

**PLAYING WITH THE UMWELTEN:
SEEING THE WORLD THROUGH THEIR EYES**

KELLY L. KRAUS
Bachelor of Arts, University of Lethbridge, 2018

A Thesis/Project
Submitted to the School of Graduate Studies
of the University of Lethbridge
in Partial Fulfillment of the
Requirements for the Degree

MASTER OF SCIENCE, NEUROSCIENCE

Department of Neuroscience
University of Lethbridge
LETHBRIDGE, ALBERTA, CANADA

© Kelly L. Kraus, 2018

**PLAYING WITH THE UMWELTEN:
SEEING THE WORLD THROUGH THEIR EYES**

KELLY L. KRAUS

Date of Defence: October 22nd, 2018

Dr. S. Pellis Supervisor	Professor	Ph.D.
-----------------------------	-----------	-------

Dr. L. Barrett Thesis Examination Committee Member	Professor	Ph.D.
---	-----------	-------

Dr. E. Galway Thesis Examination Committee Member	Associate Professor	Ph.D.
--	---------------------	-------

Dr. P. Henzi Chair, Thesis Examination Committee	Professor	Ph.D.
---	-----------	-------

For
All The Playful Primates On The Planet

This thesis is dedicated to the memory of my dear and loving mother.

May your energy be ever free, yet always stay close to me.

Abstract

This thesis unites two contrasting projects within the framework of one concept: the *umwelt* – which stresses the need to view the world from the subject’s perspective. The first project is a comparative analysis of the play fighting in several species of Old World monkeys. All species attacked and defended the same body targets and used similar combat tactics. Surprisingly, whereas two species focused more on biting, the other two adopted tactics to enhance the opportunity for competition. The second project involves a story about play written for young children. An analysis of the parents’ impressions of the children’s responses revealed that the sex and interests of the child greatly influenced their attentiveness to the story. Thus, the thesis demonstrates that the *umwelt* is a powerful conceptual tool for understanding how the subjects perceive and react to the world, whether describing behaviour, or communicating with an audience.

Acknowledgments

It is with deep and heartfelt gratitude that I thank Dr. Sergio Pellis for his role as my thesis supervisor. I am grateful to have had his time and expertise, along with his steadfast support, which contributed significantly to the completion of my thesis. Dr. Pellis enthusiastically shared his knowledge of animal play behaviour with me, which largely influenced my interests in, and appreciation for, the subject matter. He has been a guiding force during this process and will remain as an inspiration and mentor to me.

My sincere gratitude is extended to Dr. Elizabeth Galway and Dr. Louise Barrett for their roles on my thesis committee. I am thankful to have had their time, support, and intellectual contributions, which were all crucial to the development of my thesis. I was inspired by Dr. Galway's knowledge of and passion for children's literature and by Dr. Barrett's expertise in articulating primate behaviour. Their unique perspectives motivated me to stretch the limits of my thinking.

Thank you to Dr. Vivien Pellis, for the time and effort that you, along with your husband, put in to film and capture the monkey play behaviour that I used in my project. Without this footage, it would not have been possible for me to conduct this research.

Finally, I am profoundly grateful for the love and support given to me by my family. Thank you to my husband Kyle, my mom and dad, and my brother and sister-in-law, for all of your help during my time as a graduate student. From the very beginning to the very end, your strength and encouragement helped me to endure when I needed it the most - I love you all.

Table Of Contents

Supervisory Committee	ii
Dedications	iii
Abstract	iv
Acknowledgments	v
Table of Contents	vi
List of Tables	vii
List of Figures	viii
List of Abbreviations	ix
1. Introduction	1
2. Examining The Rough and Tumble Play of Two Closely Related Cercopithecinae Genera: A Comparative Analysis	3
Introduction	3
Methods	4
Results	12
Discussion	27
3. Informal Pilot Study: Children’s Story - Target Audience Assessment	36
Introduction	36
Methods	37
Results & Discussion	38
Conclusion	41
4. Story: Every Day I Like To Play, I Like To Play In Every Way	42
5. Conclusion	52
6. References	54
7. Appendix	57
Informal Pilot Study Survey	57

List of Tables

Table 2.1: Duration Of Offensive And Defensive Bites Shown In Seconds (Mean \pm SD).

Table 3.1: Summary of the Most Significant Results For Determining the Success of the Story.

List of Figures

Figure 2.1: A section of an EWMN analysis grid along with a spherical representation of body/limb positions in which the measurements for the grid are based.

Figure 2.2 (a-i): Still frames taken from the computer screen illustrate play fighting in Guinea baboons.

Figure 2.3 (a-i): Still frames taken from the computer screen illustrate play fighting in drills.

Figure 2.4: Shows the duration (percent) of biting by both opponents during a play fight. The monkey delivering the first bite, the offensive bite, is shown above the horizontal scale line for percent duration.

Figure 2.5 (a-i): Still frames taken from the computer screen illustrate play fighting in Hamadryas baboons.

Figure 2.6 (a-i): Still frames taken from the computer screen illustrate play fighting in mandrills.

Figure 2.7 (a-i): Still frames taken from the computer screen illustrate leaping play fighting with no bite attempts in mandrills.

Figure 2.8: The frequency distribution of offensive bites across the body is shown for both species. Number of offensive bite attempts: G. baboons = 78, H. baboons = 85, drills = 104; mandrills = 57.

Figure 2.9: The frequency distribution of defensive bites across the body is shown for each species. Number of defensive bite attempts: G. baboons = 46, H. baboons = 30, drills = 45; mandrills = 14.

Figure 2.10: Actively rolling over on to its side or back as an initial defensive tactic is more common in *Papio* than in *Mandrillus* species. (Number of initial tactics: G. baboons = 161, H. baboons = 38, drills = 71; mandrills = 51.) Ending up lying on the ground sometime during the encounter is also more common in *Papio* than in *Mandrillus* species (Number of play fights: G. baboons = 167, H. baboons = 38, drills = 69; mandrills = 51.)

Figure 2.11: The frequency of biting during play fights is shown for both successful offensive and defensive bites. Number of bite attempts: Guinea baboons = 124, Hamadryas baboons = 85, drills = 149; mandrills = 71.

Figure 2.12: The duration of play fights involving biting is significant when comparing all species ($H = 9.424$; $p = 0.0242$).

Figure 2.13: The percent of the play bout involving biting is significant when comparing all species. ($H = 16.626$; $p = 0.0008$).

Figure 2.14: Shows the correlations in both the *Papio* and *Mandrillus* species between the variability of overall bite times and the variability of bite overlap times. The correlation only achieves significance in the Guinea baboons and Mandrills.

Figure 2.15: The percent of the play bout involving torso-torso contact is significant when comparing all species. ($H = 14.719$; $p = 0.0021$).

List of Abbreviations

Methodological Abbreviations:

EWMN	Eshkol Wachmann Movement Notation
WMV	Windows Media Video
H/F/C	Head/Face/Cheek
N/S/UA	Neck/Shoulder/Upper Arm
B	Body
LA/H	Lower Arm/Hand
L/Ft	Leg/Foot
UT	Unidentified Target
U	Upright
R	Rolling
S	Supine
GB	Guinea Baboon
HB	Hamadryas Baboon
D	Drill
M	Mandrill

Statistical Symbols

X^2	Chi Square
U	Mann-Whitney U
r_s	Spearman's rho
Z	z-score or standard score
p	p-score or probability
H	Kruskal-Wallis

Introduction

The *umwelt* is a concept that was developed by the German biologist, Jakob Von Uexküll (von Uexküll, 1934/2010). The key aspect of this concept is that only a limited number of environmental stimuli available to an animal are used, so only certain aspects of an organism's environment are meaningful. Due to differences in sensory systems, certain features of the environment might hold salience, or value, only to organisms that can sense and perceive the existence of these features or stimuli. Therefore, the *umwelten* of diverse species, equipped with various sensory organs, cannot be the same - implying that the internal experience of the external environment would also differ. So, in that vein, a human should not assume that, for example, a bat is having the same subjective experience that they have, despite being in the same location at the same time.

Recognizing that differences in *umwelten* are possible is a powerful initial framework from which to observe, analyze, and attempt to answer questions about animal behaviour.

Taking the *umwelt* in to consideration, a descriptive study including qualitative and quantitative elements was performed in order to investigate the play fighting behaviour of four closely related species of Old World monkeys: two of the several extant *Papio* species and both of the remaining *Mandrillus* species. Previous research has identified a characteristic pattern of the play fighting in other Old World monkey species closely related to those in this study (Pellis & Pellis, 1997; Pellis, Pellis, Barrett & Henzi, 2014; Reinhart, Pellis, Thierry, Gauthier et al., 2010); therefore, it was hypothesized that the same elements would be present in both the *Papio* and *Mandrillus* species. More specifically, the goal was to provide a detailed description of the elements of their play fights, including the body targets bitten and the tactics of defense used to protect those targets, and to determine if these similarities are sufficient to account for all aspects of

play in these papionins. The umwelt should be considered because the monkey's subjective experience of the play fight could define the elements of the patterns revealed using behavioural analysis methods, allowing human observers to go beyond what they consider to be useful to measure.

Applying the concept of the umwelt may be useful when trying to understand the behaviour of a species other than your own, such as humans studying non-human animals. However, individual members of the same species can have differing subjective experiences of their environments despite sharing the same sensory systems. This is most evident in humans because they can communicate to each other, generally with language, and inform others of what particular experiences are like to them personally. Thus, one stimulus might invoke many different reactions and/or emotions across many individuals. When trying to understand human behaviour, the umwelt can be applied by basically putting yourself "in the shoes" of the other person/people producing the behaviour(s) in question. This view is considered in the second part of the thesis.

Following the empirical monkey play study, this thesis also includes a children's story about human and animal play behaviour, along with the conclusions from an informal pilot study. In order to write an effective story for children aged 3-4, the author must get in to the heads, so to speak, of the intended audience. Which is not exactly an easy feat; differences in age and cognitive ability can exist between the author and the audience. By taking in to consideration the umwelt of a preschool aged child, the author can better consider the kind of story content that may be enjoyed and appreciated by the target audience. The purpose of the informal pilot study is to do just that - tap in to mind of the child by attempting to assess their experience of hearing the story.

Examining The Rough and Tumble Play of Two Closely Related Cercopithecinae Genera: A Comparative Analysis

When species of catarrhine primates (i.e., Old World monkeys and apes) engage in rough and tumble play, or play fighting, they strive to gently bite one another on the neck, shoulder, and upper arm area (e.g., Pellis & Pellis, 1997; Pellis et al., 2014; Reinhart et al., 2010; Schaller, 1963). Despite this common target area, the tactics used for attack and defense can differ markedly across species. For example, some are more likely to remain standing whereas others are more likely to roll over on to the ground (e.g., Emory, 1975). Several factors have been implicated in producing such variation, including social systems, with more egalitarian systems leading to more on the ground wrestling than is the case for more despotic ones (Palagi, 2006; Reinhart et al., 2010), body morphology, with lithe body builds enabling more acrobatic maneuvers than more robust ones (e.g., Pellis et al., 2014; Reinhart et al., 2010) and possibly phylogeny (e.g., Pellis & Iwaniuk, 1999, 2000). Given the importance of peer-peer play in the juvenile period in refining social skills (Palagi, 2018; Vanderschuren & Trezza, 2014), it is important to determine whether the variation in experiences afforded by differing styles of play is related to species differences in which skills are being modified by the experiences arising from play (e.g., Ciani, Dall'Olio, Stanyon, & Palagi, 2012; Reinhart et al., 2010). Consequently, it is necessary to understand both the variation in styles of play and the mechanisms that produce that variation.

The present study compares the play fighting of four closely related Afro-papionin species, the Guinea baboon (*Papio papio*), the Hamadryas baboon (*Papio hamadryas*), the drill (*Mandrillus leucophaeus*), and the Mandrill (*Mandrillus sphinx*). The comparison aimed to identify whether the same suite of targets and tactics, typical of other Old World

monkeys, were also present in these four species, and whether given the similarities in morphology and social systems (see below), their play would also be similar.

Both these species of *Papio* and the *Mandrillus* species live in social systems that are *single-male units within fission-fusion bands* (Barton, 2000). This means that groups generally consist of a dominant alpha male, a few adult females, and their infants. These groups meet with other groups during the day to form large aggregates and later return to their original size. The females are philopatric and stay in the groups they are born in to, while young adult males will leave and find a new group to join (Jolly, 2007). Similarities between both genera include: a common ancestor, social systems, body sizes, and living in mostly terrestrial habitats (Jolly, 2007). Given what is known about the factors that influence play behaviour, I predicted that the biological similarities among all four species should lead to similar play fighting styles. The baboons, the drill, and the mandrill should use similar tactics to gain access over similar targets, and if differences occur, they will be small and non-significant. However, other paired comparisons of closely related species, with similar terrestrial lifestyles, body size and social organization suggest that there can still be differences in the tactics used during play fighting (e.g., Emory, 1975), suggesting that such a confluence of factors may not be sufficient to account for all aspects of playing style.

Methods

Subjects

Videotaped sequences of play fighting from troops housed in zoos were analyzed. The Guinea baboons were from the Paris Zoo, the drills were from the Barcelona Zoo, the Hamadryas baboons were from the Melbourne Zoo and, finally, the mandrills were from the Schönbrunner Zoo in Vienna. There were 10 male Guinea baboons, 19 females, and

14 juveniles in the troop. The cage was mostly a barren earth sloped area extending upwards to the rear wall, ending on a flat concrete platform at the front (about 1m wide), ending at a wall that led to a trough in front of the viewing area). The total area was about 500m². Most of the play filmed was in the flatter areas of the main cage. The troop of Hamadryas baboons included 3 males, 11 females, and 8 juveniles (5 males aged 2-3.5 years; 3 females aged 2-3years). The enclosure had a concrete floor and was enclosed by a cyclone wire fence with a floor space of 450.53m² and had logs and some vertical steel rods for climbing. For the drills, there were 3 males, 5 females, and 1 juvenile under 3 years of age (note: two of the males and at least one of the females were adolescents 4-5 years old). The film was taken in their outdoor cage, which comprised a peninsula of 700m² surrounded by a moat on three sides, with grassy areas intermingling with trees and shrubs. The troop of Mandrills was comprised of 3 males, 5 females, 8 adolescents and juveniles, and 1 infant (2 months). The 7 most likely to have engaged in play were 3 males (22 months, 29 months, and 65 months) and 5 females (15 months, 20 months, 46 months, and 2 at 16 months). The outdoor enclosure had a moat on three sides and was about 400m² with logs and trees, interspersed with grassy areas and raised platforms. As the least amount of videotape available was from the drill, 2.5 hours, the total amount of video used for each species was standardized to the same length of analysis.

