of time individuals were observed for that day. Descriptive statistics were then calculated for the activity budget of each species. Since none of the species were observed over more than 30 days, nonparametric tests were used. To ascertain if the different species had different proportions of each play behavior, the Kruskal-Wallis Rank Sum test was used ($\alpha=0.05$). After the Kruskal-Wallis test, the post-hoc Dunn test with the Bonferroni adjustment for multiple comparisons was run to calculate pairwise comparisons of each play behavior between species ($\alpha=0.05$).

Sex Differences in Rough-and-Tumble Play

The next phase of analysis was to calculate the proportion of rough-and-tumble play in males and females. This calculation was done by first separating the males and females observed in each day and calculating separate activity budgets for rough-and-tumble play. The sum of time engaged in play-chasing or play-wrestling was divided by the total time each sex was observed for that day. These daily activity budgets for males and females for each species were then averaged and a Wilcoxon Rank Sum test was used to examine potential differences ($\alpha=0.05$).

Results

Hypothesis 1: Play Behaviors by Species

Each of the play behaviors in the ethogram were observed in all four species, except for parental play, which was not observed in red colobus or redbtail monkeys. The results only partially agreed with Prediction 1, as species differences were only significant for solitary locomotor play, sexual play, and parental play. Solitary locomotor play was observed in all four species, and the proportion of solitary locomotor play in the activity budget was different among the two colobus monkey species ($\chi^2 = 25.274$, $n_{RC} = 24$, $n_{MG} = 28$, $n_{BWC} = 26$, $n_{RT} = 22$, $p = 1.353 \times 10^{-5}$) (Figure 1; Table 2).

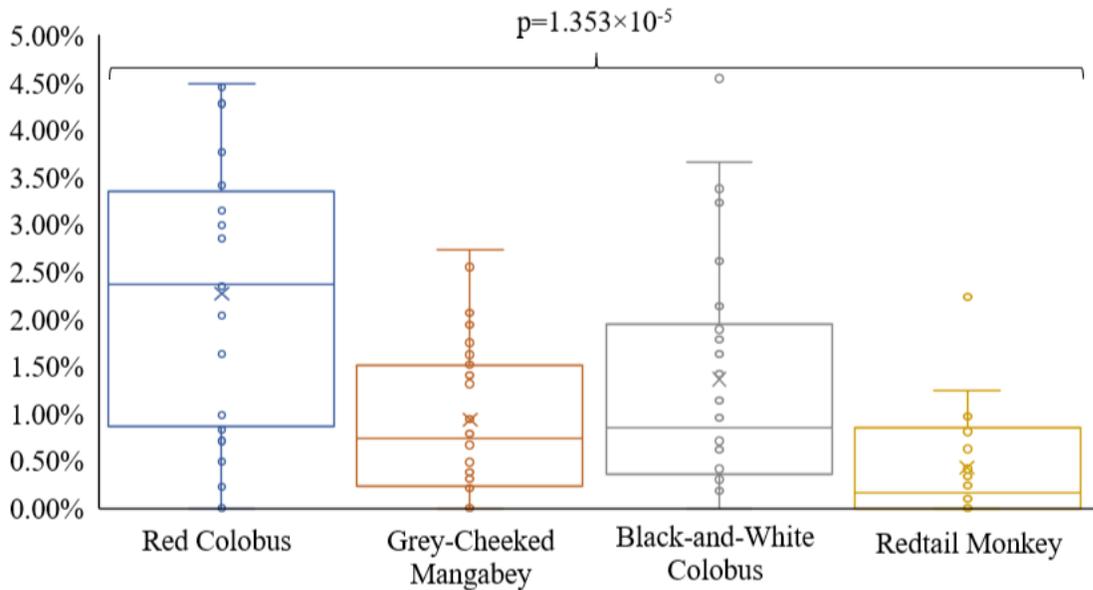


Figure 1: Distribution of solitary locomotor play within the daily activity budget of red colobus, grey-cheeked mangabeys, black-and-white colobus, and redbtail monkeys. Each circle represents the percent of solitary locomotor play in the activity budget for one day, the inner horizontal lines represent medians, the “x” indicates the means, and the boxes show inter-quartile range.

