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# Targets, Tactics, and Cooperation in the Play Fighting of Two Genera of Old World Monkeys (*Mandrillus* and *Papio*): Accounting for Similarities and Differences

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Play fighting in many species involves partners competing to bite one another while avoiding being bitten. Species can differ in the body targets that are bitten and the tactics used to attack and defend those targets. However, even closely related species that attack and defend the same body target using the same tactics can differ markedly in how much the competitiveness of such interactions is mitigated by cooperation. A degree of cooperation is necessary to ensure that some turn-taking between the roles of attacker and defender occurs, as this is critical in preventing play fighting from escalating into serious fighting. In the present study, the dyadic play fighting of captive troops of 4 closely related species of Old World monkeys, 2 each from 2 genera of *Papio* and *Mandrillus*, was analyzed. All 4 species have a comparable social organization, are large bodied with considerable sexual dimorphism, and are mostly terrestrial. In all species, the target of biting is the same – the area encompassing the upper arm, shoulder, and side of the neck – and they have the same tactics of attack and defense. However, the *Papio* species exhibit more cooperation in their play than do the *Mandrillus* species, with the former using tactics that make biting easier to attain and that facilitate close bodily contact. It is possible that species differences in how rigidly dominance relationships are maintained are expressed in the play of juveniles by altering the balance between competition and cooperation.

*Keywords*: social styles, egalitarian, despotic, play asymmetry, reciprocity, social tolerance

Both play fighting and serious fighting involve competition over gaining some advantage (Aldis, 1975; Geist, 1978). For many species, the advantage gained involves biting or otherwise contacting a particular area of the opponent's body (Aldis, 1975; Biben, 1998; Blanchard, Blanchard, Takahashi, & Kelley, 1977; Geist, 1966; Pellis & Pellis, 1987, 2018; Symons, 1978). Therefore, many of the maneuvers performed may be viewed as tactics of attack and defense associated with gaining access to or protecting that body target (Blanchard & Blanchard, 1994; Geist, 1978; Pellis, 1997; Pellis & Pellis, 1998). The target over which the animals compete can affect both the tactics that are used and how they are executed (Blanchard et al., 1977; Geist, 1978). Rats (*Rattus norvegicus*), in which play fighting and serious fighting differ in the body areas attacked (Pellis & Pellis, 1987), illustrate the effects of targets on the tactics used within the same species.

In rats, play fighting involves attacking and defending the nape of the neck, which, if contacted, is nuzzled with the snout (Pellis & Pellis, 1987; Siviy & Panksepp, 1987), whereas serious fighting involves the attack and defense of the lower flanks

and rump, which, if contacted, are bitten (Blanchard et al., 1977). Superficially, it appears that rats use similar tactics in both types of fighting (Takahashi & Lore, 1983; Taylor, 1980), but their execution is greatly modified by the differences in the targets (Pellis & Pellis, 1987). For instance, the lateral maneuver is used for attack in serious fighting, but only for defense in play fighting (Pellis & Pellis, 2015). Similarly, the tactics used by other rodents that nuzzle the nape during play fighting, such as deer mice (*Peromyscus maniculatus*), prairie voles (*Microtus ochrogaster*), and montane voles (*M. montanus*), are more like those used by rats (Pellis, Pellis, & Dewsbury, 1989) than is the case for species that target different body areas, such as Syrian golden hamsters (*Mesocritus auratus*), which nibble the cheeks (Pellis & Pellis, 1988) and Djungarian hamsters (*Phodopus campbelli*), which lick the mouth (Pellis & Pellis, 1989).

While both playful and serious fighting involve competing for an advantage (Aldis, 1975; Blanchard & Blanchard, 1994), there is also a key difference. During serious fighting, role reversals only occur because one animal is able to overcome the defenses of their opponent and so gain the advantage (Geist, 1978). In contrast, during play fighting, the animals incorporate some cooperative actions that ensure reciprocity, thus allowing partners to take turns in gaining the advantage (Altmann, 1962; Palagi, Cordoni, Demuru, & Bekoff, 2016; Pellis, Pellis, & Reinhart, 2010). While the degree of turn-taking can vary depending on species, age, sex, and dominance relationships (e.g., Bauer & Smuts, 2007; Biben, 1998; Cordoni & Palagi, 2011; Essler et al., 2016; Pellis et al., 1989; Pellis, Pellis, & McKenna, 1993), some minimum level has to be present for play fighting to be sustained (Suomi, 2005; Wilmer, 1991).

In play fighting, different species incorporate reciprocity in different ways. Some use the same tactics as they use in serious fighting and execute them just as vigorously. However, once they gain the upper hand, they either refrain from taking the advantage (Pellis, Pellis, & Reinhart, 2010) or cease prosecuting the advantage if their partner signals submission (Pellis & Pellis, 2016). In both cases when an attacker ceases its attack, its partner can execute a counterattack that leads to a role reversal (Pellis & Pellis, 2017). In other species, the animals may incorporate movements and postures that compromise their ability to maintain the advantage once it is gained (Foroud & Pellis, 2003) or fail to incorporate defensive elements in their attacks that can attenuate the likelihood of retaliation by their partners. Similarly, when defending, the animals may be less vigorous in the execution of a maneuver, increasing the chance of successful contact by their partners (Pellis & Pellis, 1998).

Because animals need to incorporate cooperation in their play fighting, not all aspects of the actions performed during play can be interpreted as tactics of attack and defense. However, given the variety of ways in which different species incorporate cooperation in their play fighting (Pellis & Pellis, 2017), a necessary first step for cross-species comparisons is to characterize the species-typical targets and the associated combat tactics. Doing so provides a framework for identifying actions that are not compatible with combat and so are likely present to facilitate cooperation (e.g., Norman, Pellis, Barrett, & Henzi, 2015; Pellis & Pellis, 2016; Pellis, Pellis, Barrett, & Henzi, 2014).

Using this approach, detailed comparisons across a variety of species of rodents have revealed differences both in the targets and tactics involved and in the degree of cooperation present. The most complex play fighting, that is, cases in which there are many role reversals and bodily contact is facilitated, occurs in species with the most cooperation (Pellis & Pellis, 2009), and broad comparative surveys have indicated that the most complex play fighting is commonly reported in species that have more complex social systems (Fagen, 1981). Leaving aside the possibility of sampling error, as more social and charismatic animals are more likely to be studied (Burghardt, 2005), this possible association was tested in rodents. An index of play complexity based on a combination of attack, defense, and cooperation (Pellis & Pellis, 2009) was statistically compared to an index of sociality. The two variables were not correlated (Pellis & Iwaniuk, 1999).

A potential limitation in the above study was with the sociality index. The two features used to construct the sociality index were social organization and mating system, and both are based on the spatial and temporal associations between the animals (Kappeler & van Schaik, 2002). A third feature of sociality, social structure, may be more important, as it involves the pattern of social interactions and relationships among group members (Kappeler & van Schaik, 2002). Indeed, species with more egalitarian social relationships and less rigid dominance associations tend to engage in more cooperation during play fighting than do more despotic species (e.g., Ciani, Dall'Olio, Stanyon, & Palagi, 2012; Cordoni, Norscia, Bobbio, Palagi, 2018; Essler et al., 2016; Llamazares-Martín, Scopa, Guillén-Salazar, & Palagi, 2017; Petit, Bertrand, & Thierry, 2008; Reinhart et al., 2010). Detailed studies are needed to develop a suitable comparative database to test this relationship explicitly using appropriate statistical techniques that take into account the phylogenetic relationships among the species (e.g., O'Meara, Graham, Pellis, & Burghardt, 2015; Pellis & Iwaniuk, 2000).