Data Collection

Over the course of 10 days at each zoo, sequences of play fighting were videotaped using 8mm Sony Camcorders, by two observers stationed at different vantage points. Although, it was not possible to be certain of the identity of the subjects, the fewer drills and mandrills present meant that more often than not, sequences could be attributed to particular pairs of individuals. For the baboon species, such individual tracking was not

possible, but age (based on size) and sex differences could be ascertained for pairs and, given the much larger number of juveniles present, sequences of multiple pairs playing within the same video frame was available. As much as possible, we verified species-typical patterns by including as many different individuals as possible in the analyses. Videotapes were converted in to Windows Media Video files (WMV) in order to be played by the *Avidemux* player on a Mac computer.

Data Analysis

Sequences identified as play fights were analyzed frame-by-frame so that the details of the play fight were visible and could be scored on to a spreadsheet.

Criteria for most of the play fights included in the analysis were that they must be dyadic and that the beginning and the end of the sequence must be visible. Generally, the play fights began when both monkeys appeared to be fully engaged with one another, either by making eye contact and/or by approaching the partner. When the play fight started, there was an *offender* who made the first bite attempt, and a *defender* who might retaliate with a bite if given the opportunity. These roles may change throughout the bout depending on which player made the bite attempt first in successive attacks. The monkeys were labeled as *Player A* and *Player B*, and were designated so that the monkey making the first bite attempt was *Player A*. These labels did not change even if *Player A and B* reversed roles, taking turns being the offender and defender.

Qualitative Analysis

From the available play fights, two protracted sequences were selected for detailed frame-by-frame analysis using Eshkol Wachmann Movement Notation (EWMN) (Eshkol & Wachmann, 1958). These sequences were selected from the Guinea baboons and the drills. The two sequences were as comparable as possible with regard to: length of

encounter, similarity of terrain, visibility of bite targets, successful offensive and defensive bites, and that the monkeys approached each other from an upright position. EWMN is a notation technique in which the positions and movements of each animal's body (e.g., head/neck, torso, limbs) are tracked over video frames in a globographic sphere with coordinates on the surface (see left panel in Figure 2.1). In addition to the movements of the body parts of each animal, the relative position, orientation and distance between the social partners are also recorded over time. Together, these enable the observer to detect which animal initiates changes in relationship between partners and allows for the detection of correlated movements between subjects (see panel on left in Figure 2.1). For further details on EWMN see Golani (1976) and for a recent example of its use see Pellis et al. (2013).

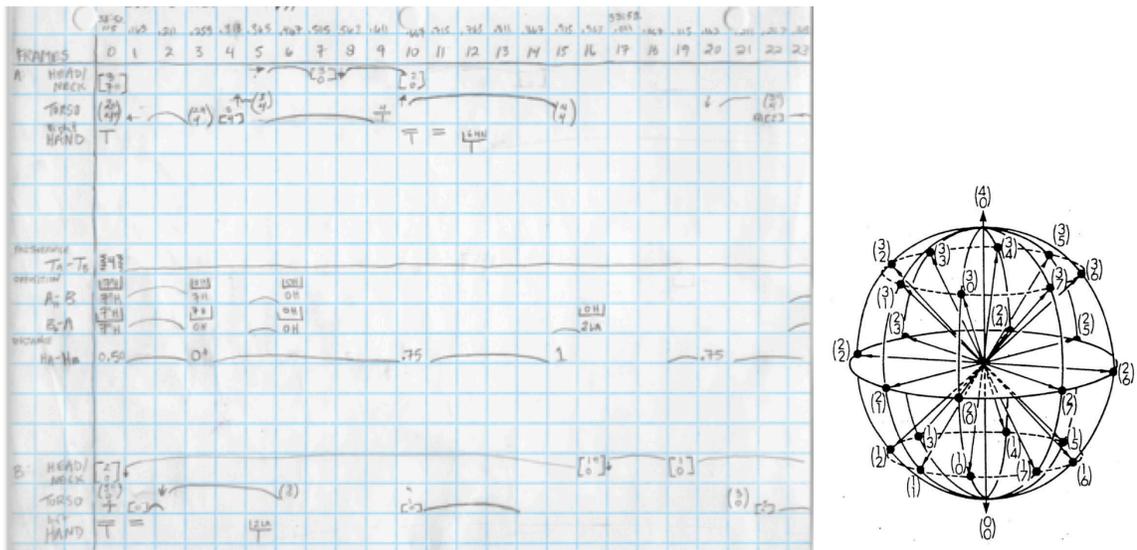


Figure 2.1: A section of an EWMN analysis grid along with a spherical representation of body/limb positions in which the measurements for the grid are based.

For the present analysis, the location in space of each monkey's head/neck, torso, and hands were notated, as was the orientation of each monkey's head in opposition to the closest body part of its partner. The distance between both players was recorded using an

approximate distance measure of ‘head length’ measured from the tip of the nose to the back of the head for each species. The locations of the body parts combined with the opposition and distance information provide a picture of the dynamic interactions occurring between both players. Because the EWMN permits the observer to juxtapose the same movements in different frames of reference, it permits the detection of what is most salient to the animals at any given moment in the interaction (Golani, 1976). In this way, the analytical approach helps the human observer to decipher the *umwelt* of the participants in an encounter.

Quantitative Analysis

EWMN derived measurements: Following the EWMN analyses, an additional set of 20 Guinea baboon sequences and 18 drill sequences fitting the above criteria were chosen for less detailed frame-by-frame analysis, but one that allowed us to verify that the general pattern revealed by EWMN was consistently present. The beginning frame of each play sequence was identified as before, then the frame of the first bite by one partner and that of the other were identified, as was the cessation of biting. The first and last frame of physical contact was also identified, along with the first and last frame of torso-torso contact. Finally, the frame on which play fighting ceased was identified. This simplified EWMN-type score enabled sequences to be juxtaposed to evaluate similarities and differences among sequences and between the species (see Figure 2.4 below).

Furthermore, this qualitative analysis provided the framework from which to extract quantitative measurements that reflected the differences in the pattern of play in the two genera *Papio* and *Mandrillus* (see below).

Targets: The offensive and defensive bites were recorded from play fight scenes where the targets could be clearly determined; this included successful and unsuccessful bite

attempts. If the target was not clear, it was labeled as an unidentified target (UT) and the bite was not included. The number of offensive bite attempts recorded from each species are: G. baboons = 78, H. baboons = 85, drills = 104, and mandrills = 57. The number of defensive bite attempts recorded from each species are as follows: G. baboons = 46, H. baboons = 30, drills = 45, and mandrills = 14. The location of the bites were scored onto five divisions of the body (based on Reinhart et al., 2010): (1) Head/Face/Cheek (H/F/C), (2) Neck/Shoulder/Upper Arm (N/S/UA), (3) Body (B), including all areas of the back, side, stomach, and rump, (4) Lower Arm/Hand (LA/H), and (5) Leg/Foot (L/Ft). Since differences in tactics can arise from differences in the body areas being targeted (Pellis & Pellis, 1997), the distribution of bites by the monkey giving the offensive bite and the defensive bite were noted separately.

Tactics: In order to defend oneself, different tactics may be adopted while play fighting. In this case, the monkeys could remain standing or adopt a supine position to protect their own target. To assess whether supine postures arise because of the tactics adopted by the defending monkey, the use of two types of tactics when the monkeys initially confronted one another face-to-face were scored. In one tactic the defender raised up onto its hind feet and grasped the attacker with the hands (upright tactic/*U*) and in the other, the defending monkey rolled around its longitudinal axis (rolling tactic/*R*). These data were obtained from 161 Guinea baboon scenes, 38 Hamadryas baboon scenes, 71 drill scenes, and 51 mandrill scenes. To assess the use of tactics throughout the length of the scene, play fights were scored for whether one or both partners were laying on the ground, either on their sides or backs (supine/*S*) at any time, as such postures promote bodily contact and prolonged bouts of play. These data were from 167 Guinea baboon scenes, 38 Hamadryas baboons, 69 drill scenes, and 51 mandrill scenes.

Bite Attempts (Success vs. Failure): For this measurement, cases of offensive and defensive bite attempts were included, even if the bites were made to unidentified targets, in order to calculate the total number of successful and failed bite attempts for each species. The number of offensive and defensive bites, respectively, are: Guinea baboons = 78, 46; Hamadryas baboons = 55, 30; drills = 104, 45; and mandrills = 57, 14. The success rate of each species was converted to a percentage in order to compare relative bite successes between the offending and defending monkey.

Play Fight and Bite Durations: To assess the length of encounters when a successful offensive bite was followed by a successful defensive bite, a number of play fights from all four species were compared. The Guinea baboon scenes (n = 20) and the drill scenes (n = 18) were the same ones first identified for use in the qualitative analysis. For the Hamadryas baboon and the mandrill, 13 play fights were chosen for each species using the same criteria as the Guinea baboon and drill scenes in regards to comparability: the monkeys approached each other from an upright position, the terrain was similar, bite targets were visible, and a successful defensive bite followed a successful offensive bite. The length of each bout was recorded in seconds and begins once the monkeys are engaged with one another, either by making eye contact or by approaching one another.

In addition, the duration of biting during play fighting was measured in two ways: as the number of frames of biting (converted to sec) and as the proportion of time in which bites lasted relative to the length of the play bout. A bite was considered to have begun at the first moment of contact with the target and ends at the last moment of contact with the target. The length of each offensive bite and each defensive bite were recorded separately. Also recorded were the frames that encompassed mutual biting,

where both animals are contacting their respective targets, in order to examine the percent of the play fight where biting overlaps.

Torso-Torso Contact Durations: An additional measure was taken for each species from the same scenes used to collect the duration data above, except the asymmetric drill pairs were removed (G. Baboon = 20; H. Baboon = 13; drill = 13; mandrill = 13). These play fights were removed because they were not comparable to the other three species, but play fights with similar sized pairs were. For example, larger drills use their size to hold the smaller drill down on the ground, creating longer than usual torso-torso contact while in a horizontal position, rather than in a vertical face-to-face position. As soon as monkey A and monkey B begin to have any physical contact during the play fight, the starting frame was recorded along with the frame the contact ended. Also recorded were the first and last frames that the monkey's torsos were in contact. The number of frames was converted to seconds in order to measure the proportion of time in which the monkeys were in torso-to-torso contact relative to the length of total physical contact.

Statistical Analysis

Given that in most cases members of each troop could not be consistently tracked as individuals, this limitation was taken in to consideration during the analysis. Although, it should be noted that in many videotapes more than one dyad was playing in the frame, which revealed that different pairs played in a similar manner, making it unlikely that species-typical patterns arose due to one aberrant member from each troop. For data involving categorical and interval scales, nonparametric tests, such as the Kruskal-Wallis, the chi-square, the Mann-Whitney U, and Spearman's rho were used (Siegel & Castellan, 1988). Appropriate Bonferroni corrections were used to adjust for multiple pairwise

comparisons following a successful nonparametric ANOVA or Chi square analysis.

Results were considered significant if $p < 0.05$.

Results

Qualitative analyses

The EWMN analysis of the two sequences revealed the basic organizational similarity in the play fighting of the Guinea baboon and the drill, but also highlighted how they may differ. In both species, the sequences begin similarly, as one partner approaches, grabs its partner and lunges to bite the shoulder area. The recipient of the attack can move to avoid the bite and/or deliver a retaliatory bite, typically to the side of the face.

Repeated sequences of such attack and defense proceed during the playful encounter, but as Figures 2.2 and 2.3 show, there are also some marked differences. The drills keep their bodies separated at arms length, whereas the baboons hold each other close, pressing their bodies close together, moreover, throughout the sequence the drills remain upright, whereas the baboons often roll around the ground. Most striking is the difference in the pattern of biting. In Figure 2.4, the percentage of the play fight involving biting is illustrated, with the top panel showing a sequence from the baboons (5.66 s) and the bottom panel showing a sequence from the drills (4.50 s). The offensive and the defensive bites in the baboon sequence encompass 75% to 81% of the bout, respectively, compared to 18% and 6% for the drills.



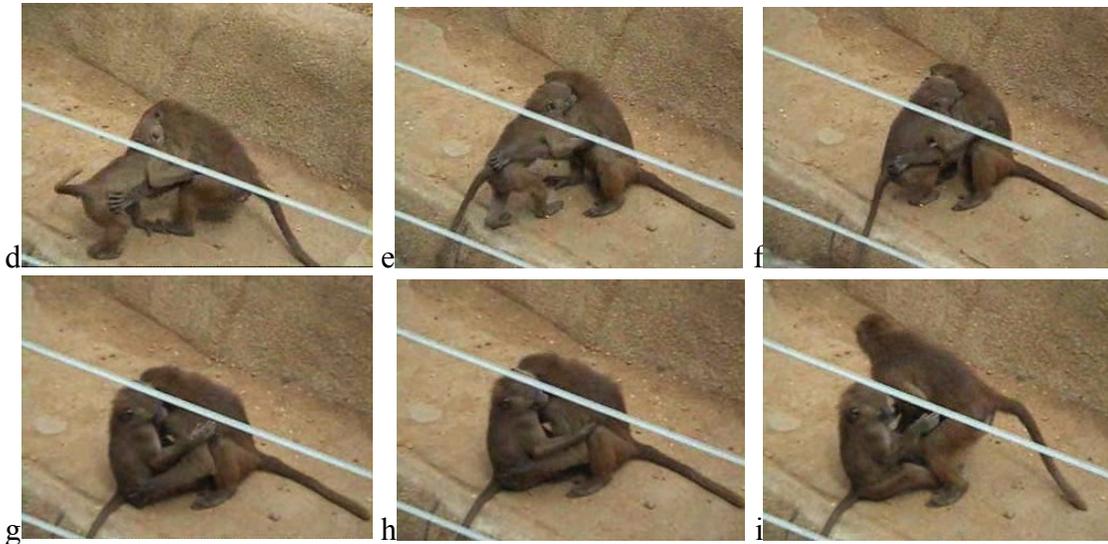


Figure 2.2 (a-i): Still frames taken from the computer screen illustrate play fighting in Guinea baboons (see text for a detailed description).



Figure 2.3 (a-i): Still frames taken from the computer screen illustrate play fighting in drills (see text for a detailed description).

