MONKEYING AROUND: COMPARING PLAY BEHAVIOR IN RELATION TO PREDATION RISK IN SYMPATRIC OLIVE BABOONS (PAPIO ANUBIS) AND VERVET MONKEYS (CHLOROCEBUS PYGERYTHRUS)

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Abstract:
Predation has long been considered a strong selective pressure on primate behavior, including foraging and feeding. However, its effects on play behavior, a crucial aspect of primate life, are unknown. Feeding is necessary for survival, but play is imperative for later reproductive success. Olive baboons (Papio anubis) and vervet monkeys (Chlorocebus pygerythrus) are often sympatric but baboons are larger and more aggressive, suggesting that they may be less vulnerable to predation and thus may have longer or more frequent play bouts. Similarly, within species, male primates, being more aggressive than female primates, may be less vulnerable to predation and so may play more than females. I observed play behavior of baboons and vervets in Nyungwe and Akagera National Parks, Rwanda, to test these predictions. I used all-occurrence sampling to record frequencies and durations of play bouts and analyzed the data with nonparametric statistical tests. There were significant differences in play bout frequencies but not durations both between the species and between males and females within species. Future research should explore whether life history differences also contribute to differences in play behavior.

Keywords: Vervet | olive baboon | play | predation

Introduction
Primates and their predators have been in an evolutionary arms race for over 70 million years (Isbell, 2009). The effects of predation as a strong selective pressure on primate behavior have been studied in numerous contexts. Ecological tradeoffs lie at the root of predation as a selective pressure, specifically in regards to feeding and foraging behaviors and habitat use (Cowlishaw 1997; Lima 1998; Hart 2007; Coleman and Hill 2013). For instance, in a study conducted by Cowlishaw (1997), chacma baboons (Papio ursinus) were observed under different conditions of predation risk and food availability in a given habitat. He found that the baboons did not use the habitats proportionally to their availability and they spent less time in food-rich areas than expected due to the higher risk of predation in those areas. In a similar study, Coleman and Hill (2014) found that samango monkeys (Cercopithecus mitis erythrarchus) decide on habitat usage based on predation risk rather than on resource availability. Ultimately, predation may lead to trade-offs in foraging, habitat use, or another common behaviors in primates (Lima 1998; Hart 2007). Though predation has obvious effects on the daily lives of all primates, certain characteristics may make some primates more prone to predation than others. Smaller-bodied primates are more susceptible to predator attacks than are larger-bodied.
primates (Isbell 1994; Enstam 2007). For this reason, different primate species tend to have different predator avoidance or deterrent strategies. Shultz et al. (2004) noticed that terrestrial primates are more likely to live in large groups or to be large in body size as a predator deterrence strategy. One hypothesis regarding extreme sexual dimorphism in some species is that large males act as predator deterrents, implying that large body size does, in fact, reduce risk of predation (Leutenegger and Kelly 1977). In addition to large body size, alarm calls are another popular predator deterrent (Enstam 2007; Isbell and Bidner 2016). In a study by Enstam and Isbell (2002), predation responses were compared between vervet monkeys (Chlorocebus pygerythrus) and their slightly larger relatives, patas monkeys (Erythrocebus patas). They found that vervet monkeys tend to alarm call and flee while the larger, more aggressive patas monkeys would sometimes engage in “active defense” (Isbell and Enstam 2002). Like patas monkeys, red colobus (Piliocolobus tephrosceles) males have also been observed to use aggression as a predator deterrent (Struhsaker and Leakey 1990; Boesch 1994; Mitani and Watts 1999). In three separate studies, researchers noticed that chimpanzees attacked younger red colobus and avoided adult males due to their aggressive responses (Struhsaker Leakey 1990; Boesch 1994; Mitani Watts 1999).