For several reasons, primates are a particularly good mammalian taxon for such an endeavor. First, there is a considerable knowledge on the socioecology and life history traits of many species (e.g., Campbell, Fuentes, MacKinnon, Bearder, & Stumpf, 2011; Mitani, Call, Kappeler, Palombit, & Silk, 2012). Second, there is considerable variation in social systems (e.g., Kappeler & van Schaik, 2002; Shultz, Opie, & Atkinson, 2011). Third, to our knowledge, there are no species of primates that have not been reported to engage in social play as juveniles (Burghardt, 2005; Fagen, 1981). Moreover, the content of play fighting varies across species in terms of the targets competed over and the degree of cooperation involved (e.g., Antonacci, Norscia, & Palagi, 2010; Palagi, 2006; Palagi, Norscia, & Spada, 2014; Pellis & Pellis, 1997, 2018), and, most critically, at least some of this variation seems to coincide with differences in social relationships (e.g., Ciani et al., 2012; Cordoni et al., 2018; Petit et al., 2008; Reinhart et al., 2010).

However, as noted above, the body targets competed over can greatly influence the tactics used by the contestants (Pellis & Pellis, 1987, 2015). If the targets competed over differ between species, this makes characterizing and comparing the tactics and the modes of cooperation more difficult (Pellis et al., 2010). Therefore, selecting a group within the primates that have similar targets during play fighting is

preferable. Studies of the play fighting in several species of cercopithecine monkeys have shown that they compete to bite the same general body area – the upper arm, side of the neck, and shoulder (e.g., Owens, 1975a; Pellis & Pellis, 1997; Pellis et al., 2014; Reinhart et al., 2010; Symons, 1978). If this pattern of targeting is consistent across this subfamily, this could be an excellent taxon for testing the hypothesis that the degree of cooperation during play fighting is associated with more relaxed social relationships, as cercopithecines vary across many dimensions of sociality (Cords, 2012).

The present study compared four species of cercopithecines from two genera of the tribe Papionini, Guinea baboons (*Papio papio*), hamadryas baboons (*P. hamadryas*), drills (*Mandrillus leucophaeus*), and mandrills (*M. sphinx*) to identify the targets and tactics of their play fighting. All four species live in single-male harems, with those core units coalescing with other such units to form larger bands (Barton, 2000). They are all highly sexually dimorphic, large bodied, and mostly terrestrial (Swedell, 2011). Although aspects of play fighting have been studied in some of these species (e.g., Emory, 1975; LeResche, 1976; Mellen, Littlewood, Barrow, & Stevens, 1981; Pereira & Preisser, 1998; Terdal, 1996), the available literature does not provide the analyses needed to discern the targets over which these species compete. Therefore, a descriptive analysis was conducted on videotaped recordings of play fighting sequences using methods allowing comparison with equivalent data obtained from other species of cercopithecines (Pellis & Pellis, 1997; Pellis et al., 2014; Reinhart et al., 2010).

Although the current study found that the targets and tactics were similar across the four species, we also found some aspects of competition that differed between the two genera that could not be accounted for by differences in body targets. Therefore, the paper is organized into two sections. In Part 1, the findings with regard to targets and tactics are presented; in Part 2, the additional analyses used to explore the genus-level differences are presented. Then, in the *General Discussion*, the implications of the findings on the role of social style in influencing cooperation in play fighting are considered.

## General Method

**Subjects**

Videotaped sequences of play fighting from five troops housed in zoos were analyzed. The Guinea baboons were from the Paris Zoo (2002), the drills were from the Barcelona Zoo (2002), the hamadryas baboons were from the Melbourne Zoo (2001), and, for the mandrills, one troop was from the Schönbrunn Zoo in Vienna (1997), and the other troop was from the Colchester Zoo (2009).

In the Guinea baboon troop, there were 10 adult males, 19 adult females, and 14 juveniles (ranging between 1.5-6.0 years). Nine of the juveniles were males. The cage was mostly a sloping area of barren earth that extended upwards to a rear wall. Most of the play occurred at the front of the cage on a flat concrete platform (about 1 m wide), with a wall that led to a trough in front of the viewing area. The total area was about 500 m$^2$. Most of the play was filmed in the flat areas of the cage. The troop of hamadryas baboons included 3 adult males, 11 adult females, and 8 juveniles (5 males, aged 2-3.5 years; 3 females, aged 2-3 years). The enclosure had a concrete floor, was enclosed by a cyclone wire fence with

a floor space of 450.53 m$^2$, and had logs and some vertical steel rods for climbing.

In the drill troop, there was 1 adult male, 4 adult females, 2 adolescent males, and 1 adolescent female (4-5 years old), with 1 juvenile male under 3 years of age. The film was taken of their outdoor cage, which comprised a peninsula of 700 m$^2$ surrounded by a moat on three sides, with grassy areas interspersed with trees and shrubs. The troop of mandrills from the Schönbrunn Zoo was comprised of 3 adult males, 5 adult females, 8 adolescents and juveniles, and 1 infant (2 months). The 8 most likely to engage 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 400 m$^2$ with logs, trees, grassy areas, and raised platforms.

The second troop of mandrills from the Colchester Zoo consisted of 3 adult males (10-11 years), 5 adult females (8-21 years), and 14 immature animals. Four mandrills (aged 6 months to 1 year) did not play in the area filmed. Most of the play recorded was by the juveniles – 3 females (2-4 years) and 7 males (2-5 years). The main enclosure was at a considerable distance from the walkway available for public viewing, and the play recorded was restricted to a smaller portion of the overall cage. This area was approximately 80 m$^2$, containing an open patch of grass scattered with trees and wooden scaffolding strung with rope webbing, limiting the number of interactions that were not obscured.

## Data Collection

Over the course of 10 days at each zoo (except for the mandrills at the Colchester Zoo, which were videotaped for only three days), sequences of play fighting were videotaped using 8-mm Sony Camcorders by two observers (SMP and VCP). A continuous, all-instances sampling procedure was used. Once we became accustomed to the troops' daily routine and places in the enclosures in which play was most likely to occur, each observer was stationed at a location that provided a good vantage point from which to videotape. The camera was not fixed to one view but was hand held, which enabled the observer to track the animals as they moved about. The enclosure was continuously scanned, and any instance of play fighting that occurred was videotaped. If different play fights occurred simultaneously in different locations, the play fight that was closer to the observer or the one with the most unobstructed view was videotaped.

The amount of videotaped material ranged from 90 min (the mandrills from the Colchester Zoo) to 5.5 hr (the Guinea baboons). Given this range, the troops from the Barcelona, Melbourne, Paris, and Schönbrunn zoos were the primary focus for comparison, with each providing between 100 and 600 play fights. Because of the number of obstacles blocking the view of the mandrills at Colchester Zoo, only 35 interactions were available for which the various kinds of quantitative analyses could be scored. Therefore, this troop was mainly used to evaluate within-species consistency across troops. Similarly, because the largest number of interactions was available for the Guinea baboons, a second independent sample was used to test within troop consistency in that species.

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, the 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 some pairs and, given the large number of juveniles present, sequences of multiple pairs playing within the same video frame were 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 Mac computers.

## Data Analysis

Play fighting is embedded in sequences of rough-and-tumble play that can include both chasing and wrestling (Blurton Jones, 1967). The focus of the present study was the fighting component. As play fighting in some species can involve competition for the same body targets competed over during serious fighting (Aldis, 1975; Owens, 1975a), the two forms of fighting can be difficult to differentiate (Pellis &

Pellis, 2016). Encounters were judged to be playful if they met the criteria established by Smith (1997: (1) A resource, such as a piece of food, is not gained or protected; (2) the contact is restrained, or at least there are no combat-induced injuries; (3) there are role reversals between a pair, with partners alternating as to which is the attacker and which is the defender; (4) even if chasing ensues following contact, further affiliation is likely; and, (5) the presence of play signals, such as the open mouth play face (van Hooff, 1967).