Table 3: Comparisons for percent of solitary locomotor play in activity budget between red colobus, grey-cheeked mangabeys, black-and-white colobus, and redbtail monkeys.

| Comparison | Z-score | p-value unadjusted | p-value with Bonferroni adjustment |
|------------|---------|--------------------|------------------------------------|
| BWC-MG | 1.12 | 0.261 | 1.000 |
| BWC-RC | -1.89 | 0.0590 | 0.354 |
| MG-RC | -3.02 | 0.00252 | 0.0150* |
| BWC-RT | 3.15 | 0.00164 | 0.00987* |
| MG-RT | 2.14 | 0.034 | 0.201 |

| | | | |
|-------|------|-------------|-------------|
| RC-RT | 4.90 | 0.000000957 | 0.00000574* |
|-------|------|-------------|-------------|

*Significant differences determined using Post-hoc Dunn test with Bonferroni adjustment. (RC=Red colobus, MG=grey-cheeked mangabeys, BWC=black-and-white colobus, RT=redtail monkeys).

Rough-and-tumble play occupied 2.14 +/- 2.04% of the activity budget of red colobus, 2.62 +/- 2.80% for grey-cheeked mangabeys, 2.31 +/- 2.78% in black-and-white colobus, and 1.53 +/- 1.71% in the activity budget for redtail monkeys with no differences among species ($\chi^2 = 2.6679$, $n_{RC} = 24$, $n_{MG} = 28$, $n_{BWC} = 26$, $n_{RT} = 22$, $p = n.s.$). Object play was observed less than solitary locomotor play and rough-and-tumble play, but was not different among species: 0.0236 +/- 0.0638% for red colobus, 0.107 +/- 0.274% for grey-cheeked mangabeys, 0.378 +/- 1.23% in black-and-white colobus, and 0.101 +/- 0.364% in redtail monkeys ($\chi^2 = 4.8911$, $n_{RC} = 24$, $n_{MG} = 28$, $n_{BWC} = 26$, $n_{RT} = 22$, $p = n.s.$).

Sexual play was also observed to a lesser extent than solitary locomotor play or rough-and-tumble play, but the differences among species were significant ($\chi^2 = 10.632$, $n_{RC} = 24$, $n_{MG} = 28$, $n_{BWC} = 26$, $n_{RT} = 22$, $p = 0.01389$) (Figure 2). The post-hoc Dunn test showed that differences were significant mainly due to the redtail monkeys (Table 3).