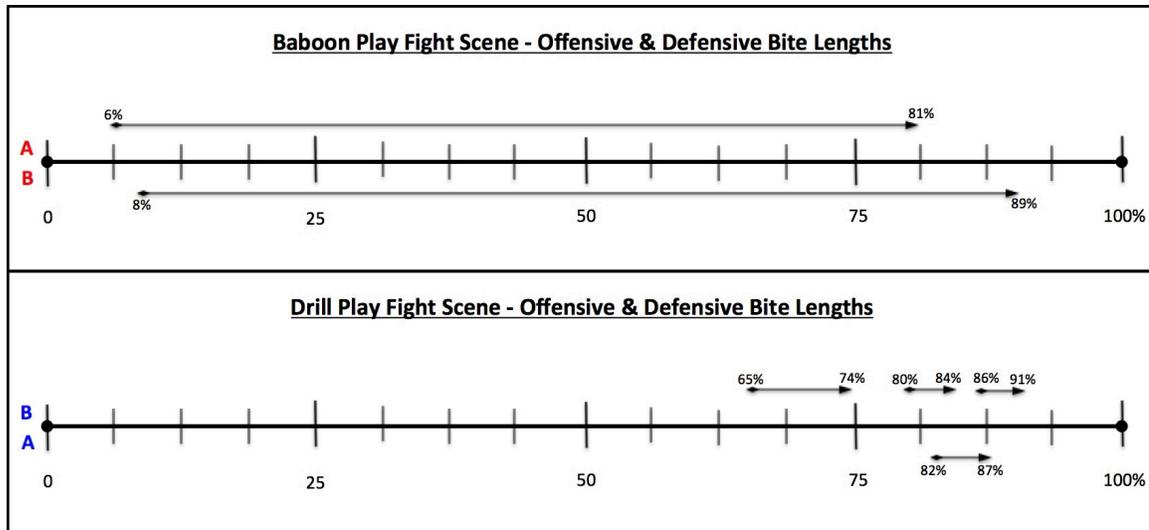


Figure 2.4: Shows the duration (percent) of biting by both opponents during a play fight. The monkey delivering the first bite, the offensive bite, is shown above the horizontal scale line for percent duration.

Not only does Figure 2.4 reveal the difference in the proportion of the encounter spent in biting, but also in how offensive and defensive bites relate to one another. The offensive and defensive bites have a long period of overlap in baboons, whereas in drills the offensive bite is quickly terminated with the onset of the defensive bite. This is illustrated in Figures 2.2 and 2.3: baboon A contacts the shoulder of baboon B (c) who retaliates with a shoulder bite and the baboons stay in this mutual biting position for most of the play fight (h) until baboon B stands up, turns, and leaves (i); drill A is about to bite drill B's shoulder (g) who in turn is about to retaliate with a bite to drill A's cheek (h) and subsequently drill A releases its bite, ducks under drill B's body to avoid being bitten, and then drill B turns and leaves (i).

The hamadryas baboons look similar to the guinea baboons in regards to overlapping bites, close contact, and rolling on the ground. In Figures 2.5 both baboons approach each other and baboon A contacts the shoulder of baboon B (b) who also bites

the shoulder of his attacker (c), when they stop biting one another they still remain close (e) until they roll on the ground and baboon A bites the neck of baboon B (g-i).

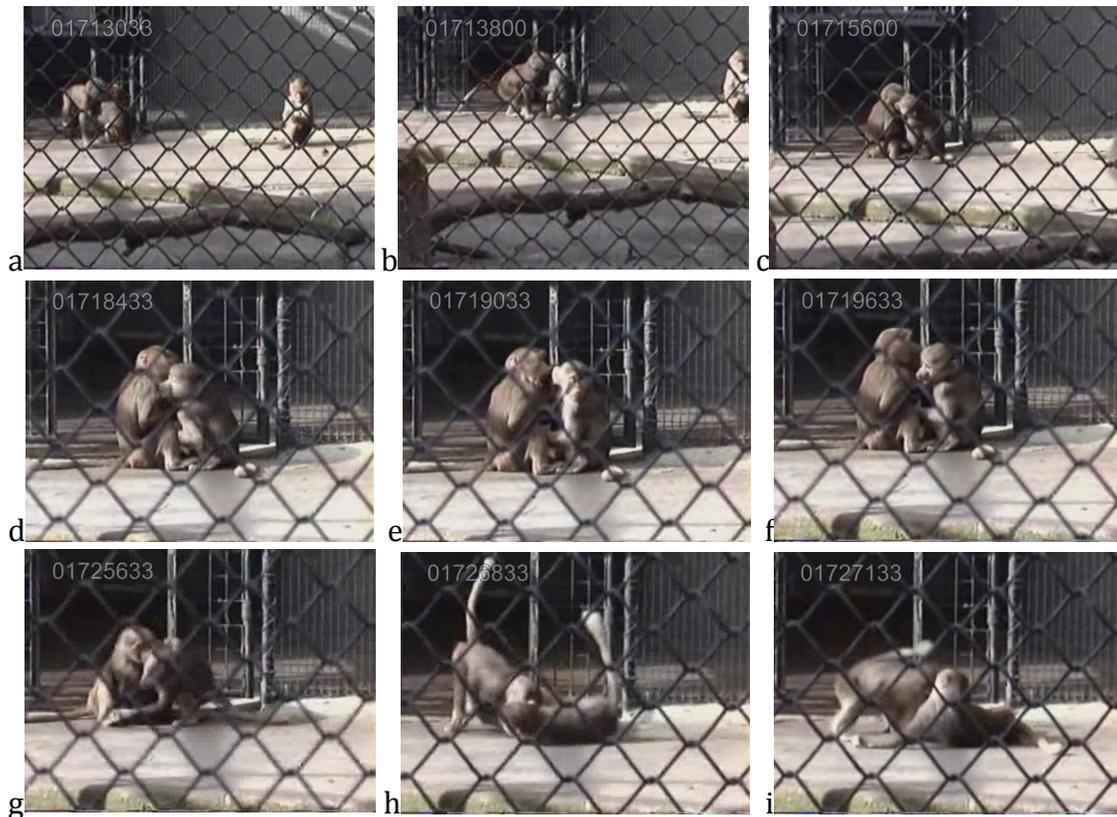


Figure 2.5 (a-i): Still frames taken from the computer screen illustrate play fighting in Hamadryas baboons (see text for a detailed description).

After analyzing the play of *Mandrillus sphinx*, two things became evident: the mandrills appear similar to the drills in that they use their arms to keep their distance from one another and similarly less bite overlap occurs (Figure 2.6), but also, they engage in a type of leaping play that lacks physical contact (Figure 2.7). The presence of the leaping play makes the mandrills different from the other species in this study that did not exhibit this type of play. That this was not an aberrant pattern limited to the troop that I examined is suggested in Emory's (1975) paper on mandrill and gelada play interactions, which included a category of non-contact bouncing play that he observed in both species, but found to be more frequent in the mandrills.



Figure 2.6 (a-i): Still frames taken from the computer screen illustrate play fighting in mandrills (see text for a detailed description).



Figure 2.7 (a-f): Still frames taken from the computer screen illustrate leaping play fighting with no bite attempts in mandrills (see text for a detailed description).

Overall, the results from the qualitative analyses indicate that while both *Papio* and *Mandrillus* species compete to bite the same body target, there are differences in the use of tactics used to block the partner from biting the target, differences in how they respond to being bitten, and differences in the amount of biting and physical contact. Also, the less temporal overlap between offensive and defensive bites (see Figure 2.4) suggest greater opportunity for more attempts to deliver bites in drill play fights than in baboon play fights.

Quantitative analyses

Targets and tactics: The frequency of offensive bites is not randomly distributed across the body in all four species (G. baboons: $X^2 = 68.024$, $df = 4$, $p < 0.001$; H. baboons: $X^2 = 48.464$, $df = 4$, $p < 0.001$; drills: $X^2 = 67.684$, $df = 4$, $p < 0.001$; mandrills: $X^2 = 42.862$, $df = 4$, $p < 0.001$). The most frequently bitten area of the body in all species encompasses the neck, upper arm, and shoulder (N/UA/S) (Figure 2.8). Likewise, defensive bites were not randomly distributed in three of the four species: the Guinea baboons ($X^2 = 97.719$, $df = 4$, $p < 0.001$), the Hamadryas baboons ($X^2 = 42.062$, $df = 4$, $p < 0.001$), and the drills ($X^2 = 41.75$, $df = 4$, $p < 0.001$). The trend was similar, but not significant for the mandrills - a larger sample size would be required for a clearer assessment.

However, differences were found in the body area most frequently bitten defensively. Comparisons of the distribution of retaliatory bites to the HD/F/C and the N/UA/S areas in all four species were significant ($X^2 = 9.5352$, $df = 3$, $p = 0.02296$). *Papio* species were more likely to retaliate with bites to the N/UA/S area, whereas *Mandrillus* species were more likely to direct retaliatory bites to the H/F/C area (Figure 2.9). Although, the largest difference is seen in the drills when they are compared in a pairwise fashion with both baboon species (GB+D: $X^2 = 8.1065$, $p = 0.004411$; HB+D: X^2

= 5.7841; p 0.016172). Meaning that the drills and the mandrills are similar in their defensive targets, but the drills differ the most from both of the baboon species.

With regard to initial defensive maneuvers used when evading a bite to the play target, there is a significant difference when comparing all four species ($\chi^2 = 20.8826$, $df = 3$, $p = 0.000111$). The Guinea baboons drive this difference as they significantly differ from the other three species when compared pairwise (GB+HB: $\chi^2 = 4.357$, $p = 0.036857$; GB+D: $\chi^2 = 12.1476$, $p = 0.000491$; GB+M: $\chi^2 = 11.6329$, $p = 0.000648$). Figure 2.10 illustrates that while all four species are most likely to adopt an upright tactic, both baboons are more likely to actively gain the supine position, especially the Guinea baboon.

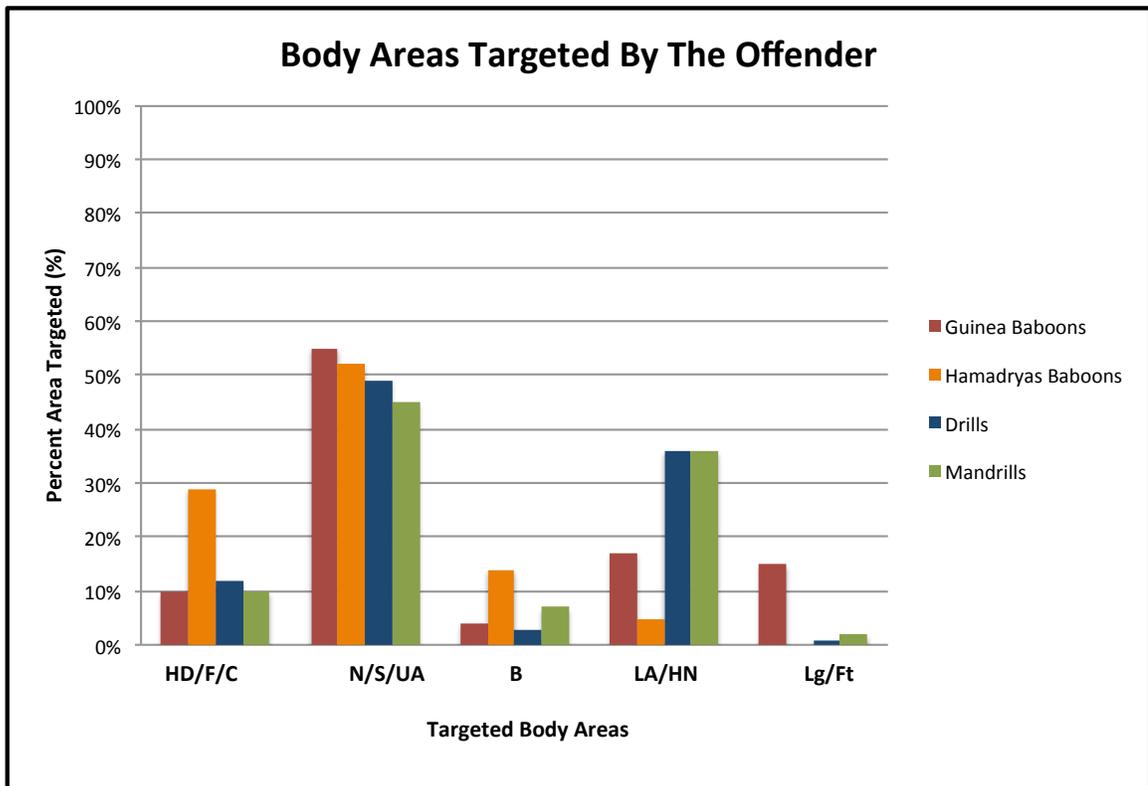


Figure 2.8: The frequency distribution of offensive bites across the body is shown for both species. Number of offensive bite attempts: G. baboons = 78, H. baboons = 85, drills = 104; mandrills = 57.

During the entire length of the play fight, it is possible that one or both partners may end up lying on their sides or back in defense even if it was not the initial tactic. Comparing these instances of supine positions in all four species shows a significant difference amongst them ($X^2 = 55.872$, $df = 3$, $p < 0.00001$). The pairwise results reveal that both *Papio* species are similar to one other, as are the *Mandrillus* species, and that the difference is at the genus level (GB+D: $X^2 = 31.175$, $p < 0.001$; GB+M: $X^2 = 26.7638$, $p < 0.001$; HB+D: $X^2 = 26.3515$, $p < 0.001$; HB+M: $X^2 = 24.4262$, $p = 0.000001$). Both baboon species are more likely to adopt defensive tactics during a play fight that lead to the increased prevalence of supine positions when compared to the drill and mandrills. The rare use of supine positions throughout a play fight by the *Mandrillus* species is also shown in Figure 2.10.