Dyadic sequences meeting these criteria were used. In addition, for inclusion in the main analyses, only play fights that were observable from their onset to their termination and were not obscured over the course of the interaction were used. Play fights were judged to have begun when both monkeys appeared to be fully engaged with one another, either by making eye contact and/or by approaching one another. The play fight was considered to have terminated when they stopped interacting and either remained sitting near one another or moved apart. Depending on the comparisons being made, different numbers of sequences were used for analysis. As we had a different number of play fights available for each of the four species so as to ensure unbiased selection, the interactions meeting the requisite criteria were accepted as they appeared chronologically in the videotaped material.

**Statistical analysis.** The data mostly involved categorical and ordinal scales. For the categorical data, the chi-squared test was used; for the data involving ordinal scales, various nonparametric tests, such as Friedman two-way analysis of variance (ANOVA), Kruskal-Wallis one-way ANOVA, Mann-Whitney $U$, and sign tests were used. Following significant ANOVAs, appropriate post hoc pairwise tests were used (Siegel & Castellan, 1988). The alpha level was set at 0.05. Because the exact values for $p$ varied markedly in number of decimal places (from as low as two to over 12), to standardize the presentation, the value to the closest standard level of significance given in Siegel & Castellan (1988) is shown (e.g., 0.05, 0.02, 0.01, 0.001). Also, because we could not always be certain that samples from a troop were fully independent (i.e., not including more than one contribution from the same individual), statistical tests were not used to identify patterns but rather to test the generalizability of the patterns identified from the frame-by-frame qualitative analyses (see below).

**Inter-observer reliability.** The qualitative techniques for frame-by-frame analyses of play fighting sequences produced notated score sheets (see Part 1). These were read by one of the authors (either SMP or VCP) who had not previously seen those sequences. The reader then verbally described the sequence to the person who produced the notation. This ensured that the abstracted notations adequately described the key features of the interactions.

The primary quantitative data for the four main troops were scored by KLK. The second sample of Guinea baboons and the sample of mandrills from Colchester Zoo were scored by VCP, who at the time was not privy to the patterns found by KLK. For the Guinea baboons, the interactions scored by KLK were from the first three hours of videotaped material, whereas those scored by VCP were from the last two hours. For both species, VCP used the same selection criteria and scoring scheme as that used by KLK. Most of the data from the two scorers did not differ significantly, indicating that the scoring scheme used by KLK could be replicated. These findings also indicate that, irrespective of the interactions used (Guinea baboons), a troop was consistent in its pattern of play and that different troops of the same species (mandrills) consistently showed the species-typical pattern of play. The few differences that did emerge from the analyses between the two scorers reinforced the genus-level differences that emerged from the main comparisons. Therefore, the findings from the samples analyzed by VCP are incorporated into the appropriate sections of the *Results*.

## Part 1: Targets and Tactics

Scoring the location of actual bites or the lesions and scars likely resulting from bites can reveal the body targets attacked during playful and serious fighting (e.g., Aldis, 1975; Brain, 1981; Hausfater, 1972; Kinsey, 1976; Owens, 1975a; Ruehlmann, Bernstein, Gordon, & Balcaen, 1988). However, such an approach has its limitations because as one animal lunges to bite, its partner may perform a defensive action that

either blocks or redirects the bite (Blanchard et al., 1977; Pellis & Pellis, 1988), and so the actual body area bitten may not be an accurate reflection of the body area that is the target of attack. For example, serious fights between adult male Richardson's ground squirrels (*Urocitellus richardsoni*) involve attack and defense of the shoulder, which is bitten if contacted. However, once one squirrel turns and flees, the other frequently chases and delivers bites to the other's rump (Pellis, MacDonald, & Michener, 1996). Simply counting bites would overestimate the rump as a target. If a squirrel is stationary, its attacker maneuvers to bite its opponent's shoulder and not the rump. Similarly, the recipient of the attack maneuvers to protect its shoulders and not its rump. That is, tracking the offensive maneuvers of one protagonist with the correlated defensive maneuvers of the other can provide clues as to which body areas are more likely to be attacked and protected (Blanchard & Blanchard, 1994; Geist, 1978; Pellis & Pellis, 2015).

The same problem exists for scoring the combat tactics. A common approach is to quantify the occurrence of predefined behavior patterns (e.g., Breed, Meaney, Deuth, & Bell, 1981; Dempster & Perrin, 1989; Emory, 1975; Essler et al., 2016; Owens, 1975a). Again, as particular tactics of attack are correlated with particular tactics of defense (e.g., Blanchard et al., 1977; Geist, 1966; Pellis & Pellis, 2015), the absence of a given tactic by one animal cannot necessarily be attributed to that animal. Their partner may have failed to provide the opportunity for them to perform that tactic. The defensive tactic adopted may also be constrained by the direction of attack (e.g., from the rear, side, or front; Pellis et al., 1989). Whichever tactic is executed, a continued attack by another animal may force a defender to switch to different tactic (Pellis & Pellis, 1987). As in identifying targets, characterizing the preferred tactics of the interacting animals requires that the correlated actions by each be tracked. However, tracking several cycles of these correlated moves and countermoves over the course of an encounter can be logistically daunting. The Eshkol Wachmann Movement Notation system (EWMN) provides a formal framework for facilitating such analyses (Eshkol & Wachmann, 1958).

EWMN is a geometric system, designed to express relations and changes of relation between parts of the body, with the body treated as a system of articulated axes (i.e., body and limb segments). A limb is any part of the body that either lies between two joints (e.g., the lower arm is bounded by the elbow and the wrist) or has a joint and an unbound extremity (e.g., the hand is bound by the wrist at one end, but the tips of the fingers are free of a constraining joint). These are imagined as straight lines (axes) of constant length, which move with one end fixed to the center of a sphere. The body is represented on a horizontally ruled page into columns that denote units of time (e.g., frames of a video). The signs for movement are read from left to right and from bottom to top. Movements by any limb segment or the body as a whole can be described as the distal end moving across the surface of the sphere, with the proximal end being anchored in the center of the sphere. Typically, the locations on the sphere (horizontal and vertical) are at 45º angles, but the unit of angular measurement can be reduced (e.g., 22.5º) if finer grain comparisons are needed. An important feature of EWMN is that the same movements can be notated in several polar coordinate systems – the surrounding and static environment, the subject's own

body, or relative to the body of another animal. By transforming the description of the same behavior from one coordinate system to the next, invariance in the behavior may emerge in some coordinates but not others (Golani, 1976).

Critically, for interactions involving pairs of animals, by examining the notated sheet (which resembles a musical score sheet), the relationship between the two animals' movements can identified, and the body area that may be the focus of attack and defense can thus be identified. For example, while both birds in a pair of playing Australian magpies, *Gymnorhina tibicen*, may make moves and countermoves, the notation score revealed that the relationship between one bird's beak and the other bird's side of the head remains constant, revealing the side of the head as the target for the contest (Pellis, 1981). Using this approach, the tactics used to defend those targets can also be characterized because the video frames when the tactic is first initiated can be distinguished from the succeeding frames when the partner's actions can lead to a different outcome (Reinhart et al., 2010). For an example of how the system is used and notated sequences are read, see *Appendix A* in Pellis et al. (2013). For the present paper, frames from videotaped sequences and written descriptions are used to represent the patterns of behavior detected from the EWMN scores.