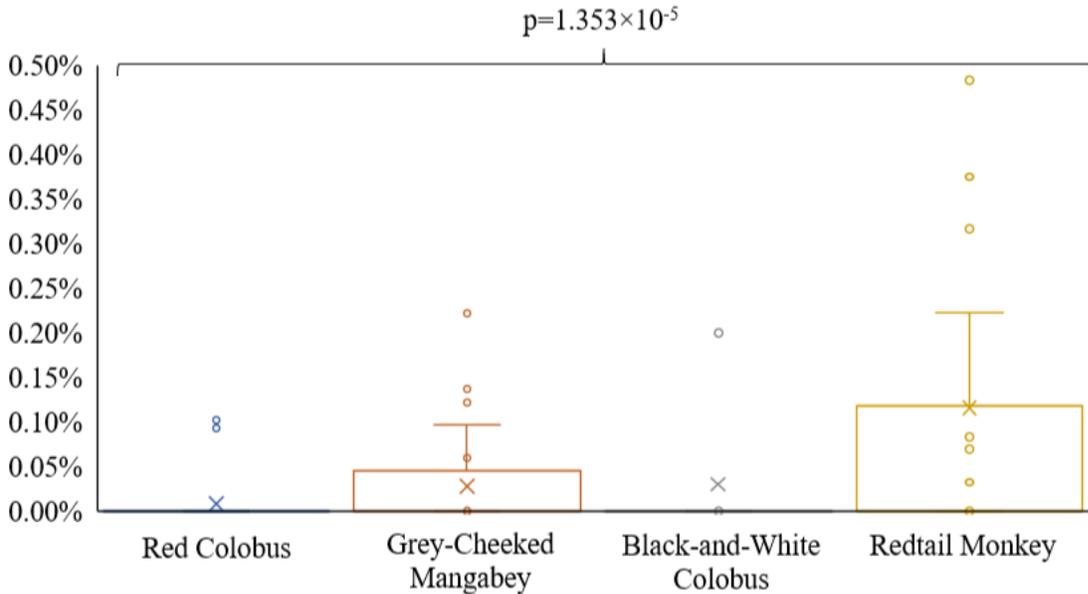


Figure 2: Distribution of sexual play within the daily activity budget of red colobus, grey-cheeked mangabeys, black-and-white colobus, and redbtail monkeys. Each circle represents the percent of sexual play in the activity budget for one day, the inner horizontal lines represent medians, the “x” indicates the means, and the boxes show inter-quartile range.

Table 4: Comparisons for percent of sexual play in activity budget between red colobus, grey-cheeked mangabeys, black-and-white colobus, and redbtail monkeys.

| Comparison | Z-score | p-value unadjusted | p-value with Bonferroni adjustment |
|------------|---------|--------------------|------------------------------------|
| BWC-MG | -1.39 | 0.163 | 0.980 |
| BWC-RC | 0.0397 | 0.968 | 1.00 |
| MG-RC | 1.41 | 0.160 | 0.960 |
| BWC-RT | -2.81 | 0.00494 | 0.0296* |
| MG-RT | -1.53 | 0.127 | 0.763 |
| RC-RT | -2.80 | 0.00516 | 0.0310 |

*Significant differences determined using Post-hoc Dunn test with Bonferroni adjustment. (RC=Red colobus, MG=grey-cheeked mangabeys, BWC=black-and-white colobus, RT=redtail monkeys).

Finally, while parental play was not observed in red colobus and redbtail monkeys, it was observed in grey-cheeked mangabeys (0.0256 +/- 0.126%) and black-and-white colobus (0.0751 +/- 0.0227%) and was significantly different among species ($\chi^2 = 9.3644$, $n_{RC} = 24$, $n_{MG} = 28$, $n_{BWC} = 26$, $n_{RT} = 22$, $p = 0.02482$). The Dunn test showed several pairwise differences that contributed to the differences among the four species (Table 4).

Table 5: Comparisons for percent of parental play in activity budget between red colobus, grey-cheeked mangabeys, black-and-white colobus, and redtail monkeys

| Comparison | Z-score | p-value unadjusted | p-value with Bonferroni adjustment |
|------------|---------|--------------------|------------------------------------|
| BWC-MG | 1.74 | 0.0819 | 0.491 |
| BWC-RC | 2.65 | 0.00799 | 0.0480* |
| MG-RC | 0.995 | 0.319 | 1.00 |
| BWC-RT | 2.59 | 0.00955 | 0.0573 |
| MG-RT | 0.972 | 0.331 | 1.00 |

*Significant differences determined using Post-hoc Dunn test with Bonferroni adjustment. (RC=Red colobus, MG=grey-cheeked mangabeys, BWC=black-and-white colobus, RT=redtail monkeys).