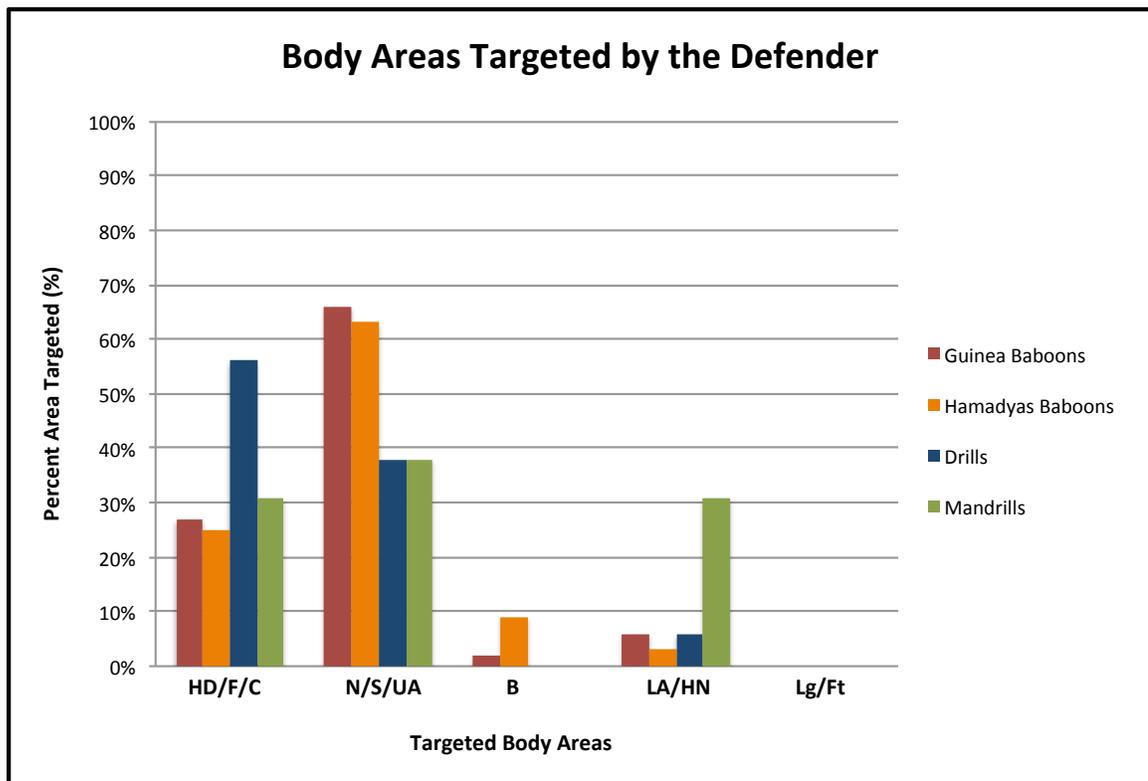


Figure 2.9: The frequency distribution of defensive bites across the body is shown for each species. Number of defensive bite attempts: G. baboons = 46, H. baboons = 30, drills = 45; mandrills = 14.

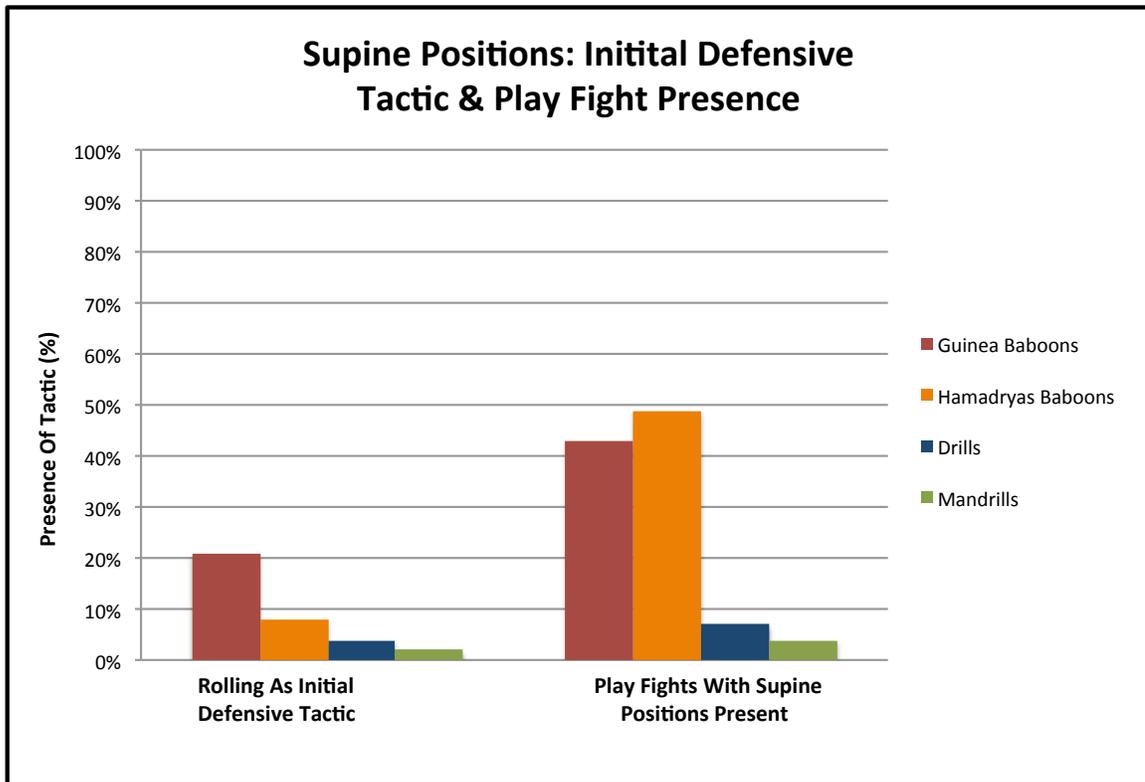


Figure 2.10: Actively rolling over on to its side or back as an initial defensive tactic is more common in *Papio* than in *Mandrillus* species. (Number of initial tactics: G. baboons = 161, H. baboons = 38, drills = 71; mandrills = 51.) Ending up lying on the ground sometime during the encounter is also more common in *Papio* than in *Mandrillus* species (Number of play fights: G. baboons = 167, H. baboons = 38, drills = 69; mandrills = 51.)

Bite success vs. failure: When comparing the total number of offensive and defensive bite attempts in all four species, there is a significant difference in the frequency of success rates ($X^2 = 87.1208$, $df = 3$, $p < 0.00001$). Pairwise comparisons revealed that both *Papio* species are similar to one another, but they each differ from the *Mandrillus* species, which, in turn, differ from each other (GB+D: $X^2 = 42.9496$, $p < 0.001$; GB+M: $X^2 = 70.9658$, $p < 0.001$; HB+D: $X^2 = 17.845$, $p = 0.000024$; HB+M: $X^2 = 38.1593$, $p < 0.001$; D+M: $X^2 = 8.6166$; $p = 0.00331$). Though the drills had the most bite attempts ($n = 149$) of all four species, they experienced less success than the Guinea baboons ($n = 124$)

and the Hamadryas baboons (n = 71), who had less bite attempts, but experienced more success. In general, the *Papio* species have more successful bite attempts than the *Mandrillus* species when offensive and defensive bite attempts are combined.

Upon repeating this analysis, but for offensive and defensive bites separately, the results also showed that the frequency of successful and unsuccessful bites are not randomly distributed (Offensive: $\chi^2 = 69.9868$, $df = 3$, $p < 0.00001$; Defensive: $\chi^2 = 15.6256$, $df = 3$, $p = 0.001353$). For offensive bites, a pairwise comparison showed that the Guinea baboon and the Hamadryas baboon were similar in regards to success rates, but they differ significantly from the drill and mandrill, who also differed from one another (GB+D: $\chi^2 = 30.3666$, $p < 0.001$; GB+M: $\chi^2 = 57.2375$, $p < 0.001$; HB+D: $\chi^2 = 13.1044$, $p = 0.000295$; HB+M: $\chi^2 = 32.9362$, $p < 0.001$; D+M: $\chi^2 = 9.2529$, $p = 0.002351$). In regards to defensive bite attempts, a pairwise comparison showed that the Guinea baboons were significantly different from both the *Mandrillus* species (GB+D: $\chi^2 = 12.1604$, $p = 0.000488$; GB+M: $\chi^2 = 9.0186$, $p = 0.002672$), while the Hamadryas baboons differed significantly only from the drills (HB+D: $\chi^2 = 4.6091$, $p = 0.031802$). Figure 2.11 illustrates the success rates of offensive and defensive bite attempts and shows that the *Papio* species are more successful than the *Mandrillus* species are for both bite types. In other words, the drill and mandrill are organizing their play fights in such a way that bites do not contact the intended target area as easily, or as often, as they do in both baboon species.

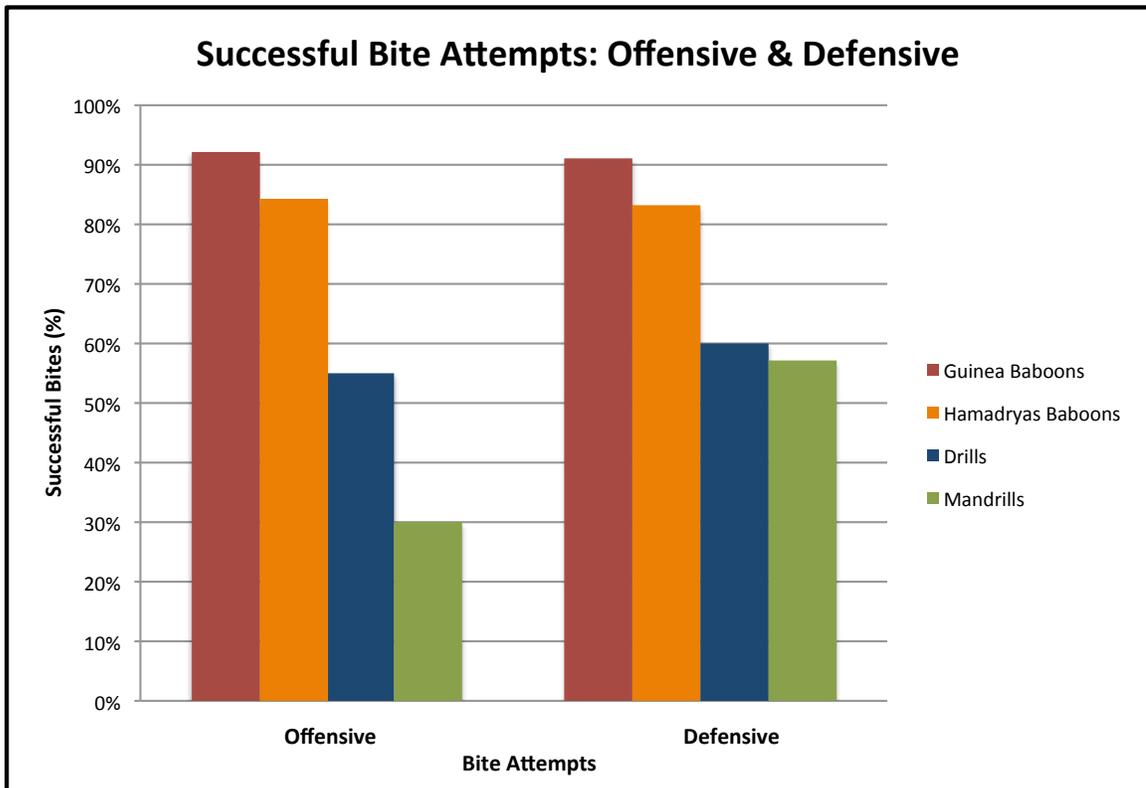


Figure 2.11: The frequency of biting during play fights is shown for both successful offensive and defensive bites. Number of bite attempts: Guinea baboons = 124, Hamadryas baboons = 85, drills = 149; mandrills = 71.

Duration of play fights and of biting: The duration of play fights in which a successful offensive bite is followed by a successful defensive bite showed significance for all four species ($H = 9.424$, $p = 0.0242$). Figure 2.12 shows the median play fight lengths for the Guinea baboon, the Hamadryas baboon, the drill, and the mandrill. It is apparent in the figure that the Hamadryas baboons have the largest median value; moreover, results from the pair-wise comparisons showed that they were significantly different from the Guinea baboons ($U = 58$, $X^2 = -2.63433$, $p = 0.00854$) and the mandrills ($U = 38.5$, $X^2 = 2.33333$, $p = 0.0198$). The Guinea baboons, drills, and mandrills, however, were similar to one another in this regard. When comparing the lengths of the successful offensive and defensive bites that occurred in the aforementioned play fights, all four species did not

significantly differ from one another (Table 2.1), meaning that when these bites do occur, they are relatively similar in length from start to end.

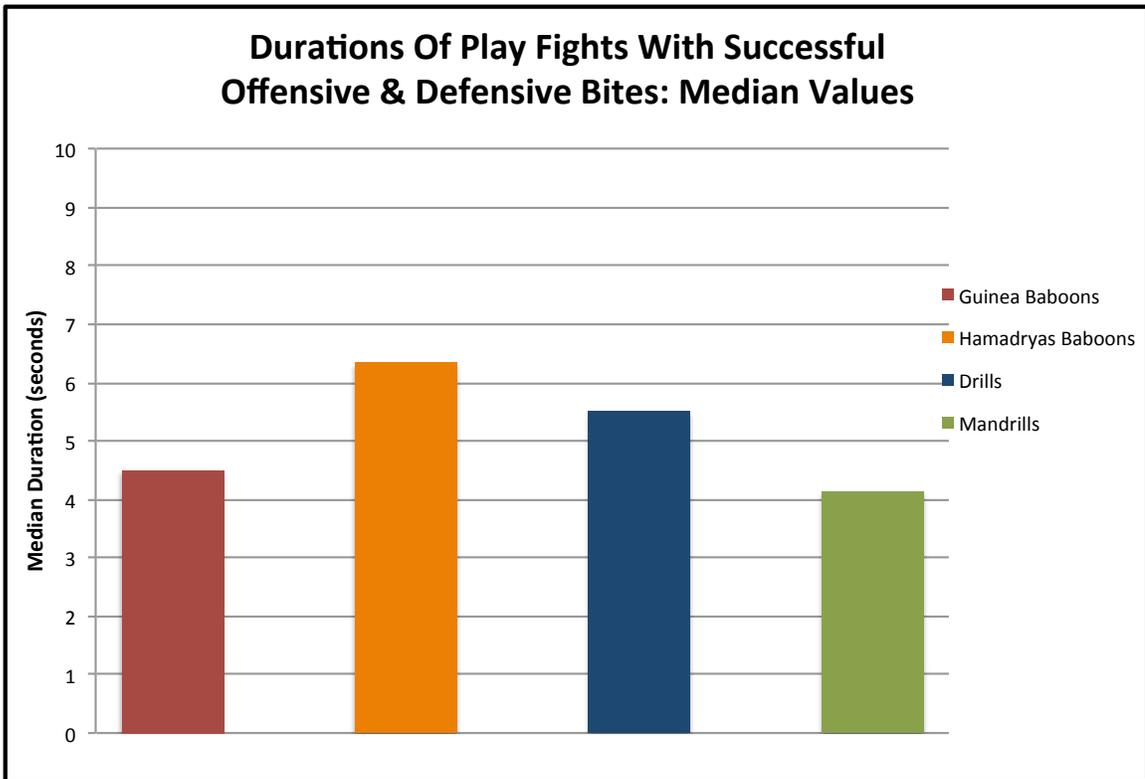


Figure 2.12: The duration of play fights involving biting is significant when comparing all species ($H = 9.424$; $p = 0.0242$)

Table 2.1: Duration Of Offensive And Defensive Bites Shown In Seconds (Mean \pm SD)

Guinea Baboon	2.19 \pm 2.17	1.67 \pm 1.60
Hamadryas Baboon	4.09 \pm 4.03	3.51 \pm 3.38
Drill	1.52 \pm 1.34	1.25 \pm 1.98
Mandrill	1.32 \pm 0.88	1.36 \pm 1.30

The durations were not significantly different ($p > 0.05$).