Once what appeared to be the targets and the preferred tactics were identified by EWMN analyses, a quantitative approach was used to test whether the patterns discerned were robust across species and troops.

## Method

For the EWMN analyses, three comparable sequences of fully observable play fighting from pairs of each species were used. We selected sequences from across the taped material to ensure that the three play fights from each species involved different individuals. Following this detailed analysis, which included all the body parts of both partners, an additional 18-20 sequences that were fully observable and were from the same partner wise orientation (face-to-face) from all four species were analyzed frame-by-frame. The movements of the partners for these additional sequences were tracked using a simplified version of the EWMN score sheet. This simplified score sheet sufficed to track how the partners positioned themselves relative to one another, what the tactics used were during the encounter, whether bites were delivered, and, if so, for how many frames they were sustained. For these qualitative analyses, only the mandrills from the Schönbrunn Zoo were included.

The first bite delivered by the approaching monkey was scored as an *offensive bite*. If that monkey's partner delivered a retaliatory bite on receiving an offensive bite, it was scored as a *defensive bite*. The location of these bites were mapped onto various parts of the body: (1) Head/Face/Cheek (HFC), (2) Neck/Shoulder/Upper Arm (NSUA), (3) Body (B), including all areas of the back, side, stomach, and rump, (4) Lower Arm/Hand (LAH), and (5) Leg/Foot (LFt) (Reinhart et al., 2010). Only bites in which the area of the body bitten or to which bites were directed could be identified were included in the analysis, with more than one bite being possible within any particular play fighting sequence (Pellis & Pellis, 1997; Pellis et al., 2014).

To defend against a bite, different tactics may be adopted while play fighting (Reinhart et al., 2010). For the present study, these tactics were divided into two broad categories – as the defender turned to face its partner, it either remained standing or sitting (upright tactic) or rolled over onto its side or onto its back (supine tactic). As an attack may continue after the initial defensive action taken by the recipient, this can influence further defensive actions taken (Pellis & Pellis, 2015). Therefore, the first 2-3 video frames following the initiation of a bite were used to ascertain whether the defender began to adopt

a supine or upright defense (Reinhart et al., 2010). The percentage of initial defenses involving the supine tactic was calculated. Because the tactics used can change over the course of an interaction, the percentage of play fights in which a supine tactic occurred at any time during the interaction was also scored.

# Results

All 12 playful sequences analyzed with EWMN had the same basic structure. One monkey would approach another, grab it, and lunge to bite its NSUA area. The recipient of the attack then moved to avoid the bite and/or deliver a retaliatory bite, typically to the side of its attacker's face. Moreover, when defending themselves, monkeys from all species were most likely to use the upright tactic (Figures 1 and 2). The other 60 play fights that were subjected to frame-by-frame analysis (i.e., simplified EWMN scores) were consistent with the pattern described above. These additional sequences were also used to quantitatively assess the generality of these commonalities in the pattern of play fighting.
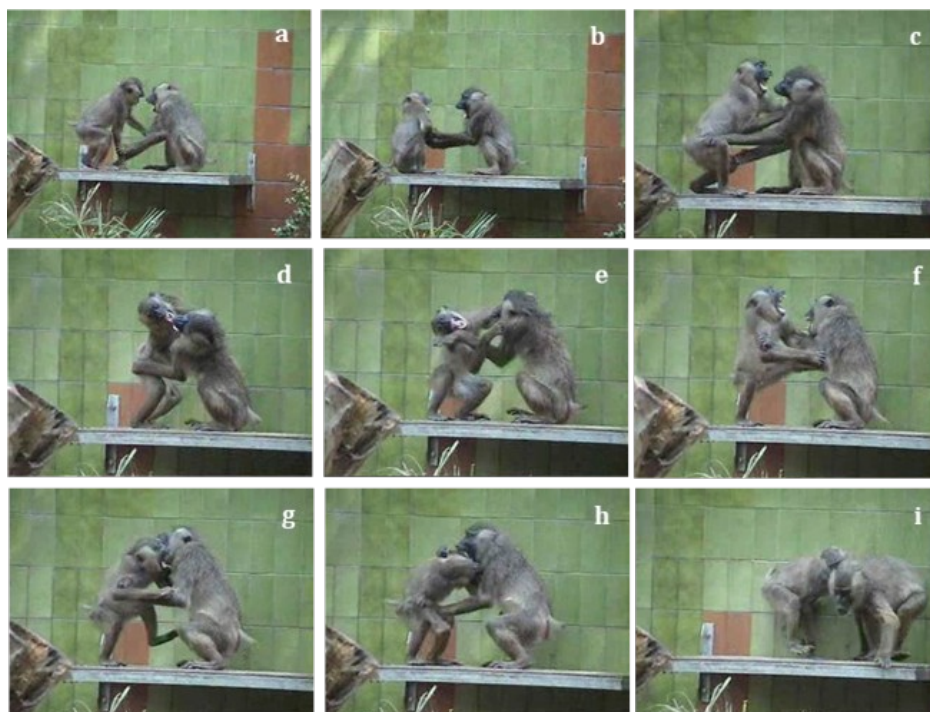


*Figure 1.* **Still frames from a videotaped sequence illustrate a play fighting sequence in a pair of drills (see text for a detailed description).**
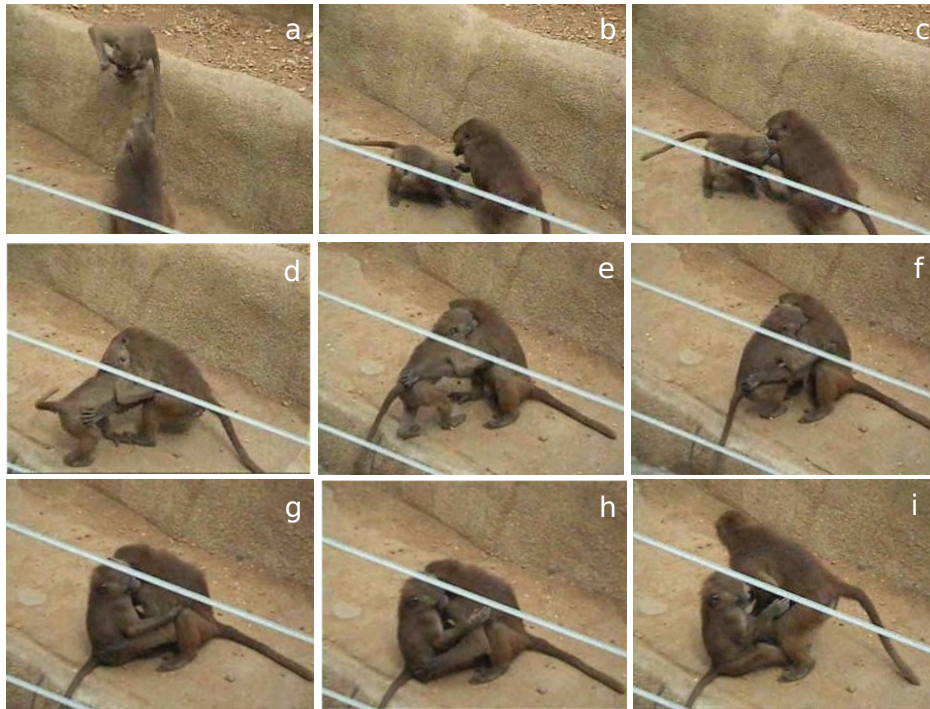
*Figure 2.* **Still frames from a videotaped sequence illustrate a play fighting sequence in a pair of Guinea baboons (see text for a detailed description).**

If the NSUA was the primary target, it was predicted that this body area should receive the most bites. A Friedman ANOVA of the tabulated bites, including both offensive and defensive bites, revealed that bites were not randomly distributed across the body ($F_r = 9.35$, $N = 4$, $k = 5$, $p < 0.05$). The modal area bitten by all species was the NSUA area (Table 1). Pairwise comparisons showed significant differences between the NSUA and both the torso and the legs/feet ($p < 0.05$). Retaliatory bites tended to be more frequently directed at the anterior of the partner's body (head and NSUA), but this was complicated by a higher frequency of bites directed to the hands in the *Mandrillus* species (Table 1; see below for more details on this genus-level difference).