Just as all primates are subject to predation risk, all primates play. Play is defined by Burghardt (2005) as satisfying several conditions including arising spontaneously, having no immediate function, and occurring in a stable environment. While many primatologists agree that the benefits of play occur much later than when the act itself takes place, the specific benefits are still debated (Chalmers 1987; Pellis 1988; Struhsaker and Leakey 1990; Lima 1998; Lewis 2000; Fagen 1993; Fairbanks 1993; Maestripieri and Ross 2004). Developing good motor skills is one of the primary hypothesized functions of play (Fagen 1993; Maestripieri and Ross 2004). A second widespread theory on the functionality of play is honing social skills that can be utilized throughout the animal’s life (Chalmers 1987; Lewis 2000; Fairbanks 1993). Play often necessitates cooperation and communication between partners which inherently works to increase social competency. Lewis (2000) noted that primate social play was positively correlated with neocortex ratio. She attributed this to the fact that social play requires a number of complex cognitive function such as predicting behaviors and reacting appropriately which, in turn, helps the animals develop skills useful in their adult lives. Fairbanks (1993) noted that even the motor skills acquired through play can aid in primate reproductive success. She argues that male primates develop fighting skills through play and that fighting ability in male cercopithecines often precipitates greater reproductive success. Social competency is even more crucial to reproductive success because successfully integrating into a new group post-dispersal requires appropriate social skills (Platt et al. 2016). Ultimately, playing during the juvenile period helps build the skills necessary for later acceptance in future social circumstances including dispersal and, later, courting behavior.

Even though play eventually produces benefits, there are immediate costs. Play is a very risky behavior because it puts individuals in precarious situations and leaves them susceptible to predation (Struhsaker and Leakey 1990; Lima 1998; Fagen 1993). During play, individuals are not completely aware of their surroundings and are prone to falls. A number of studies involving lethal falls cited by Fagen (1993) indicate the high risk that often correlates with play. Furthermore, play reduces the capacity for vigilance as attention is directed toward the object of play rather than surroundings. For instance, in a study of yellow baboon (P. cynocephalus) predatory behaviors, Hausfater (1976) noted that the baboons preyed upon mostly younger vervets who were in play groups away from the more vigilant adults. In addition to reducing vigilance, play makes individuals more
conspicuous to their predators. In its most simple yet justifiable form, increasing activity leads to an increased risk of predation (Lima 1998). Struhsaker and Leakey (1990) found that crowned hawk-eagles (*Stephanoaetus coronatus*) did not randomly select primate prey, but rather targeted adult males in four primate species (except red colobus as noted above) because they tended to be more demonstrative, give more alarm calls, and be less cautious overall which made them very conspicuous, easy targets. Similarly, play reduces vigilance and increases noticeability making the players easy targets for predation. Evolutionarily speaking, risky behaviors should not be performed unless they have benefits that outweigh the costs. This necessitates that play does in fact lead to benefits such as those stated above in order for the tradeoff to be worth it evolutionarily.

While play involves risk of predation, the risks themselves vary across species and habitats (Enstam 2007). In order to account for these variables, I selected vervet monkeys and olive baboons, two species very similar in habitat and that share common predators, to examine how predation may affect play behavior. Vervets and olive baboons both share leopards (*Panthera pardus*) as a common predator and are both found in East Africa, in places such as Rwanda where I observed them. While these two species may live in the same areas and share a common predator, they differ quite obviously in other respects. Body size is the first evident difference between these two species. On average, olive baboons are approximately five times the size (weight) of vervets (Dechow 1983; Isbell and Jaffe 2013). Olive baboons are also much more aggressive toward predators than vervet monkeys; vervets are known for their species-specific alarm calls while baboons tend to actively defend and even attack during times of predation (Cowlishaw 1994; Enstam 2007; Isbell and Bidner 2016). In fact, Cowlishaw (1994) found that in four of the eleven documented instances of baboon retaliation against leopards, the primates actually killed the felid. As mentioned previously, both body size and aggression have been shown to be negatively correlated with predation risk so baboons should therefore have a lower risk of predation than vervet monkeys do in the same general environment.