When examining the total bite lengths converted to percentages of the total play fight, differences between all four species emerged ($H = 16.626$, $p = 0.0008$). These differences were found at the genus level, with both *Papio* species differing from both *Mandrillus* species (GB+D: $U = 75$, $Z = 3.05509$, $p = 0.00222$; GB+M: $U = 43$, $Z = 3.18699$, $p = 0.00142$; HB+D: $U = 56$, $Z = -2.42194$, $p = 0.01552$; HB+M: $U = 37$, $Z = -2.41026$, $p = 0.01596$). The amount of the play fight spent biting is very similar in the Guinea baboons (47.5%) and the Hamadryas baboons (48%), while the drills (35.25%) and mandrills (29%) are also similar (Figure 2.13). These latter results suggest that even though bite lengths do not significantly differ, it is the amount of time devoted to biting in each play fight that is notably different when all four species are examined.

When comparing the total time spent biting to the amount of mutual biting occurring in the same frames, there was no significant difference found between the species. However, when the data were re-examined in terms of the correlations between the variability in total bite time available and the variability in bite overlap time, significance was reached in the Guinea baboons ($r_s = 0.68452$, $p = 0.00087$) and the mandrills ($r_s = 0.95991$, $p < 0.0001$). The correlations are illustrated in Figure 2.14 for both *Papio* and *Mandrillus* species; the results show that for the Guinea baboons and the mandrills, 53% and 80%, respectively, of the variability in the bite overlap time can be attributed to the variability in the amount of the whole interaction that involves biting. The Guinea baboons and mandrills are more likely to exhibit mutual biting than the Hamadryas baboons and the drills are. In other words, there is more of a chance for bites to overlap if more of the play fight involves biting in general, however, this seems to be true only for the Guinea baboons. It was shown above that both of these species significantly differ from one another when total bite proportions are compared. In this

case, there must be another factor responsible for the high correlation seen in the mandrills.

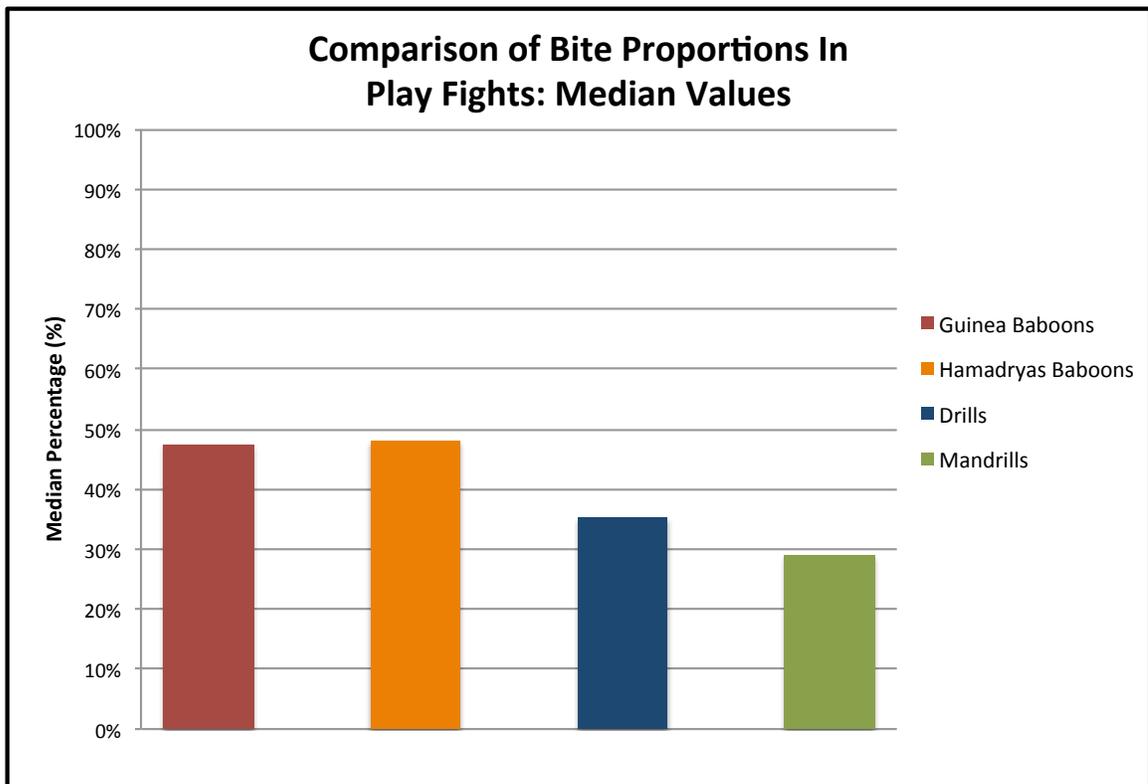


Figure 2.13: The percent of the play bout involving biting is significant when comparing all species. ($H = 16.626$; $p = 0.0008$).

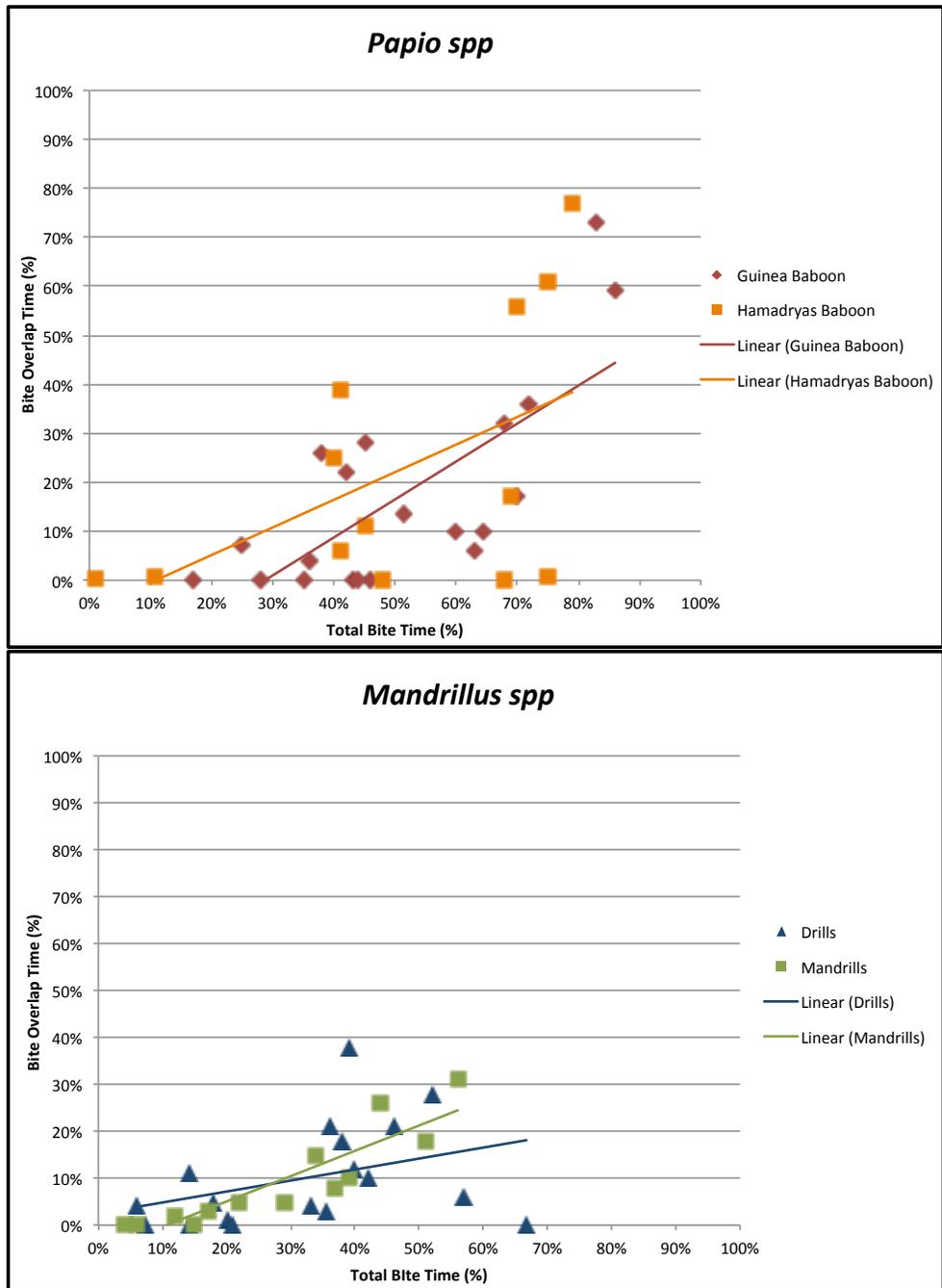


Figure 2.14: Shows the correlations in both the *Papio* and *Mandrillus* species between the variability of overall bite times and the variability of bite overlap times. The correlation only achieves significance in the Guinea baboons and Mandrills.

Duration of torso-torso contact: The proportion of torso-torso physical contact made by the monkeys while playing is significant when all four species are compared ($H = 14.719$, $p = 0.0021$). Pairwise analyses followed the same pattern shown for the bite proportion

results: the *Papio* species do not differ from one another, nor do the *Mandrillus* species, but significance is achieved at the genus level (GB+D: $U = 60.5$, $Z = 2.54222$, $p = 0.01108$; GB+M: $U = 59.5$, $Z = 2.57907$, $p = 0.00988$; HB+D: $U = 32$, $Z = 2.66667$, $p = 0.00758$; HB+M: $U = 32$, $Z = 2.66667$, $p = 0.00758$). Both baboon species spend a larger proportion of physical contact in a torso-torso configuration, while the drill and mandrill appear to try harder to prevent such positions. Figure 2.15 illustrates the median percentage of time each species spent torso-torso while play fighting.

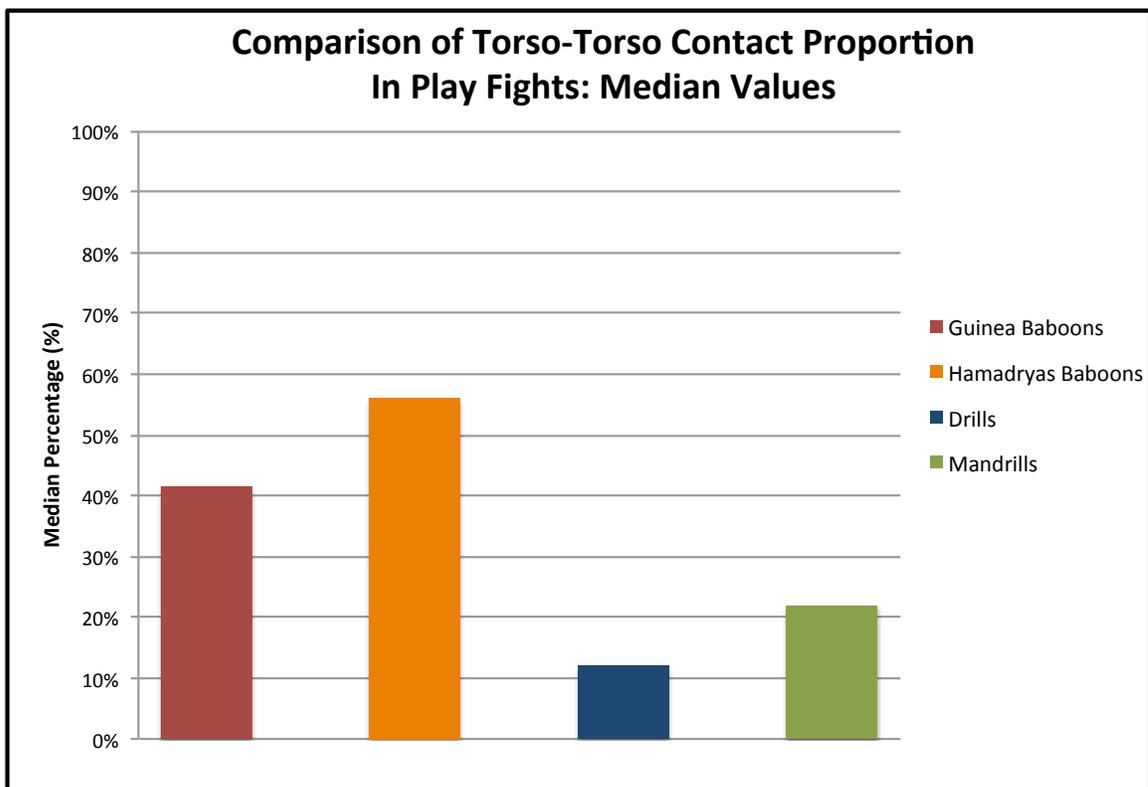


Figure 2.15: The percent of the play bout involving torso-torso contact is significant when comparing all species. ($H = 14.719$; $p = 0.0021$).

Discussion

The results show that the target areas competed over when attempting to deliver a playful bite are similar in all four species - Guinea baboons, Hamadryas baboons, drills, and mandrills - mainly the N/UA/S area. The data are consistent with the targets sought

after in the play fighting of other Old World primates (Pellis & Pellis, 1997; Pellis et al., 2014; Reinhart et al., 2010). Species differences emerge when looking at the frequency of defensive bite locations. Retaliatory bites are mostly either directed to the primary play target (N/UA/S area) or the HD/F/C area (essentially the side of the face). In serious fighting bites to the side of the face are highly defensive, increasing the likelihood that the attacker ceases its attack as it shifts to protecting its face (e.g., Blanchard et al., 1977; Pellis & Pellis, 1987). Similarly, during play fighting species that retaliate more often to the face are more likely to induce a defensive response in the partner that leads to termination of the play session (Pellis et al., 1989). In this way, differences in the targeting defensive, retaliatory bites may reflect species differences in the degree to which the play is cooperative relative to competitive (Reinhart et al., 2010).