Table 1
*The distribution of bites is shown as a percent for each of the four species*

| Body Areas | Head | Neck/ Shoulder/ Upper Arm | Body (Torso) | Lower Arm/Hand | Leg/Foot | Total Observed |
|---|---|---|---|---|---|---|
| **Offensive Bites** | | | | | | |
| Drills | 22.15 | 46.38 | 2.10 | 28.86 | 0.50 | 194 |
| Mandrills | 12.94 | 44.71 | 5.88 | 35.29 | 1.18 | 85 |
| Guinea baboons | 14.12 | 57.65 | 3.53 | 14.12 | 10.58 | 170 |
| Hamadryas baboons | 28.60 | 53.81 | 13.09 | 4.50 | 0.00 | 115 |

Similarly, the quantitative data confirmed that, for all species, rolling over to

supine, as an initial defense against a bite, was the least likely tactic (Table 2). Sign tests using a binomial distribution, applied to the data from each species, showed that upright defense occurred more frequently than expected by chance ($zs \geq 2.98$, with associated $p$-values of 0.01 or less).

Table 2
*The percent of play fights involving the rolling over tactic*

| Species | As the Initial Defensive Tactic | At Any Time in the Encounter |
|---|---|---|
| Drills | 4.23 (71)* | 6.76 (74) |
| Mandrills | 1.96 (51) | 3.92 (51) |
| Guinea baboons | 21.12 (161) | 43.11 (167) |
| Hamadryas baboons | 7.89 (38) | 48.65 (37) |

*Note.* *The numbers in parentheses show the number play fights used to calculate the percentage. Only play fights in which the action by the performer can be unambiguously observed were included.

For the troop of mandrills from Colchester Zoo, the modal area bitten was also the NSUA (52.83%; data based on 53 bites). The distribution of bites across body areas was compared to that of the mandrills from the Schönbrunn Zoo by using the distribution in that troop (Table 1) to calculate the expected values for the Colchester Zoo troop. A goodness of fit chi-squared test showed no significant difference ($p > 0.05$). Similarly, for the second sample of Guinea baboons, the modal bite target was the NSUA (62.50% of 72 bites). Again, a goodness of fit chi-squared test based on the distribution for the Guinea baboons in Table 1 showed no significant difference ($p > 0.05$).

Based on 35 play fights for the troop of mandrills at the Colchester Zoo, the players were unlikely to roll over to supine as the initial defensive response to an upper body bite (3.03%). A two-by-two chi-squared test comparing supine versus standing between the two mandrill troops showed no significant difference ($p > 0.05$). Similarly, as was the case for the first sample of Guinea baboons, based on 40 play fights for the second sample, the incidence of supine defense was relatively low as an initial defense tactic (20.00%) and did not significantly differ from the first sample (Table 2).

Even though species from both genera attacked and defended the same target with similar use of tactics, closer examination of sequences of play fighting indicated that there are some consistent genus-level differences. The sequence of play fighting in a pair of drills in Figure 1 illustrates the pattern typical of *Mandrillus*. As the monkey on the left (1) approached the monkey on the right (2), both reached out to grasp each other's hands and arms (Panel a). As they held on to each other, they maintained an arm's length distance between their torsos (Panel b). Monkey 1 then began to close the distance, aiming its open mouth towards 2's shoulder (Panel c), but Monkey 2 turned to face Monkey 1, blocking the bite (Panel d). As they pulled apart from each other, Monkey 2 bit Monkey 1's left hand (Panel e). Monkey 1 then moved forward while pushing Monkey 2's mid-ventrum with its left foot (Panel f) and lunged to bite Monkey 2's left shoulder (Panel g). As it did so, Monkey 2 lunged to bite the side of

Monkey 1's face (Panel h). As Monkey 1 ducked, it raised itself so that its mouth faced Monkey 2's right shoulder. Before a bite ensued, Monkey 2 swerved to its right and began to disengage from the bout (Panel i; for the real time behavior, see also Supplementary Video Clip 1).

The sequence of play fighting in the pair of Guinea baboons in Figure 2 illustrates the pattern typical of *Papio*. The baboon on the upper left (1) approached the baboon below (2) (Panel a). As Monkey 2 grabbed at Monkey 1's arm (Panel b), Monkey 1 bit Monkey 2 on its left shoulder (Panel c). Both animals then grabbed each other's upper arms and, while maintaining close contact between their bodies, delivered and sustained bites directed at each other's shoulders, the side of their necks, and their cheeks (Panels d-h). Monkey 2 then stood up, turned to its right, and disengaged from the bout (Panel i; for the real time behavior, see also Supplementary Video Clip 2).

The close inspection of all the notated play sequences (illustrated by Figures 1 and 2) revealed two core differences between the two genera. First, while all species held each other's arms, the drills and mandrills held each other at arm's length, whereas the baboons held each other closely, maintaining torso-to-torso contact for long periods of the interaction. Second, biting by the drills and mandrills tended to occupy less of the interaction than did the biting by the baboons, which were more sustained. The consequences of this difference in fighting style were further examined both qualitatively and quantitatively using the larger sample of simplified EWMN scores.

Although the duration of bouts of play fighting did not differ significantly across species, they were variable in length (range: 1.05-17.38s). Therefore, to contrast the notated sequences across the four species on a standardized scale, the duration of each bite as a percentage of the total length of the play fight was calculated (i.e., the number of video frames for each bite divided by the total number of frames encompassing the play fight). A bite was considered to have begun at the first frame of contact with the target and end at the last frame of contact. The partners were labeled as A and B and the bites by both were tracked,.