Here I test the prediction that risk of predation affects olive baboon and vervet monkey play behavior differently. Specifically, I predicted that baboons would have both longer and more frequent play bouts compared to vervets due to lower risk of predation because of their larger body sizes and more aggressive nature. To examine the relationship between predation risk and body size and aggressiveness further, I also predicted that female baboons would play more often or for longer than female vervets, male baboons would play more often or for longer than male vervets, and within each species, males would play more often or for longer than females.

**Methods**

**Study sites**

I collected data from June 14 to June 30, 2016 in two of Rwanda’s national parks: Akagera National Park (1.60° S, 30.72° E) and Nyungwe Forest National Park (2.53° S, 29.28° E). Akagera is situated in a warm, dry savanna and Nyungwe is a mountain rainforest. In Akagera, I observed both lodge groups (situated next to a hotel) and groups located away from constant human habitation. The only group in which play was observed in Nyungwe was also situated next to a small hotel.

**Study subjects**

The two species I observed for this study were olive baboons and vervet monkeys. Another researcher and I recorded data from several baboon troops; group sizes ranged from five non-adults to thirteen non-adults (adults were not counted in demographies due to the challenge of counting large groups in a short period of time). The only vervet group in which play was observed consisted of two adult males, two adult females, four subadult females, two juvenile females, one infant male,
and one infant female. All of the groups observed were semi-habituated.

Data collection and analysis

My data collection partner and I first tested our inter-observer reliability in identifying age-sex classes of individuals by comparing our observed demographics and defining age class based on visual observation. We collected observational data on play using all-occurrences sampling. Upon arrival at a study site, we would collect demographics of the group and then immediately watch for play behavior. Whenever play was observed, we recorded the sex and age class of the player(s) and the duration of the play bout. If group composition changed during the study period in the area of observation, we collected demographics again and continued observing play. We compared our data regularly to ensure accuracy and consistency of data collection.

We observed the animals for 421 minutes which included approximately 78 minutes of play (play made up 18.6% of the total observation time). In total, 164 separate play bouts were recorded, 124 play bouts for baboons and 40 play bouts for vervets.

I used Mann-Whitney U tests to analyze the data for play bout durations and Chi-square Goodness-of-Fit tests to analyze the data for frequencies of play bouts. In total, I tested for differences in play bout duration and frequency between baboons and vervets, male and female baboons, male and female vervets, male baboons and male vervets, and female baboons and female vervets.

Results

Duration of play bouts
Baboons vs. vervets

Baboon play bout durations ranged from 5-145 seconds and averaged 29.8 seconds. Vervet play bout durations ranged from 5-51 seconds and averaged 25.1 seconds. Baboons did not play for significantly longer periods than vervets did despite their larger body size and increased aggression towards predators (Mann-Whitney U test: \( U_A = 2428, P_{(1)} = 0.42, 1\text{-tailed}; \) Figure 1).

Female baboons vs female vervets

I observed 40 individual play bouts by female baboons and 34 play bouts by female vervets. Female baboon play bout durations ranged from 5-73 seconds with an average of 23.7 seconds while female vervet play bout durations ranged from 5-51 seconds with an average of 24.9 seconds. Female baboons did not play significantly longer than female vervets (Mann-Whitney U test: \( U_A = 740.5, P_{(1)} = 0.26, 1\text{-tailed}; \) Figure 2).

Male baboons vs. male vervets

I recorded 84 individual play bouts for male baboons and 6 individual play bouts for male vervets. The duration of play bouts for male baboons ranged from 5-145 seconds with an average of 32.7 seconds while the duration of play bouts for male vervets ranged from 6-44 seconds with an average of 26.5 seconds. Male baboons also did not play significantly longer than male vervets (Mann-Whitney U test: \( U_A = 252.5, P_{(1)} = 0.5, 1\text{-tailed}; \) Figure 3).