The *Mandrillus* species had a stronger preference for targeting the HD/F/C area than did the *Papio* species, although this preference was weaker in the mandrills than the drills. In addition, Figure 2.8 shows a higher tendency in the *Mandrillus* species to target the LA/HN area offensively, however, these bites may have actually been defensive bites, but, due to the way the data was scored, they fell in the offensive category. During data collection, the first monkey to deliver a bite was labeled as *offender*, but in the case of the drills and the mandrills, many bites were aimed at the hands of the *would-be* offender as they were reaching to grab the partner - meaning that those bites were most likely more of a preemptive defensive bite rather than a purposeful lunge toward that target as an offensive preference. A similar methodological problem in differentiating between offensive and defensive bites to the partner's hands has been encountered in other species that do a lot of grappling in their play, such as is the case with spider monkeys (Pellis & Pellis, 1997). So, the primary genus level difference that would seem most important in

comparing the four species is that *Mandrillus* is more likely to retaliate against the face than is *Papio*.

The defensive tactics adopted during the play fights also showed species differences at the genus level. While the rotating to supine defensive tactic was the least likely to be used to face the offender, it was more frequently used as the initial pattern of defense in *Papio* compared to *Mandrillus*. The genus difference became even greater with the general appearance of supine positions at any time during the encounter, not just as the opening maneuver (Figure 2.10). The use of these supine positions influenced the content of play fights. For example, these positions, which include laying on either the back or the side, provide more opportunity for close body contact, which can then facilitate more biting as the targets are more readily available. The Guinea baboons are more likely than the other three species to actively roll to a supine position as an initial defensive tactic, while both baboon species show similar use of these tactics throughout the length of the play fight. The drill and mandrill use supine positions very rarely and are similar to one another in this aspect. In contrast, actively remaining upright to defend against an attack, which is more common in the *Mandrillus* species, produces a different structure than those play fights that include supine positions - there is less bodily contact and the opportunities for biting are fewer. Thus, although the bite targets are relatively similar for all species, differences in the structure of play fighting emerge when defensive tactics are compared. These differences in tactics led to differences in several of the measures scored.

The success rates of biting when offensive and defensive bites are combined show a significant difference between *Papio* and *Mandrillus*, with the baboon species being more successful at biting the target. The same was true for both offensive and

defensive bites (Figure 2.11). The lengths of play fights that include both successful offensive and defensive bites differed when all species were compared. Closer analysis showed it is the Hamadryas baboons that have the longest median play fight length (6.339 s), and they differ significantly from the Guinea baboons and the mandrills, with the drills being the closest in length (median = 5.505 s). In order to see if the lengths of the individual offensive and defensive bites were contributing to the differences in lengths of play fights, each bite in the successive play fights was recorded in seconds and the species were all compared. However, no significant differences were found. Meaning that even though the lengths of play fights differ among the species, especially the Hamadryas baboons, when successful bites were made the length of contact from start to end was relatively similar in all four species. Given that the baboon species have a similar pattern of play, the difference between them in play fight lengths cannot be attributed to target preference, tactic use, bite success rate, or bite length. There must be something else, therefore, in causing the Hamadryas baboons to have longer play fights than Guinea baboons.

In an attempt to further analyze the content of the play fights, the duration of offensive and defensive bites was converted to a percentage of the total duration of the play fight. Both *Papio* species devoted more of the play fight to biting than the *Mandrillus* species did; this suggests that no matter the length of the play fight, the *Papio* species are spending more time biting than the *Mandrillus* species are. Conversely, this implies that the time spent *not* biting in the *Mandrillus* species is being used in a different manner, namely, to prevent successful bites by maintaining their distance from one another. Before the measure of distance is explored further, one more measure of biting was examined: mutual bite overlap.

The results showed that the time spent mutually biting is not significantly different across species, meaning that most bites occur in more of a back and forth pattern between the offender and the defender. However, the range is very large and the highest values are found in the Hamadryas baboons. It appears that the *Papio* species are more likely to be observed in close bodily contact than are the *Mandrillus* species, which allows for the opportunity to mutually bite one another during a play fight. When the variability of total bite time was compared with the variability of bite overlap time, the results showed strong correlations in the Guinea baboon and the mandrill, meaning that the more time that biting occurs for, the higher the chance that mutual biting will also occur.

The differences between the distances the two playing partners kept from one another was visually evident in the play fights; the different use of tactics confirms that the *Papio* species are more likely to adopt positions allowing for close-contact. In order to quantitatively evaluate this apparent difference, the proportion of time during play fights in which the partners were in torso-to-torso contact was measured. Again, the difference was found at the genus level, with the drills and mandrills spending less time with their torsos in close contact with one another than was the case for the baboons (Figure 2.15).

Play Fighting - Emphasizing Pleasurable Rewards?

The study showed that as predicted all four species compete to bite the same body targets and use a similar suite of tactics to do so. That is, the organization of their play fighting is like that of other Old World monkeys. However, given the similarities in body morphology and social organization across the four species, it was also predicted that the style of competition should also be similar among these species. This prediction was not

confirmed, as some aspects of the style of play fighting differed across the genera and to some extent within the genera.

Both baboon species seem to emphasize biting the target as the goal of the play fight; while drills and mandrills seem to emphasize the tussle, the act of defending their own target (with mandrills also injecting many jumps in to their play fights). When the baboons make contact with their partner's target area, they can end up in a mutual biting position if their partner has also reached their respective target. On the other hand, dyads of similar-sized drills intensely defend their targets with lots of hand/arm blocking, subsequently sacrificing their own contact with (or length of contact with) their partners target area. For them, it seems that the primary goal could be keeping their own target free from contact, while biting their partner's target is more of a secondary goal. This difference could be related to the amount of close bodily contact that each species is able to withstand. In this way, it seems that both *Papio* species are more tolerant of contact than are the *Mandrillus* species.

Both baboon species spent more time during play fighting biting one another and doing so while maintaining close bodily contact, with the play of *Hamadryas* baboons being more exaggerated in these regards. Similarly, both *Mandrillus* species spent more time competing for access and less time in actually biting, with the non-contact playful interactions by the mandrills being an exaggerated version of this pattern. There are two issues to be resolved concerning these genus and species differences. The first concerns the mechanisms that produce play fighting and how these may be varied to produce these different styles. The second concerns why species so similar to one another in so many regards should play in these different styles.

In a seminal comparative study of play fighting, Aldis (1975) showed that participants of play fights gain two rewards from such engagement – bite the play target and generally mouth the partner. That these two represent two separate motivating factors has subsequently been corroborated. For example, when play fighting, a pair of oriental small-clawed otters compete to bite each other on the cheeks, but when a third joins in, it will target the animal in the defensive position and mouth its hind feet and tail (Pellis, 1984). This pattern has been further documented in other primate and non-primate species (Pellis, 1981; Reinhart et al., 2010). These findings suggest that players find both biting/mouthing the partner rewarding and competing to access a particular body target rewarding. The two may overlap, but they are distinct motivating factors. Decades of work on the play fighting of rats has shown that engagement in play activates the reward mechanisms of the brain (Vanderschuren et al., 2016; Siviý, 2016), but that while successfully contacting the play target is rewarding it is not as rewarding as when the animal actively competes with the partner to gain that access (Pellis & McKenna, 1995). Indeed, in a recent study of play fighting in wart hogs, it was found that even when the play target was readily accessible, the animal bypassed the target to initiate a play fight with the partner to only then maneuver to overcome the partner's defensive actions to contact the same body target it previously bypassed (Pellis & Pellis, 2017a). Together, these experimental and comparative studies show that there may be multiple rewards emanating from engaging in play fighting and it is possible that different rewards may have a different salience in different species.

Both the *Mandrillus* and *Papio* species engage in competitive play fighting as the partners maneuver to gain access to the partner's play target and simultaneously protect their own play target from the partner's mouth. However, given what we know

about the reward mechanisms motivating play, it is possible that different mechanisms are predominant in the two genera. For *Papio* the salience of biting is greater than the salience of competing, whereas for the *Mandrillus*, the salience of competing is greater than the salience for biting. A greater emphasis on one reward relative to the other may be sufficient to account for the genus-level differences in style of play fighting. A simple way to produce these differences could be in how much an animal tolerates being bitten – for the baboons biting is sufficiently rewarding to tolerate being bitten back. That for *Mandrillus*, biting the partner is rewarding is suggested by the asymmetrical contests when a larger partner plays with a smaller one. The larger partner held the smaller animal firmly pressed to the ground and then proceeded to deliver bites. These bites were of longer duration than the case for symmetrical contests, when the partner was better able to retaliate with its own bites. That is, drills find biting a partner rewarding, but being bitten is aversive, so in symmetrical contests bites are brief and intermittent. In contrast, in baboons bites are longer because to maintain the bite the animal tolerates being bitten.

In these regards, some of the idiosyncrasies within genera may also be explained – the Hamadryas baboon shows a more exaggerated baboon pattern and the mandrill shows a more exaggerated version of the *Mandrillus* pattern. Unfortunately, insufficient knowledge exists about the psychological and neural mechanisms underlying play fighting beyond what is known in rats (Vanderschuren et al., 2016; Sivi, 2016), to develop suitable experimental tests to evaluate whether these hypothesized mechanisms account for the differences between *Mandrillus* and *Papio*. What the present study does highlight is that what animals find rewarding may differ even amongst closely related species, and so caution should be exercised when generalizing from a supposedly ‘model’

species. Our comparative knowledge is far from sufficient to know what would be an ideal model species (Pellis & Pellis, 2017b).

There is evidence that species that differ in social style also differ with regard to their style of play fighting as juveniles – species with more despotic social systems have styles of play that emphasize competition, whereas species with more egalitarian social systems have styles of play that emphasize cooperation (Cianni et al., 2012; Palagi, 2006; Reinhart et al., 2010). Moreover, species with a more lithe build generally incorporate more acrobatic maneuvers into their play fighting compared with heavier set animals (Pellis et al., 2014; Reinhart et al., 2010). However, given the similarities in social systems and body morphology across the four species in this study, it is unclear why they should differ in play styles. Given that the biggest differences were across the genera, one possibility is that there are historical factors involved that are not evident in the current biology and lifestyles of the extant species. For some features of social behaviour, including play, sometimes the phylogenetic ancestry of the species can explain more of the variance than can current aspects of their socioecology (Thierry et al., 2000). A much larger data set of species across the full range of lineages comprising the Old World monkey family would be needed to test statistically whether a phylogenetic signal influences the style of play or whether some other, more subtle socioecological factors need to be taken into account (O’Meara et al., 2015; Pellis & Iwaniuk, 2000). Again, though, the present study suggests caution in assuming that animals with similar social systems and similar body morphologies are likely to play similarly.

Informal Pilot Study: Children's Story - Target Audience Assessment

The children's story entitled "Every Day I Like To Play, I Like To Play In Every Way!" was written in partial fulfillment of the requirements for a Master's of Science degree. The story is about human and animal play behaviour and is intended for children, both boys and girls, in the age range of 3-4 years old. It is meant to be more entertaining than educational, though the content is factual and based on the real characteristics of play. Children's literature can be a useful medium for introducing scientific concepts to young children. By presenting factual information in the form of a narrative, children might find it easier to understand difficult scientific concepts (Morrow et al., 1997, as cited in Sackes, Trundle, & Flevares, 2009). Also, developmentally appropriate scientific literature can foster curiosity and create opportunities for children to ask questions about the content (Sackes et al., 2009).

The main character in the story is a little girl who describes the events of her day, from morning to night, which are largely focused around the play activities she engages in. Different types of play are represented throughout the story: object, social, and locomotor, as defined in Bekoff (1984). Animal play behaviour is introduced when the little girl asks her mom "Do animals play too?", and her mom answers the question by reading the information from a book. The story ends with a section for parents; the purpose is to inform them of the importance of play during early childhood in relation to social and cognitive development.

In order to assess if the story is appropriate for the projected age range, an informal pilot survey was created to gather insight from the target audience. The perception of the child and the parent reader is valuable information for determining the effectiveness of the story and its content. Also, the results could be useful in designing a

formal survey in the future for further development of the story. Galliot and Graham (2016) suggest that the use of focus groups in the initial phase of data collection can enhance the final survey design. This is especially true if the target population contains members at different stages of literacy due to differing levels of physical and cognitive development (Scott, 1997, as cited in Galliot & Graham, 2016). This pilot study did not use a focus group in its true form; however, the informal survey and the participants were intended to act in the same way - to provide information and insight that will aid in the construction and wording of a formal questionnaire (Borgers et al., 2000; Scott, 1997, as cited in Galliot & Graham, 2016). The results that Galliot and Graham (2016) collected from their informal survey informed them of: participant diversity, survey constructs, complexity of response options, variety of possible response options, and participant-friendliness of their draft survey. Due to the participation of adults and children in this pilot study, all of the aforementioned items are of particular interest and should be somewhat measurable from the survey results.

Methods

Survey participants were recruited through the use of social media, and thus, are acquaintances of the writer. The requirements for participation include: having a child within the target age range (3-4 years), agreeing to read the story to their child/children, and to fill out a short survey afterwards. A total of 12 parents were recruited, with a total of 13 children. The story and the surveys were sent to participants through email, and the surveys, once completed, were sent back via email. The survey contains 8 questions: 3 pertain to the children and 5 pertain to the adult reader. The child's age and gender were collected along with whether or not they liked the story ("Yes" or "No") and if they wanted to hear it more than once ("Yes" or "No"). The primary reader was asked for their

age, gender, and education level, and to answer “Yes” or “No” if they: enjoyed reading the story to their child/children, read the information for parents at the end, and if they learned something new from the information for parents. The last question was meant to solicit extra feedback from the parent, or the primary reader, by asking them to write a paragraph including any suggestions or comments that they may have regarding the story and/or their child’s reaction to it.

Results & Discussion

There were fewer surveys returned than sent out; six out of twelve were received and thus provided the following data. The number of children included in the informal study was six along with six parents. There were two female children, both 3 years of age, and four male children, aged 3 (2) and 4(2) years. All parents were females, aged 29-42, with education ranging from high school (2) to college/doctorate degrees (4). Five children reported liking the story, while four of them wanted to hear it again when asked. All of the parents reported that they enjoyed reading the story to their kids, that they read the parental information at the end of the story, and four of those parents reported that they learned something new about play.