As can be seen in Figure 3, which juxtaposes the pattern of biting in a sequence from drills with one from Guinea baboons, the differences are readily noticeable. Compared to the baboons, each bite by the drills tended to encompass a smaller percentage of the encounter. Comparing these simplified notations across all four species showed that the two *Papio* species were more like each other and different than the two Mandrillus species, which in turn were more similar to each other. The same approach was used to track and evaluate torso-to-torso contact during bouts of play fighting, and this revealed a similar genus difference: There were longer periods of close contact present in the *Papio* species than in the *Mandrillus* species.
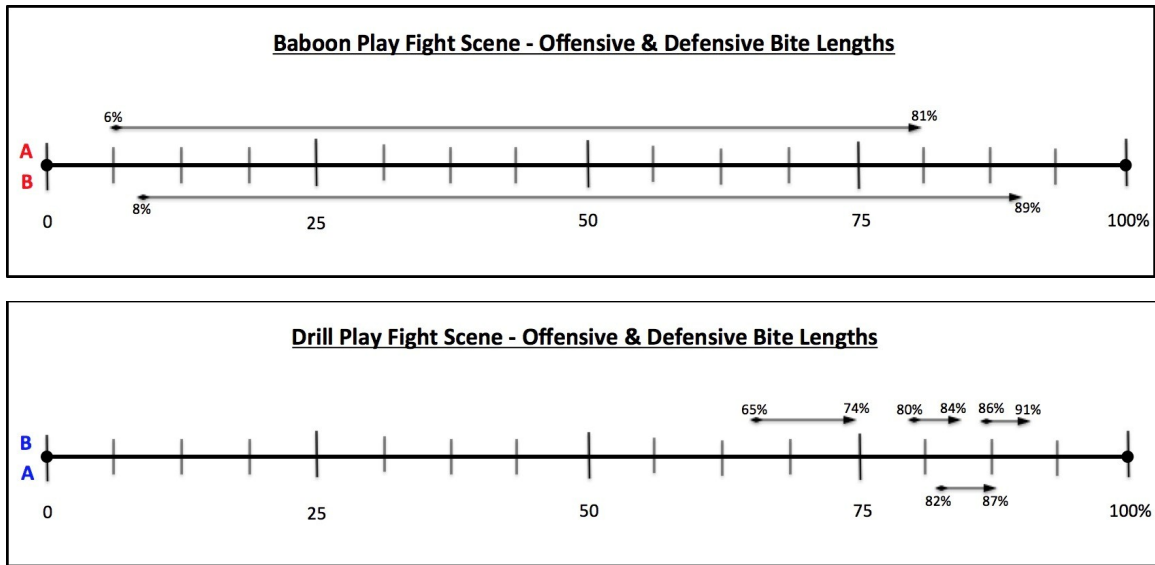
*Figure 3.* **An example of biting during play fighting is shown for a pair of Guinea baboons (upper panel) and drills (lower panel).** The total length of the play fight is standardized to 100%, and the bites by the partner that delivered the first bite is placed above the scale and one that delivered the first retaliatory bite is placed below the scale.

To test these differences quantitatively, the total number of frames in each interaction in which biting by either partner was present were summed and divided by the total number of frames in the bout. This was also done for torso-to-torso contact. Based on the qualitative analyses, it was predicted that the total percent of time spent in biting and in torso-to-torso contact should be greater for the *Papio* species than for the *Mandrillus* species (Table 3).

Table 3
*Percent of time during play fighting involving two types of contact is shown for the four species*

| Species | Biting Contact | Torso-to-Torso Contact |
|---|---|---|
| Drills | 35.25 (6-67)* (18)** | 12.00 (0-54)* (13)** |
| Mandrills | 29.00 (4-56) (13) | 22.00 (0-48) (13) |
| Guinea baboons | 47.50 (17-86) (20) | 41.50 (11-93) (20) |
| Hamadryas baboons | 48.00 (0.9-79) (13) | 56.00 (3.7-95) (13) |

*Note.* *Data are shown as median and range. **The number in parentheses shows the number of play fights scored for each measurement

A Kruskal-Wallis ANOVA showed that the percentage of time spent biting differed significantly across species ($KW = 23.21$, $df = 3$, $p < 0.01$, corrected for ties). While both *Papio* species were similar and both *Mandrillus* species were similar, the *Papio* species had longer durations than did the *Mandrillus* species (Table 3). Pairwise comparisons showed that Guinea baboons differed significantly from drills ($p < 0.01$)

and mandrills ($p < 0.01$), as did hamadryas baboons from drills ($p < 0.01$) and mandrills ($p < 0.01$). The *Papio* species did not differ significantly from each other, nor did the *Mandrillus* species ($p > 0.05$).

Similarly, the percentage of time spent in torso-torso contact differed significantly across species ($KW = 7.98$, $df = 3$, $p < 0.05$). While both *Papio* species were similar and both *Mandrillus* species were similar, the *Papio* species had longer durations than did the *Mandrillus* species (Table 3). Pairwise comparisons showed that Guinea baboons differed significantly from drills ($p < 0.01$) and mandrills ($p < 0.01$), as did hamadryas baboons from drills ($p < 0.01$) and mandrills ($p < 0.01$). Hamadryas baboons had significantly longer torso-torso contact than Guinea baboons ($p < 0.01$), whereas the two *Mandrillus* species did not differ significantly from one another ($p > 0.05$).

Too few of the play fights of the mandrills from the Colchester Zoo met the criteria for conducting the simplified EWMN analyses from which to derive the quantitative values for these two measures, but this was possible for the second sample of Guinea baboons. The scores from the second sample were compared with those from the first (Table 3) with a Mann-Whitney $U$ test. The percentage of time in the encounter in which the animals spent biting (median: 48.07%; range: 22.89-83.11%) did not differ significantly from Sample 1 ($p > 0.05$). The percentage of time in the encounter in which the animals spent in torso-to-torso contact was significantly larger in the second sample ($U = 21$, $n_1 = 8$, $n_2 = 20$, $p < 0.01$). Even so, this larger value (median: 70.9%; range: 16.4-87.2%) was consistent with the larger values for the baboons as compared to the lower values for the *Mandrillus* species (Table 3).

Holding each other at arm's length, as the *Mandrillus* species tended to do (see Figure 1), appeared to increase the difficulty in an attacker accessing its partner's NSUA. To reach toward the NSUA, the lunging partner would have to relax its hold, but, by holding its arms rigidly extended, the defending partner could keep its attacker at bay. Consequently, the *Mandrillus* species were more likely to bite each other on the hands (Figure 1e), seemingly attempting to break free from the hold. To test this greater likelihood of biting the hands, the data in Table 1 were collapsed within each genus, and the likelihood of biting the lower arms and hands was compared to biting other body areas. A two-by-two chi-squared analysis showed a significant deviation from the expected distribution ($X^2 = 37.00$, $df = 1$, $p < 0.01$), with *Mandrillus* biting their opponents' hands more often than expected and *Papio* biting their opponents' hands less often than expected. For the mandrills from Colchester Zoo, 18.87% of the bites were directed bites at the hands. This was significantly less than expected based on the value for the mandrills from the Schönbrunn Zoo ($X^2 = 5.59$, $df = 1$, $p < 0.02$) but still higher than the values for the *Papio* species (Table 1). For the second sample of Guinea baboons, 5.00% of bites were directed at the hands, and this did not differ significantly ($p > 0.05$) from the first sample (Table 1).

The greater propensity for torso-to-torso contact in the baboons (Table 3) is

consistent with the qualitative analyses of the style of play fighting in the *Papio* species. While for all species, the initial bite was most likely defended by the upright maneuver, as encounters progressed, more of the notated sequences of the baboons led to the defender rolling to supine. This pattern was confirmed by quantitatively scoring whether at any point in the encounter one or both animals ended up lying on the ground (Table 2). The data for each genus were collapsed, and rolling to supine was compared to remaining upright. A two-by-two chi-squared analysis showed a significant deviation from the expected distribution ($X^2 = 55.29$, $df = 1$, $p < 0.001$), with *Papio* more likely to adopt supine postures than was the case for *Mandrillus*. The mandrills from the Colchester Zoo and the second sample of Guinea baboons similarly conformed to the genus-typical patterns (Table 2). The Colchester Zoo mandrills had a relatively low value (9.09%), the second Guinea baboon sample had a higher value (45.00%), and neither differed significantly from the other troop and sample from the same species (Table 2).

## Discussion

The organization of play fighting in all four species involves attack and defense of the NSUA area, with the adoption and maintenance of upright postures being the primary tactic of defense. Therefore, these cercopithecines have a basic structure to their play fighting that is similar to that of other species from this subfamily (Owens, 1975a; Pellis & Pellis, 1997; Pellis et al., 2014; Reinhart et al., 2010; Symons, 1978). Despite the basic similarity in their play fights, there are some notable genus-level differences. The baboons are more likely to maintain close bodily contact and sustain prolonged periods of biting. In contrast, the drills and mandrills are more likely to maintain an arm's length distance and are less likely to deliver a bite. Also, because drills and mandrills use their hands to grasp and hold their partners at bay, their hands are also more likely to be targeted for biting. The greater likelihood of the baboons wrestling while rolling onto the ground further illustrates the difference in their style of play fighting compared to the *Mandrillus* species.