Male vs. female baboons

I recorded 84 individual play bouts for male baboons and 40 for female baboons. The duration of play bouts for males ranged from 5-145 seconds with an average of 32.7 seconds while the duration of play bouts for females ranged from 5-73 seconds with an average of 23.7 seconds. These data indicate that male baboons played significantly longer than female baboons (Mann-Whitney U test: \( U_A = 1337, P_{(1)} = 0.03, 1\text{-tailed}; \) Figure 4).

Male vs. female vervets

I recorded six individual play bouts for male vervets and 34 for female vervets. The duration of play bouts for males ranged from 5-145 seconds with an average of 32.7 seconds while female vervet play bout durations ranged from 5-51 seconds with an average of 24.9 seconds. Male vervets did not play significantly longer than female vervets (Mann-Whitney U test: \( U_A = 105, P_{(1)} = 0.46, 1\text{-tailed}; \) Figure 5).

Frequency of play bouts
Baboons vs. vervets

I recorded 124 play bouts for baboons in
the 285 minutes spent observing them and 40 bouts for vervets in the 136 minutes observing them. According to these data, baboons played significantly more frequently than vervets (Chi-square Goodness of Fit test: $\chi^2 = 45.06$, $p < 0.0001$; Figure 6).

**Female baboons vs. female vervets**

Of the 124 baboon play bouts, 40 were from females. Of the 40 vervet play bouts, 34 were due to females. Once total observation time was accounted for, the data show that female vervets played significantly more frequently than female baboons (Chi-square Goodness of Fit test: $\chi^2 = 50.88$, $p < 0.0001$; Figure 7).

**Male baboons vs. male vervets**

I recorded 84 play bouts from male baboons and six from male vervets. Taking total observation time into account, male baboons played significantly more frequently than male vervets (Chi-square Goodness of Fit test: $\chi^2 = 306.3$, $p < 0.0001$; Figure 8).

**Male vs. female baboons**

I observed 84 play bouts from male baboons and 40 from female baboons in the same total observation time. These data show that male baboons played significantly more frequently than female baboons (Chi-square Goodness of Fit test: $\chi^2 = 90.4$, $p < 0.0001$; Figure 9).

**Male vs. female vervets**

I recorded six play bouts from male vervets and 34 from female vervets in the same overall observation time. These data show that female vervets played significantly more than male vervets (Chi-square Goodness of Fit test: $\chi^2 = 238.22$, $p < 0.0001$; Figure 10).

**Discussion**

Contrary to what I predicted, I found no significant differences in play bout duration between olive baboons and vervet monkeys. In fact, there were no significant differences in durations of play bout between any of the categories compared (e.g. male baboons vs. male vervets, male vervets vs. female vervets, etc.) except between male and female baboons in which the males played significantly longer than females. Despite being larger-bodied and more aggressive, baboons may not have played longer than vervets simply due to lack of motivation. In other words the animals may just stop playing after a 30 second bout, for instance, because they have lost interest in the object of play or other player.

In contrast to duration of play bouts, frequencies of play bouts were significantly different across all comparison groups. Baboons played significantly more than vervets overall, female vervets played more than female baboons, male baboons played more than male vervets, male baboons played more than female baboons, and female vervets played more than male vervets. These data do not seem consistent with each other in the context of my hypotheses, but sample size is probably to blame. Based on my hypotheses, I expected males to play more than females due to their larger body sizes and baboons to play more than vervets across all categories due to both larger body size and greater aggression. The data are not consistent with this in the female baboons vs. female vervets and male vervets vs. female vervets comparisons. I believe that this is the case because the vervet group that played was very small and consisted of far more females than males (seven non-adult females, one non-adult male) so data will skew accordingly.