The following table describes the results of four survey questions, two that pertain to the child and two that pertain to the primary reader, which was the biological mother in every case. The numbers of “Yes” or “No” responses were tallied for each question shown in the table. Though the survey asks if the parent read the information in the back, that item is not included in the table since it would be presumed that the parent must have read the back of the story if they were to answer whether or not they had learned something from the information.

Table 3.1: Summary of the Most Significant Results For Determining the Success of the Story.

	Did the child like the story?	Did the child want to hear the story again?	Did the parent enjoy reading the story?	Did the parent learn something new?
YES Response	5	4	6	4
NO Response	1	2	0	2

Almost all of the children (83%) surveyed liked the hearing the story while all of the parents enjoyed reading it. One child did not like the story the first time through, and four of five children who did like the story wanted to hear it again. The majority of the parents (67%) reported that they learned something new from the information provided in the back of the story. Two parents were already aware of the benefits of play and therefore reported that they did not learn anything new. The survey concluded by asking the parent to provide feedback to the writer in the form of comments, suggestions, and any other relevant information that might provide useful. All six parents wrote a comment and two of them are included here. Contrasting responses were selected in order to demonstrate differing experiences and opinions. The first response is from a parent whose female child liked the story and the second response is from a parent whose male child did not like the story.

1. *My daughter really enjoyed the story and as soon as I finished it she asked to have it read to her again straight away (which is always a good sign!). Both her and I found the rhyming verse enjoyable to read/listen to and she found the part on animals particularly engaging. I think animals in stories for kids are usually farm animals or jungle animals or dogs and cats only, so having some different animals and seeing them do different things was really interesting for her- she*

giggled a lot at the popcorn mice and was paying close attention in that part of the story. She said she liked the pictures – I think because they are simple and direct and highlight exactly what is being talked about in the story (but that's just my assumption). The third time we read the story she disputed that animals play with toys, insisting they don't, because they can't pick them up. So we talked through each animal and what they play with and how, and she thought it was amazing that otters could pick up rocks and play with them.

2. *I couldn't really get my son to pay attention to the story when I first read it to him. He seems to only like superheros right now and anything that has to do with them, I have been reading lots of Batman and Spiderman books and comics to him. I liked the information for parents, and I do know that play is very important.*

Overall, the results were positive in that the story was enjoyed and heard more than once by a majority of the children whose parents read them the story. It seems that some children were more interested in particular aspects of the story rather than the overarching theme of *play*. For example, the robot toy was popular amongst boys, which suggests that a larger focus on robots and/or technology might increase the likeability of the story for them. The intent was to attract both boys and girls to the story through the common activity of play; however, it seems to be a challenging endeavor. By trying to make the story appealing to both genders, some children who prefer very gender specific books and toys may be inadvertently excluded. In the future, it might be favorable to create a boy's version and girl's version of the story in order to cater more heavily to gender preferences. This informal pilot study was very basic in nature, and therefore it was limited by the low survey return rate (50%). However, the results were insightful and the information can be used for developing a formal survey and for refining the story.

Conclusion

From the results of the pilot study, the content of a formal survey can be designed in a manner that will elicit more effective and insightful answers from the participants. The informal survey was not without its flaws, therefore, a formal electronic questionnaire should be created with careful consideration. In order to impact the rates of participant dropout, unanswered questions, and overall completion, Vicente and Reis (2010) suggest that there are six design elements to consider when developing a web-survey: “general structure, length, disclosure of survey progress, visual presentation, interactivity, and question/response format” (p. 264). Each of the aforementioned features would be carefully considered in future survey drafts in order to reduce the problems associated with survey participation/completion.

The informal pilot study aided in understanding the effectiveness of the children’s story by assessing members of the target audience and their parents. The results suggest that the majority of the children surveyed enjoyed the story and wanted to hear it again, and that their parents also enjoyed reading the story to them. Creating an entertaining story using educational material can be challenging, however, since *play* is universal to all children, the subject matter should be easily relatable. It is common knowledge that children can benefit from having their parents read to them, and the purpose of this story is to build on those benefits by delivering factual content in an entertaining format during story time.

Every Day I Like
To PLAY,
I Like To PLAY
In Every Way!

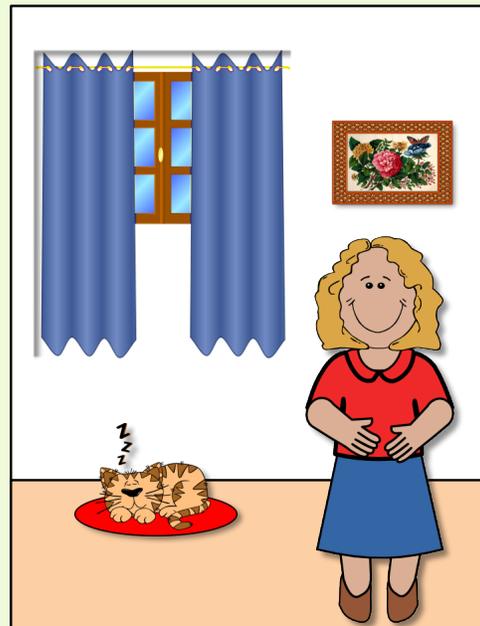
By: Kelly L. Kraus

Every Day I Like To PLAY,
I Like To PLAY In Every Way!



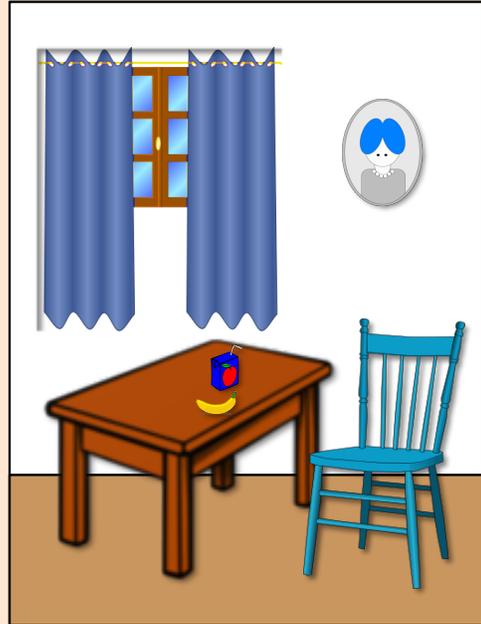
By: Kelly L. Kraus

When I wake up
and it's a new day,
I ask my Mom
"Is it time to play?"



"Yes" she says,
"But after we eat."
I go to the table,
and sit in my seat.

I wonder what I'll
Do when I'm done?
I finish my breakfast -
It's time to have fun!

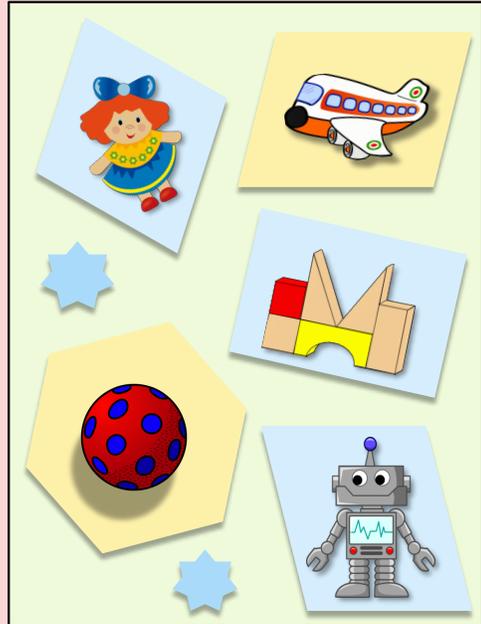


I keep my toys
In a red toy chest.
I look inside
For what I like best.



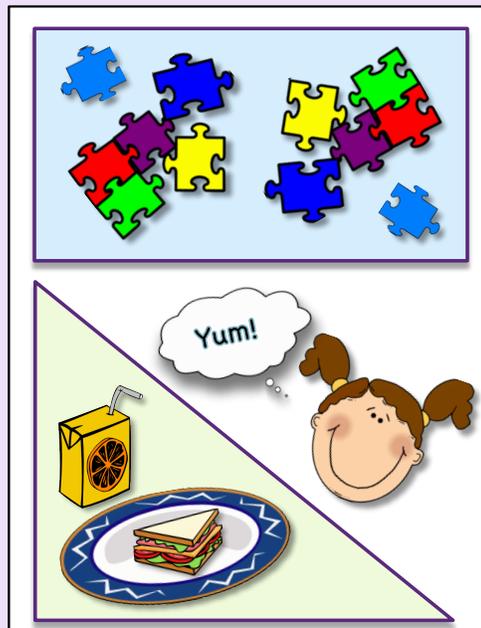
There's a ball to bounce
Way up high.
There's a toy airplane
That I can fly.

There's a pretty doll
and wooden blocks.
There's a toy robot
that blinks and walks.



There's a stack of puzzles,
I've got a bunch.
I play for a while,
then it's time for lunch.

I eat the food
that's on my plate.
I hear the doorbell -
it's my play date!

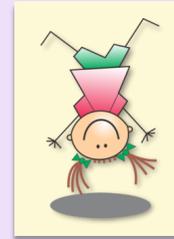


When I see my friends,
I always smile.
We go outside and
play for a while.



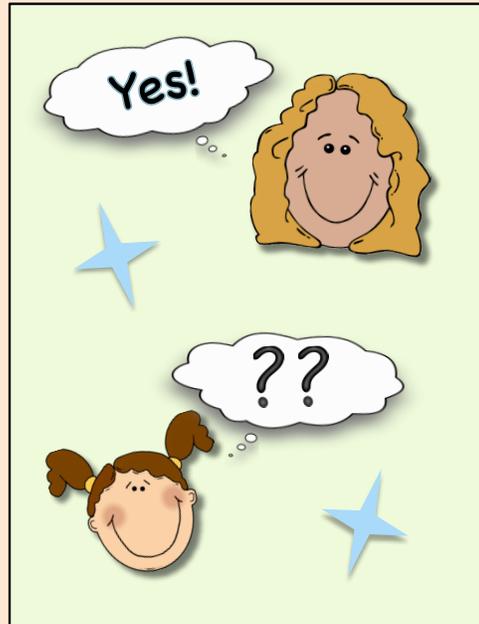
Out in the yard,
We jump, skip, and run.
Playing with my friends
Is oh so much fun!

We always take turns
and we always share.
We all like to win
so we always play fair.



Once my friends
Have gone for the day,
I'm ready for supper,
But still thinking of play.

So, I ask my mom
"Do animals play too?"
And she replies,
"Of course they do!"



She goes to the shelf
And knows where to look.
"We can find answers
inside of a book."

She reads that some pets
have a special toy,
And playing with it
can give them joy.



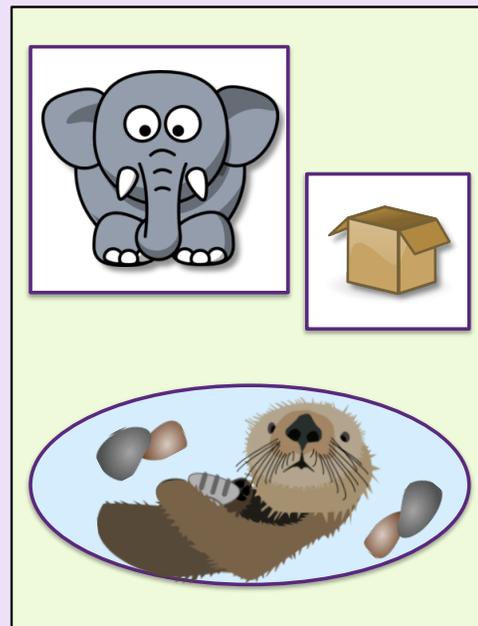
Dogs like a stick
To chase and fetch,
A bone to dig up,
Or a ball to catch.

Cats will pounce on
A fuzzy toy mouse,
Or chase a string
Around the house.



Even the animals
Who live in the zoo,
Have something special
To play with, too.

Elephants will squash
And stomp on a box.
Otters will grab and
Play with rocks.

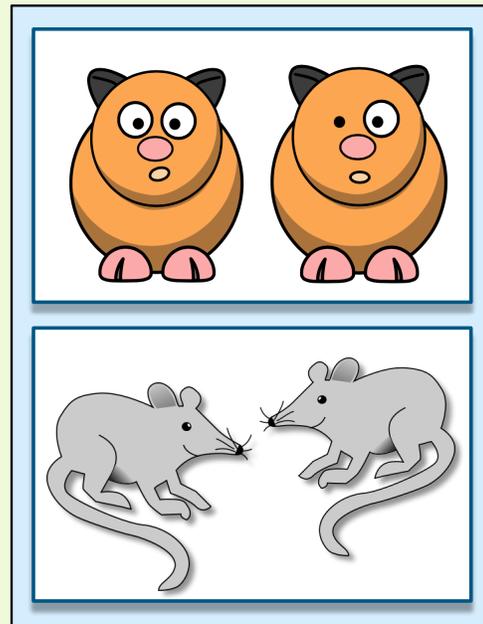


"Do animals play
With each other too?"
Mom looks in the book
And says, "Yes, they do!"



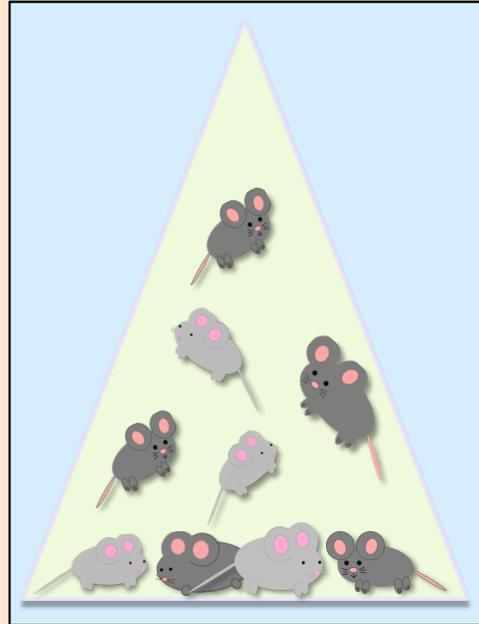
Hamsters wrestle for
The chance to kiss.
They aim for the mouth
And try not to miss.

Rats will wrestle
To give a gentle bite.
They also play fair,
When they play fight.