Overall, the play fights of baboons seem more relaxed, their bodies less tense. Maintaining close bodily contact makes it easier for partners to bite one another. In contrast, the play fights of the *Mandrillus* species seemed more competitive. They maneuver to avoid being bitten – they keep their partner at arm's length and avoid being pinned to the ground. The bites that did succeed appeared to be maintained for a shorter period of time (Figure 3, Table 3), and, as is noticeable in Figure 1, there were more unsuccessful bite attempts. Indeed, a bite was readily terminated if the partner lunged to bite the head of the monkey maintaining the bite. We hypothesize that while species from both genera compete to bite their partners while simultaneously trying to avoid being bitten (Aldis, 1975; Biben, 1998), in the *Mandrillus* species, the aversion to being bitten is greater. Consequently, *Mandrillus* individuals compete for gaining a bite, but do so in a way as to make being bitten less likely. This difference in their tactical maneuvers, compared to the baboons, makes the play of *Mandrillus* appear more competitive relative to the seemingly more cooperative play of *Papio*.

**Part 2: Competition and Cooperation**

In this section, quantitative and qualitative data are presented that test the hypothesis that *Mandrillus* species are more competitive in their play than are *Papio* species. Based on the greater success of baboons in having sustained bites (Figure 3, Table 3), it could be argued that they are more competitive in gaining bites. However, given that fighting, whether playful or serious, involves attack and defense, a low likelihood of making contact may be for two distinct reasons (Geist, 1978; Pellis & Pellis, 1998). First, few attacks are launched. Second, many attacks are launched, but few succeed because of the defensive maneuvers of the partner. Similarly, once a bite is attained, maintaining it for a prolonged period may be because the animal is able to hold the bite despite the maneuvers by its partner to extricate itself or because the animal that has been bitten does little to dislodge its attacker. Comparing the number of successful and prolonged bites independently of the actions of the partner can be misleading (Pellis et al., 2014; Reinhart et al., 2010). The opportunity to bite also needs to be taken into account.

The EWMN analyses showed that the low frequency of bites and bite duration in *Mandrillus* relative to *Papio* was not because the former launched fewer bite attempts. Rather, as is illustrated in Figure 1, one animal was effective in defending against being bitten by another. As attempting to bite but failing to make contact is a good indication that it is the defending animal's maneuvers that block the contact (Pellis, 1997; Pellis & Pellis, 1998), this measure was used to test the pattern discerned from the EWMN analyses quantitatively.

## Method and Results

A bite attempt was defined as one monkey lunging with an open mouth toward another. Bite attempts that culminated with actual contact were categorized as successful. Based on the bites shown in Table 1, the percentage of successful bites was calculated. Given that it was difficult to distinguish unambiguously between offensive and defensive bites once play fights were ongoing, for this analysis, all bite attempts were summed together. If the qualitative analyses were correct, it was predicted that the *Papio* species should have a higher success rate. There was a significant group difference in the frequency of success ($X^2 = 87.12$, $df = 3$, $p < 0.001$), with the *Papio* species having higher success rates than the *Mandrillus* species (Table 4).

Table 4
*The percent of attempted bites successfully delivered*

| Species | Successful Bites |
| --- | --- |
| Drills | 56.38 (149)* |
| Mandrills | 35.21 (71) |
| Guinea baboons | 87.80 (82) |
| Hamadryas baboons | 83.52 (85) |

For the troop of mandrills at the Colchester Zoo, like the mandrills from the Schönbrunn Zoo, success in making contact with the body area targeted was relatively low (33.33%; derived from 30 bites). A two-by-two chi-squared comparison of successful and unsuccessful bite attempts in the two troops of mandrills did not show any significant difference ($p > 0.05$). Similarly, for the second sample of Guinea baboons, bite success was higher (77.14% of 35 bites) and not significantly different from the values from the first sample ($p > 0.05$).

Two additional qualitative observations are consistent with the hypothesis that it was the *Mandrillus* species' aversion to being bitten that created their more competitive interactions. In the Guinea baboons, the drills and the mandrills from Colchester Zoo, play fights between partners of markedly different size were possible. Comparing those cases in which one partner in a pair was $\geq$ 66.7% larger (judged by the height difference when standing upright) showed that for the mandrills and the drills (five encounters from each troop), the larger partner used its size advantage to subdue the smaller partner, press it to the ground, and deliver long, sustained bites. Based on 10 encounters, larger Guinea baboons did not take such advantage – rather, the play fights of such asymmetrically-sized pairs did not differ from those of evenly matched pairs.

All four species had the kind of face-to-face wrestling and biting illustrated in Figures 1 and 2. Also, in all four species, some playful encounters could involve running at a partner, grabbing them, pulling them off balance, and running away, but these were relatively rare for the drills and baboons ($\leq$ 5.00%). In the mandrills, this pattern was exaggerated in both frequency (52.00% of 60 play fights for the mandrills from the Schönbrunn Zoo, 16.67% of 42 play fights from the mandrills from the Colchester Zoo) and in the pattern of maneuvers performed. This involved one animal approaching another and making feints at grabbing and biting; however, neither monkey made contact; if they did, it was only transitory. In Figure 4, for example, the monkey on the left (1) approached and began to jump over the seated monkey on the right (2) that was facing its partner (Panel a). Both made transitory hand contact as Monkey 1 continued its leap over Monkey 2 (Panels b and c). As Monkey 1 did so, Monkey 2 reared and turned to track Monkey 1 (Panels d and e). Consequently, Monkey 2 faced Monkey 1 as Monkey 1 landed (Panel f) and began to run away (for the real time behavior, see also Supplementary Video Clip 3).

*Figure 4.* **Still frames from a videotaped sequence illustrate a play fighting sequence in a pair of mandrills unlike that of either the drills or baboons studied (see text for a detailed description).**

## Conclusion

The data and observations presented above are consistent with the hypothesis that the apparent greater competitiveness in the *Mandrillus* species arose from their greater aversion to being bitten. The reduced biting by drills and mandrills was not for want of trying; when they attained the advantage, they were not averse to making close bodily contact and delivering prolonged bites. Indeed, the mandrills' non-contact form of play fighting may be interpreted as an exaggerated attempt by them to avoid being bitten.

## General Discussion

Studies of several cercopithecine monkey species (Owens, 1975a; Pellis & Pellis, 1997; Pellis et al., 2014; Reinhart et al., 2010; Symons, 1978) have reported that play fighting is organized around competition for biting an opponent on the side of neck, shoulder, and upper arm (NSUA). Moreover, the most common defensive and offensive tactics to do so involve standing or sitting up. The present study showed that this pattern was also true in four additional species from this subfamily (see Tables 1 and 2, Figures 1 and 2). Even though the targets and tactics in the four species were similar and consistent with that of other cercopithecines, there were some genus-level differences that suggested that the *Mandrillus* species had play fights that were more competitive than those of the *Papio* species.