Alternative explanations for the differences in play frequency between baboons and vervets include diet, group size, and group locations. Perhaps diet affected play behavior because energy is needed for play and different diets lead to varying amounts of energy. There were baboon troops that I observed both by a consistently human-inhabited lodge and troops that lived much further from constant human activity. The lodge groups often stayed on and around a large trash heap in which they often foraged through and ate from thereby consuming a lot of discarded scraps from human foods. Similarly, for vervets, the only group in which I observed play behavior was one that lived by a small hotel. While I was collecting data, one of the hotel staff threw a small banana at the monkeys to keep them out
of the hotel itself though some managed to get in and steal more fruit which implies that the group is often provisioned. Furthermore, the other groups of vervets in Akagera were far from human habitation and, therefore provisioning, and did not play at all during the time I spent observing them. The fact that the both the baboon and vervet groups that were subject to human provisioning (intentional or not) played more than the non-provisioned groups leads credence to this idea, though more empirical data collection on this subject would need to be collected. In a similar study, Kamal et al. (1997) observed that play behavior increased in juvenile hamadryas baboons (P. hamadryas) when they were provisioned compared to when they naturally foraged.

A second alternative hypothesis is due to the “group size effect” as explained by Lima (1998). In essence, the idea is that individuals in larger groups are not required to be as vigilant as individuals in smaller groups simply because there are more eyes and ears available to detect predators. Because vigilance per individual does not have to be as high, more time is available for behaviors that interfere with vigilance such as play. Baboon troops are generally larger than vervet groups so vigilance per individual should theoretically be less in baboons than it is in vervets. This concept was shown to be true for vervets in Amboseli National Park in Kenya where various groups of different sizes were observed and their activity budgets recorded (Isbell and Young 1993a). Isbell and Young found that larger groups of vervets had more overall scanning, yet fewer instances per individual compared to the smaller groups.

The third alternative explanation for the differences in play bout frequencies relates to human proximity. As noted above, the lodge groups of both baboons and vervets appeared to play more than those groups further away from human-inhabited areas. Isbell and Young (1993b) found that predation risk was reduced for vervets in closer proximity to humans and they suggested it was due to avoidance of humans by leopards. Perhaps the lodge groups have a much smaller risk of predation, at least by leopards, than the other groups simply due to close human proximity and so do not have to be as vigilant.

In the future, I would like to test these and other alternative explanations for the results I obtained. First, the “group size effect” could be tested by controlling for group size by observing groups of baboons and vervets of the same size and seeing if there were still any significant differences in play. If the group size effect was the true independent variable in play bout frequencies, I would expect no significant differences between baboons and vervets in equal sized groups. Furthermore, I could control for species as well and observe different sized groups of baboons and, separately, observe different sized groups of vervets. If play frequencies were positively correlated with group size, I could not reject this hypothesis.

For the proximity to humans hypothesis, I could look solely at baboons in Akagera and take more specific data on the differences in play between the lodge groups and non-lodge groups. If the lodge groups played significantly more than the other groups, I could not reject this hypothesis.

Ultimately, there is a difference in play bout frequencies between the species, yet the exact mechanism for why this difference exists remains unknown. There are many potential explanations for this correlation, but future studies must be done in order to come to a clearer conclusion.

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References


Figure 2. Play bout durations - females. No significant difference between female baboons and female vervets in play duration.

Figure 3. Play bout durations - males. No significant difference between male baboons and male vervets in play duration.
Figure 4. Play bout durations—baboons. Male baboons played for significantly longer than female baboons on average.

Figure 5. Play bout durations— vervets. No significant difference between male and female vervets.
Figure 6. Number of play bouts per minute observed. Baboons played significantly more frequently than vervets did.

Figure 7. Number of play bouts per minute observed- females. Female vervets played significantly more frequently than female baboons, but sample sizes were skewed.
Figure 8. Number of play bouts per minute observed—males. Male baboons played significantly more frequently than male vervets, but sample sizes were skewed.

Figure 9. Number of play bouts observed—baboons. Male baboons played significantly more frequently than female baboons did.

Figure 10. Number of play bouts observed— vervets. Female vervets played significantly more frequently than female baboons, but sample sizes were skewed.