Hypothesis 2: Rough-and-Tumble Play by Sex

The results did not support Prediction 2 for red colobus and grey-cheeked mangabeys, and it only partially supported Prediction 3 for black-and-white colobus. The Wilcoxon Rank Sum test between male and female red colobus for rough-and-tumble play indicated that their difference in proportion was not significant, which disagrees with Prediction 2. ($W = 154.5$, $n_M = 16$, $n_F = 16$, $p = n.s.$). The difference between males and female grey-cheeked mangabeys was also not significant ($W = 288.5$, $n_M = 25$, $n_F = 25$, $p = n.s.$) (Figure 3).

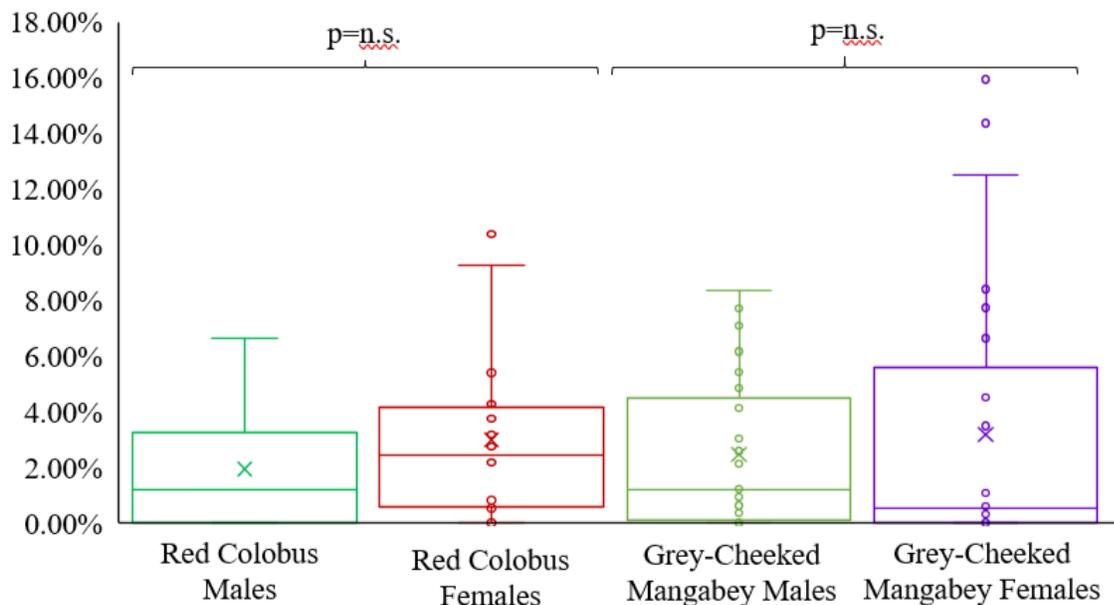


Figure 3: Distribution of rough-and-tumble play within the daily activity budget of male and female red colobus and grey-cheeked mangabeys. Each circle represents the percent of rough-and-tumble play in the activity budget for one day, the inner horizontal lines represent medians, the “x” indicates the means, and the boxes show inter-quartile range.

Rough-and-tumble play in black-and-white colobus did not occur in significantly different proportions between males and females ($W = 339.5$, $n_M = 25$, $n_F = 26$, $p = n.s.$) (Figure 4).