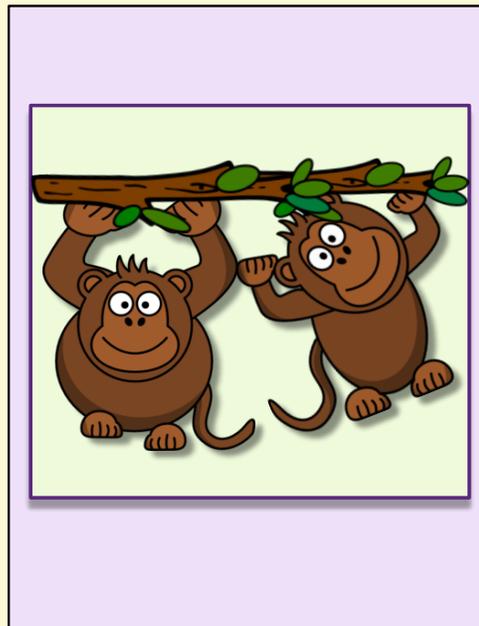
Some wild animals
Play without a toy,
They run, jump, and flip
To have some joy.

Mice jump straight up,
Hop, hop, hop!
They look like popcorn,
Pop, pop, pop!



Monkeys like to play,
While way up high.
They hang from trees,
and swing in the sky.

Now I know that
Animals play too.
And they have fun,
Just like I do!



At bedtime, I pick
a story I like.
And Mom reads to me
about a boy and his bike.

It's time to sleep,
I had a fun day.
Tomorrow I'll wake up,
Ready to play!

The End!



For Parents:

Before going to school
For part of the day,
Children learn new things
Through a behaviour called PLAY.



Play is essential
In the early years,
For children will learn
When they practice with peers.



As they grow-up
They'll enter the world,
With new social skills
That play has unfurled!



The Benefits Of Play!

Social Play: This type of play involves playing with friends and peers. Examples are: rough and tumble play, pretend play, and social games. Rules are followed during social play that ensure that fairness and turn-taking are present in order for play to remain *playful*, and to not escalate from, for example, play fighting to real fighting. Children who engage in social play are essentially practicing skills that may help them in future situations, especially those that are somewhat ambiguous. Research using rats has shown that rough and tumble play, in particular, contributes to growth in an area of the brain that correlates with the frontal cortex in humans - an area responsible for things like attention, planning, and decision-making.

Object Play: This type of play consists of playing with objects like toys. This can be done alone or with others. Toys, and non-toy items, are often used in place of the *real* objects when children engage in pretend play. Besides being fun, object play has also been associated with lowering the stress levels of children who play with toys before a particularly stressful situation, like surgery.

Locomotor Play: This type of play involves using muscle movements from one's own body that result in rapid motions like running, jumping, or skipping. Toys and friends are not required for a child to engage in, and to benefit from, locomotor play. Ideally, this type of play should be fun and unstructured, rather than rigidly controlled. Benefits for children can include an increase in the physical coordination that is required for many types of athletics.

Animal Play: Many animals play in ways that can be classified as 'social', 'object', or 'locomotor' play, and though it often looks different from human play, the benefits are similar. Also present in animal play are the rules used to keep play *playful*, like fairness and turn-taking, for example.



Illustrations created using
Public Domain
Clip Art.

Conclusion

The Eshkol Wachmann Movement Notation (EWMN) method is appropriate when considering a method of analysis that can tap in to the umwelt of a species, especially when examining interactions between animals. For the comparative analysis project, using EWMN revealed what the monkeys were paying attention to during their play fights. Even though EWMN is difficult to learn and to use, it is the complexity of the method that aids in revealing the structural intricacies of the actions performed by interacting animals. Also, analyzing behaviour with EWMN helps the observer to retain objectivity. It is important to be aware that when analyzing the behaviour of other animals, the variables that people might think are important may only be so from a human perspective, and that is why EWMN is valuable for identifying what is important to the animal(s) in question.

Of course this method was not applied in the informal pilot study and story project, but the survey was intended to gather similar results – to gain insight into the experiences of the target audience. The results revealed that the story was perceived in multiple ways across the children; though most of them liked the story, elements of it were either liked or disliked depending on the child. An adult writing for children may find it difficult to understand what is popular among them and why; therefore, a survey can be an effective tool for evaluating the preferences of someone in a different developmental stage than the writer, a factor that would most likely influence one's umwelten.

In regards to experience, the act of play fighting has multiple rewards, such as biting or wrestling one's partner, and these rewards can carry differing levels of value depending on the species. For example, obtaining a reward without working for it might

change the value that it carries, where, just like the wart hogs (Pellis & Pellis, 2017a), the drills prefer to compete over the target area - increasing the value of obtaining a bite. However, gaining a bite without much competition does not seem to affect the value of the reward as dramatically in the baboons as it does in the drills. The baboons tend to emphasize biting over wrestling, but without making some effort to obtain the reward, it may not be as 'worth it' for the drills, and so they emphasize wrestling to maximize their experience of play fighting. When extending this idea to human competitive behaviour, the prediction would be that, for example, athletes are like drills and would find winning first place proportionately rewarding in relation to the number of people they compete against. In this way, the value of a reward, for some species, is fluid and changes in relation to the level of competition exerted.

The results from the EWMN analyses directed further investigation in to the play fights revealing details contrary to the hypothesis. Though similar targets and tactics are present, the way the *Papio* and *Mandrillus* species use and emphasize these elements differ. So, despite some species having many similarities, it cannot be assumed that those similarities are sufficient to account for how an animal should play. Obviously, the results from the comparative analysis cannot explain why these differences occur, but rather, it has become apparent that they exist and should be investigated further. My thesis clearly shows that much is yet to be learned about how different species organize their play fighting. Moreover, it has revealed that methods that can gain insight into how subjects view what is important in their world, their *umwelten*, are valuable in both understanding behaviour and in communicating ideas.

References

- Aldis, O. (1975). *Play fighting*. New York, NY: Academic Press.
- Barton, R. A. (2000). Socioecology of baboons: the interaction of male and female strategies. In Kappeler, P. M. (Ed.). *Primate males: causes and consequences of variation in group composition*. Cambridge, ENG: Cambridge University Press.
- Bekoff, M. (1984). Social play behavior. *Bioscience*, 34(4), 228-233.
- Blanchard, R. J., Blanchard, D. C., Takahashi, T., & Kelley, M. J. (1977). Attack and defensive behaviour in the albino rat. *Animal Behaviour*, 25, 622-634.
- Ciani, F., Dall'Olio, S., Stanyon, R., & Palagi, E. (2012). Social tolerance and adult play in macaque societies: A comparison with different human cultures. *Animal Behaviour*, 84, 1313-1322.
- Emory, G. R. (1975). The patterns of interactions between the young males and group members in captive groups of *Mandrillus sphinx* and *Theropithecus gelada*. *Primates*, 16(3), 317-334.
- Eshkol, N., & Wachmann, A. (1958). *Movement notation*. London: Weidenfeld & Nicolson.
- Galliot, N., & Graham, L. J. (2016). Focusing on what counts: using exploratory focus groups to enhance the development of an electronic survey in a mixed-methods research design. *Aust. Educ. Res.*, 43, 567-585.
- Golani, I. (1976). Homeostatic motor processes in mammalian interactions: A choreography of display. In P. P. G. Bateson & P. H. Klopfer (Eds.), *Perspectives in ethology*, Vol. 2 (pp. 69-134). New York, NY: Plenum.
- Jolly, C. L. (2007). Baboons, Mandrills, and Mangabeys: Afro-papionin socioecology in a phylogenetic perspective. In Campbell, C. J., Fuentes, A., MacKinnon, K. C., Panger, M. & Bearder, S. K. (Eds.). *Primates in perspective*. (pp. 241-251). New York, NY: Oxford University Press, Inc.
- O'Meara, B. C., Graham, K. L., Pellis, S. M., & Burghardt, G. M. (2015). Evolutionary models for the retention of adult-adult play in primates: The roles of diet and other factors associated with resource acquisition. *Adaptive Behaviour*, 23, 381-391.
- Palagi, E. (2018.) Not just for fun! Social play as a springboard for adult social competence in human and non-human primates. *Behav. Ecol. Sociobiol.* 72, in press.
- Pellis, S. M. (1981). A description of social play by the Australian magpie *Gymnorhina tibicen* based on Eshkol-Wachman notation. *Bird Behaviour*, 3, 61-79.

- Pellis, S. M. (1984). Two aspects of play-fighting in a captive group of Oriental small-clawed otters *Amblonyx cinerea*. *Zeitschrift für Tierpsychologie*, *65*, 77-83.
- Pellis, S. M., & Pellis, V. C. (1987). Play-fighting differs from serious fighting in both target of attack and tactics of fighting in the laboratory rat *Rattus norvegicus*. *Aggressive Behavior*, *13*, 227-242.
- Pellis, S. M., Pellis, V. C., & Dewsbury, D. A. (1989). Different levels of complexity in the playfighting by muroid rodents appear to result from different levels of intensity of attack and defense. *Aggressive Behavior*, *15*, 297-310.
- Pellis, S. M., & Pellis, V. C. (1997). Targets, tactics, and the open mouth play face during play fighting in three species of primates. *Aggressive Behaviour*, *23*, 41-57.
- Pellis, S. M., & Iwaniuk, A. N. (1999). The problem of adult play fighting: A comparative analysis of play and courtship in primates. *Ethology*, *105*, 783-806.
- Pellis, S. M., & Iwaniuk, A. N. (2000). Adult-adult play in primates: comparative analyses of its origin, distribution and evolution. *Ethology*, *106*, 1083-1104.
- Pellis, S. M., Blundell, M. A., Bell, H. C., Pellis, V. C., Krakauer, A. H., & Patricelli, G. L. (2013). Drawn into the vortex: The facing-past encounter and combat in lekking male greater sage-grouse (*Centrocercus urophasianus*). *Behaviour*, *150*, 1567-1599.
- Pellis, S. M., Pellis, V. C., Barrett, L., & Henzi, S. P. (2014). One good turn deserves another: combat versus other functions of acrobatic maneuvers in the play fighting of vervet monkeys (*Chlorocebus aethiops*). *Animal Behavior and Cognition*, *1*(2), 128-143.
- Pellis, S. M., & Pellis, V. C. (2015). Are agonistic behavior patterns signals or combat tactics - or does it matter? Targets as organizing principles of fighting. *Physiology & Behavior*, *146*, 73-78.
- Pellis, S. M., & Pellis, V. C. (2017a). What is play fighting and what is it good for? *Learning & Behavior*, *45*, 355-366.
- Pellis, S. M., & Pellis, V. C. (2017b). Play behavior. In J. Vonk & T. Shackelford (Eds.), *Encyclopedia of Animal Cognition and Behavior* (pp. 1-13). Springer: New York.
- Reinhart, C. J., Pellis, V. C., Thierry, B., Gauthier, C-A., VanderLaan, D. P., Vasey, P. L., & Pellis, S. M. (2010). Targets and tactics of play fighting: competitive versus cooperative styles of play in Japanese and Tonkean macaques. *International Journal of Comparative Psychology*, *23*, 166-200.

- Sackes, M., Trundle, K. C., & Flevares, L. M. (2009). Using children's literature to teach standard-based science concepts in early years. *Early Childhood Education Journal*, 36, 415-422.
- Saczawa, M. (2005). The types and duration of play in a solitary species (*Pongo pygmaeus*) versus a social species (*Mandrillus leucophaeus*). *Oxford Journal of Anthropology*, 1, 1-10.
- Schaller, G. B. (1963). *The mountain gorilla: Ecology and behavior*. Chicago, IL: The University of Chicago Press.
- Siegel, S. & Castellan, N. J. (1988). *Nonparametric statistics for the behavioral sciences* (2nd ed.). New York, NY: McGraw-Hill.
- Siviy, S. M. (2016). A brain motivated to play: insights into the neurobiology of playfulness. *Behaviour*, 153, 819-844.
- Thierry, B., Iwaniuk, A. N., & Pellis, S. M. (2000). The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus *Macaca*). *Ethology*, 106, 713-728.
- Vanderschuren, L. J. M. J., & Trezza, V., 2014. What the laboratory rat has taught us about social play behavior: role in behavioral development and neural mechanisms. *Curr. Top. Behav. Neurosci.* 16, 189-212.
- Vanderschuren, L. J. M. J., Acterberg, E. J. M., & Trezza, V. (2016). The neurobiology of social play and its rewarding value in rats. *Neuroscience & Biobehavioral Reviews*, 70, 86-105.
- Vicente, P., & Reis, E. (2010). Using questionnaire design to fight nonresponse bias in web surveys. *Social Science Computer Review*, 28(2), 251-267.
- von Uexküll, J. (1934/2010). *A foray into the worlds of animals and humans*. English translation. University of Minnesota Press: Minneapolis, MN.

Appendix

Informal Pilot Study Survey

- These questions are to be answered by the primary reader of the story. Some details pertain to the child and some pertain to the adult reader.
- Names and/or any identifying factors will be kept private and treated confidentially. The survey results will be included in my thesis as an informal assessment of the effectiveness of my children's story.
- **Directions:** Please read the children's story about play behaviour to your 3 and/or 4 year old child. Once finished, please answer the applicable survey questions honestly and to the best of your ability. If you have multiple children, please keep the answers consistent on the survey (Ex: Child #1 remains Child #1 throughout so that the answers pertain to the same individual child).

Survey Questions

1. Please provide the following information for:

Child #1:

Age -

Gender -

Child #2:

Age -

Gender -

Child #3:

Age -

Gender -

2. Please ask your child(ren) the following and answer “YES” or “NO”:

Did they like the story?

Child #1:

Child #2:

Child #3:

3. Please ask your child(ren) the following and answer “YES” or “NO”:

Would they like to hear the story again?

Child #1:

Child #2:

Child #3:

The Following Questions Pertain To The Primary Reader / Parent:

4. Primary Reader:

Age -

Gender -

Current Level of Education -

5. Please answer “YES” or “NO” to the following:

Did you enjoy reading the story to your child(ren)?

6. Please answer “YES” or “NO” to the following:

Did you read the information for parents at the end of the story?

7. Please answer “YES”, “NO”, or N/A to the following:

Did you learn something new about play behaviour from the information for parents at the end of the story?

8. Please provide a paragraph with your honest feedback, positive and/or negative, including things like, but not limited to: what type of reaction(s) did your child(ren) have during the story; did the story hold the attention of your child(ren); did your child(ren) ask about, or comment on, the illustrations; did your child(ren) ask any questions about the story content; what suggestions do you have to improve the story - as well as any additional comments you might have.