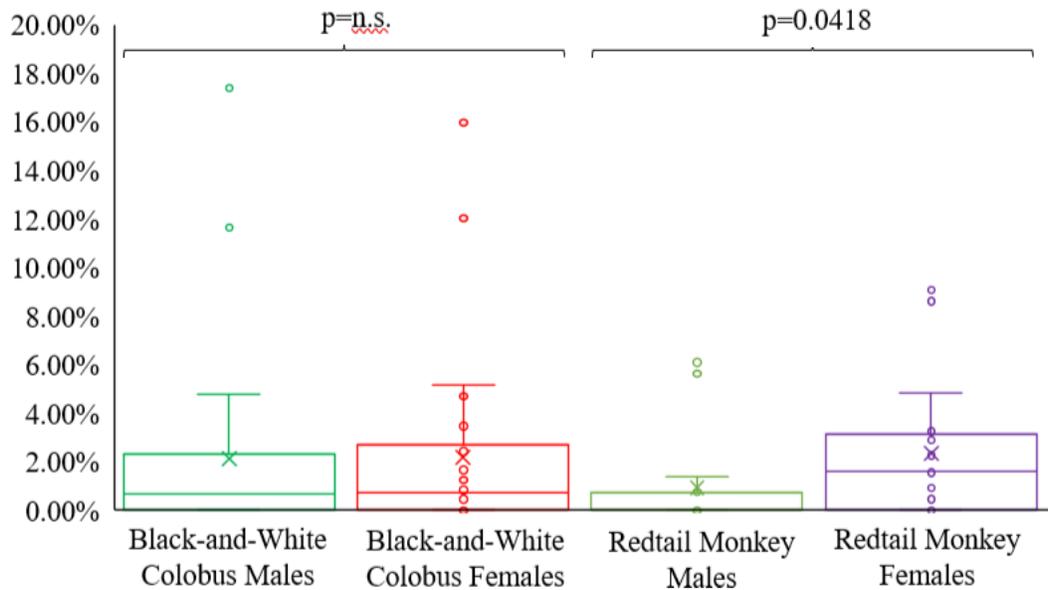


Figure 4: Distribution of rough-and-tumble play within the daily activity budget of male and female black-and-white colobus and redbtail monkeys. Each circle represents the percent of rough-and-tumble play in the activity budget for one day, the inner horizontal lines represent medians, the “x” indicates the means, and the boxes show inter-quartile range.

Finally, the Wilcoxon test between male and female redbtail monkeys showed that their difference in proportions was significant, such that females played more than males ($W = 169$, $n_M = 15$, $n_F = 16$, $p = 0.0418$) (Figure 4).

Discussion

Play Behaviors by Species

The purpose of this study was to test predictions for play behaviors made in support of the Instinct-Practice Theory and Fighting Skills Hypothesis. The four species were predicted to show differences in frequency of five different play behaviors under the Instinct-Practice Theory. Male and female red colobus and grey-cheeked mangabeys were predicted to show different frequencies of rough-and-tumble play, and the differences were predicted to be insignificant for male and female black-and-white colobus and redbelt monkeys according to the Fighting Skills Hypothesis. Among the four species, solitary locomotor play, parental play, and sexual play were observed in different frequencies, but not in rough-and-tumble play and object play. When examining differences between the sexes for rough-and-tumble play, differences between male and female red colobus, grey-cheeked mangabeys, and black-and-white colobus were not significant, and the differences between male and female redbelt monkeys were significant.

Overall, play is a very small proportion of the activity budget of immature individuals in the study species. These results are similar to those of studies on play in the activity budgets of other primate species (Barale, Rubenstein, & Beehner, 2015; Shimada & Sueur, 2017; Struhsaker, 1980; Worch, 2010). While there is variation in the exact proportion of play in the activity budget, in studies of wild primates it usually accounts for less than 10%. Wild juvenile Japanese macaques were found to spend an average of 5.4% of their activity budgets in social play (Shimada & Sueur, 2017). Wild gelada infants and juveniles also spend anywhere between about 5.5-0 minutes/hour playing, depending on their age (Barale, Rubenstein, & Beehner, 2015). A study comparing red colobus and redbelt monkey behavior found that play accounts for 1.8% of the activity budget of young redbelt monkeys, and 2.7% of the activity budget of young red colobus (Struhsaker, 1980). A later study on immature red colobus in Kibale have also been shown to play during an average of 27% of their activity budget, which is far greater than what

was observed in this study. However, the difference may be due to methodological differences, as the study used instantaneous focal sampling of individuals instead of continuous focal sampling (Worch, 2010). Low frequency of play compared to other behaviors in the primate behavioral repertoire speaks to the flexibility of play both within and across species, in that the amount of play is often curtailed in times of stress (Burghardt, 2005). As stated in the literature review, multiple studies have found that populations that undergo water and preferred food shortages decrease their play frequency (Baldwin & Baldwin, 1974; Nunes et al., 1999; Sommer & Mendoza-Granados, 1995). In addition, previous research on overall play in Kibale monkey species found that species with further daily travel distances and a higher percentage of arthropods in their diet play less than species that do not have to travel as far and eat plants such as leaves that do not require as much effort to find (Worch, 2004). Although amount of play decreases when other needs such as feeding become more imperative, in none of these studies does play cease entirely. Therefore, its continued presence, even at the low proportions found in this study, indicates an adaptive importance despite environmental stress or a demanding diet. While level of difficulty in accessing resources certainly cannot predict whether play will occur in a species or not, it may help explain why it was found at such low rates in this study, especially when compared to higher amounts of play recorded in play studies in captive settings where resources are provided (Paukner & Suomi, 2008).

This small contribution of play to the activity budget of the study species is important because the resulting differences of proportions of play behaviors between species were also small, despite the significant differences in solitary locomotor play, sexual play, and parental play. Differences between species for mean proportion of sexual play in the activity budget were all less than 0.10%. Therefore, the differences between species for sexual and parental play do

not appear to be biologically significant, in that they are too small to indicate uniquely adaptive functions in the species for which their proportion is greater. Unfortunately, studies that examine differences between species for specific types of play behavior usually analyze them in terms of presence or absence or hourly frequency, rather than proportions in their activity budgets (O'Meara et al., 2015; Palagi & Cordoni, 2012). These methods for characterizing differences between species for different play behaviors may therefore be more effective than just differences in activity budgets.

Solitary locomotor play was the only behavior for which differences among species appear to be both statistically and biologically significant. Although sexual and parental play are also significantly different, the miniscule differences in frequencies among species do not appear to be large enough to warrant evolutionary importance. The differences for solitary locomotor play are great enough to indicate relevant behavioral differences in the amount of time spent in this behavior, which leads to a partial acceptance of the first hypothesis of different proportions of play behaviors in each of the species. Solitary locomotor play is significantly greater in red colobus than grey-cheeked mangabeys and redtail monkeys, and the difference approached significance between red colobus and black-and-white colobus. As previously stated, locomotor play appears to be valuable as a method of developing motor skills as part of the Instinct-Practice Theory of play (Harcourt, 1991; Power, 2000). A greater proportion of solitary locomotor play in red colobus than other species may indicate a greater importance for play as a method of developing these motor skills in red colobus than the other species. There are several possible evolutionary explanations for this increased need for practice and development of locomotor ability in red colobus. A 2009 study recorded various injuries in red colobus, grey-cheeked mangabeys, black-and-white colobus, and redtail monkeys (Arlet, Carey, & Molleman, 2009).

Overall, the adult red colobus had the vast majority of arm, leg, and tail fractures when compared to the other species. The authors suggested that these and the other fractures seen were due to falls during locomotion, and that previous observers have noted that red colobus are much “clumsier” than the other species (Arlet, Carey, & Molleman, 2009; Struhsaker, 1975). The perceived lack of agility in red colobus has not yet been examined in detail. However, it is interesting to see that this species also shows more solitary locomotor play than the other species. This type of play may be important for immature individuals in this especially at-risk species to gain proper motor skills and prevent these types of injuries. Another explanation may be avoidance of predation. At Ngogo, a field site within Kibale, researchers recorded instances of predation by chimpanzees. They found that of all prey species, chimpanzees most frequently hunted and killed red colobus, which accounted for 88.4% of the kills observed (Watts & Mitani, 2002). As stated previously, solitary locomotor play is thought to develop motor skills in order to better avoid predation (Harcourt, 1991; Power, 2000). Red colobus may show greater frequency of solitary locomotor play because it aids in practicing locomotor behaviors that will aid in escaping chimpanzees.

Play Differences by Sex

As part of the Fighting Skills Hypothesis, it was predicted that red colobus and grey-cheeked mangabeys would show more rough-and-tumble play in immature males than females. Redtail monkeys and black-and-white colobus would also show no differences between immature males and females in occurrence of rough-and-tumble play. However, the results did not support the predictions for red colobus, grey-cheeked mangabeys, and redtail monkeys. The Fighting Skills hypothesis has been tested before in red colobus and refuted because the study found no difference in rough-and-tumble play between males and females (Worch, 2010). It has

also been studied in black-and-white colobus and showed similarly insignificant differences between males and females (Worch, 1998). These findings are important because they add to the growing body of evidence that the Fighting Skills hypothesis is an incomplete model for predicting rough-and-tumble play in infants and juveniles in a particular species (Sharpe, 2005). In addition, the fact that play has apparently evolved multiple times suggests that play may have adopted different purposes and benefits in different lineages (Pellis, Burghardt, Palagi, & Mangel, 2015). It has been found, for example, that both male and female rhesus macaques (*Macaca mulatta*) reared in social isolation are unable to perform the proper body movements for successful copulation as adults. Similar results have been noted in rats, indicating that in some species, social play, especially rough-and-tumble play, may be important for future sexual competency (Pellis & Pellis, 2009). Therefore, rough-and-tumble play may still be important for practicing behaviors needed in adulthood, but not just those required for aggressive interactions.

Another important issue is that recent studies have explored the idea that the Fighting Skills Hypothesis is less about overall frequency of rough-and-tumble play and more about differences in how this play is conducted in species where the sexes have different adult aggression levels. Multiple primate studies have compared rough-and-tumble play between species with different levels of physical aggression in adults (Reinhart et al., 2010; Palagi & Cordoni, 2012). They have found that primates with a more egalitarian and cooperative social organization tend to show rough-and-tumble play bouts that are more cooperative, in that they often involve multiple players, and bouts tend to last longer without escalating into fights. Species with stricter and more aggressive social organizations tend to have rough-and-tumble play bouts that are more often dyadic and competitive in their movements to gain the upper hand over an opponent (Reinhart et al., 2010; Palagi & Cordoni, 2012). Therefore, more detailed

studies into the components of rough-and-tumble play, rather than just their occurrence, may provide a more nuanced understanding of the Fighting Skills Hypothesis.

One final element to consider in examining sex differences is the possibility of energy intake affecting play frequency. An investigation in a sample of 11 immature savanna baboons found that individual play frequency and duration were significantly correlated with estimated milk consumption and protein availability (Altmann, 1991). In addition, males consumed more milk as well as excess protein than females, although these differences were not statistically significant. Therefore, it was suggested that males may play more partly because of their greater nutritional intake as part of the Surplus Energy hypothesis (Fagen, 2002; Altmann, 1991). Unfortunately, studies on differences in nutritional intake between the sexes in immature primates are rare, but it may be something that should be kept in mind and accounted for in future play studies.

Future Directions

This study examined differences in play behaviors within the activity budgets of four different monkey species in Kibale National Park. As of now, there has been relatively little research on the full play repertoires of these species, or even in play in these species at all. Although the study did not support previously suggested hypotheses, including Instinct-Practice Theory and the Fighting Skills Hypothesis, it did indicate important routes for future study. For example, the relatively high proportion of solitary locomotor play in the red colobus activity may be further studied in its relation to the development of locomotor skills in a species with a high frequency of locomotion-related fractures in adults. An examination of the adaptive function of solitary locomotor play would require a long-term study in which individuals are observed from infancy to adulthood, and their frequency of locomotor play is examined in relation to

developmental milestones (Berghänel, Schülke, & Ostner, 2015). Another avenue for study is the re-examination of rough-and-tumble play in these species, which would include analyses on polydyadic vs dyadic play interactions and length of play bouts.

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