The *Mandrillus* species spent more of their play fights holding each other at arm's length, and so spent less time in torso-to-torso contact (Table 3), they were less successful in delivering bites (Table 4) and were less likely to sustain biting when successful (Table 3, Figure 3), and were less likely to roll over onto the ground when

wrestling (Table 2). The greater number of bites to the hands in *Mandrillus* species (Table 1) was associated with these patterns, which appear to be attempts to break free from a partner's hold (Figure 1). Indeed, it should be noted that, given the relatively smaller area of the body encompassed by the hands relative to the NSUA (e.g., Hori, Tokura, & Tadaki, 1972), bites to the hands were likely underestimated in the current scoring scheme. We hypothesized that this combination of differences was consistent with the *Mandrillus* species being more averse to being bitten, which results in them being more competitive in their attempts to gain access to their partner's body target while simultaneously trying to prevent retaliatory bites. However, before exploring whether this is the case and, if so, what may account for these genus differences, some limitations in the data need to be considered.

**Caveats**

Behavior can vary markedly across troops of the same species (de Waal & Luttrell, 1989; Thierry et al., 2008; van de Waal, 2018), and, in captivity, novel behaviors can arise (Laidre, 2008). Therefore, we recognize that caution needs to be exercised in drawing overly firm conclusions about species-typical patterns based on a limited sample of troops, especially captive ones. Even so, it should be noted that the majority of studies on play available in the literature are based on analyses of single troops, and most of these are of captive animals (e.g., Emory, 1975; Mancini & Palagi, 2009; Mellen et al., 1981; Palagi & Cordoni, 2012; Pellis & Pellis, 1997; Pereira & Preisser, 1998; Petit et al., 2008). Confidence in what may be regarded as typical for a species is elevated when data from multiple troops of the same species consistently produce the same pattern (e.g., Ciani et al., 2012; Cordoni et al., 2018; Palagi, 2006; Palagi & Cordoni, 2012; Pellis & Pellis, 2018; Pellis, Pellis, Reinhart, & Thierry, 2011; Petit et al., 2008; Reinhart et al., 2010).

In the present study, one troop each from three species and two troops from one species were studied. Despite the differences in the number of animals per troop, the demographic composition (e.g., sex ratio, age distribution), and the type of enclosure, all the troops exhibited the same pattern of play: the attack and defense of the NSUA from a face-to-face orientation while maintaining an upright position (see Figures 1 and 2). Similarly, the differences that did emerge were at the genus level and consistent across troops. The two species of *Papio* species were more like each other than either were with the *Mandrillus* species, and the three troops of the *Mandrillus* were more like each other than any were with the *Papio* species. What these commonalities across species and genera suggest is that the patterns of play fighting are sufficiently robust to override the effects of troop-level variations in demographics and environmental context.

However, without matched samples of troops of comparable size, age-distribution, and sex composition, smaller idiosyncracies across troops are harder to interpret. For example, it is possible that the lower frequency of noncontact play fights in the mandrills from the Colchester Zoo could be due to the younger demographic profile of these animals, or it could be that the exaggerated expression of these types of encounters by the mandrills from the Schönbrunn Zoo is simply a peculiarity of that

troop. Even though the frequency of these types of play fights differed between the two mandrill troops, such encounters were much more common in both troops of mandrills than in the other three troops. Another example is the greater amount of torso-to-torso contact between pairs of hamadryas baboons compared to Guinea baboons. But, given that the second sample of Guinea baboons also had greater torso-to-torso contact than did the first sample from the same troop, it is not possible to know if the apparent species difference is little more than sampling error. However, like the variation in the mandrills, despite these troop and species differences in the *Papio* species, they are unified in being different to the lower amount of torso-to-torso contact in the *Mandrillus* species.

Although the targets attacked and defended are often robustly similar between the sexes and across ages (Pellis & Pellis, 1987, 1988, 1989), the preferred tactics of attack and defense can differ between the sexes and can change with age (e.g., Biben, 1998; Owens, 1975b; Pellis & Pellis, 1990; Symons, 1978). In particular, due to differences in preferred styles of play or social relationships, the choice of play partners can change with age (e.g., Biben, 1989; Cheney, 1978; Koyama, 1985; Lutz & Judge, 2017; Meaney & Stewart, 1981; Owens, 1975b). Therefore, it is not unreasonable to suspect that some of the subtle differences in play style that we found across the species may be an artifact of demographic differences across the troops.

However, it is unlikely that species *differences* and troop idiosyncrasies account for the *similarity* in targets and tactics across all five troops. Clearly, systematic comparisons of known individuals across ages and between sexes are needed to quantitatively evaluate the magnitude of the differences between the two genera. However, given the consistency within the two troops of *Papio* and the three troops of *Mandrillus*, despite within and between genus variation in demographics, we consider that the present data are sufficient to show that there are stylistic differences in the pattern of play between the two genera. If this is so, what may account for these differences?

**Competition versus Cooperation**

Not all defense tactics are equal. For example, when attacked, rats can use two types of tactics to defend their nape and wrestle with a partner. The defender can rotate to supine, which has the advantage of keeping the target pressed against the ground; or, the defender can partially rotate, turning its forequarters toward its attacker, and so keep its nape away from its partner's reach, yet remain standing on one or both of its hind feet. From the supine position, the defender's forepaws are free to push its partner as it stands on top and continues to reach around to its nape. However, the rat standing on top has the advantage as it can use its forepaws and body weight to restrain the movements of its supine partner, thus limiting the range of options for further defensive maneuvers and/or opportunities for launching counterattacks. From the partially rotated position, the defender can push its partner with its forepaws, rear up and push, kick with its hind foot, or hip-slam, any one of which can push its partner off balance, thus creating an opportunity for launching a

successful counterattack (Himmler, Pellis, & Pellis, 2013; Pellis & Pellis, 1987). A detailed analysis of standing and supine tactics in the play fighting of Tonkean macaques (*Macaca tonkeana*) and Japanese macaques (*M. fuscata*) showed the same difference – standing defense offered greater opportunities to block attacks, initiate successful counterattacks, and terminate encounters (Reinhart et al., 2010). Even though both *Papio* and *Mandrillus* species were less likely to adopt the supine tactic, the *Papio* species were more likely to do so (Table 2). The qualitative analyses indicated that just as in rats and macaques, rolling to supine limited the defense and counterattack options available.

Moreover, in both rats and macaques, supine defense creates more opportunities to insert actions that facilitate role reversals (Foroud & Pellis, 2003; Reinhart et al., 2010). Such self-handicapping actions are also possible from the standing position (Pellis & Pellis, 2016; Pellis et al., 2014), but they are more easily enacted when grappling with one's partner while rolling around on the ground (Palagi, 2008; Reinhart et al., 2010). Not only supine defense but also any close body contact can be antithetical to successful defense and counterattack, as is illustrated in the present paper. In the *Mandrillus* species, keeping their partners at arm's length makes successful bites more difficult, whereas the close-quarters play style by the baboons resulted in more frequent and more sustained bites. Therefore, the differences in inter-body distance between the species of the two genera suggest that the *Mandrillus* species are more reluctant to put themselves in a disadvantageous position.

We hypothesized that this may be because although species of both genera seek to bite their partner, as is the case for many species of primates (e.g., Aldis, 1975; Biben, 1998; Owens, 1975a; Pellis & Pellis, 1997; Symons, 1978), the *Mandrillus* species find being bitten more aversive. Consequently, they adopt tactics that can position themselves to launch a biting attack but also simultaneously provide a vantage point from which to block attacks and counterattacks by their partner. Tactics such as these, which are a compromise between attack and defense, have been described in the serious fighting of several species (Geist, 1966, 1978; Pellis & Pellis, 1987; Pellis et al., 2013) and for the play fighting of some species (Pellis & Pellis, 2016; Pellis, Pellis, & Reinhart, 2010).

Consistent with our hypothesis, the *Mandrillus* species did not bite less because they refrained from biting but because more of their biting attacks were foiled by the defensive maneuvers of their partners (Table 4). Of course, it is possible that the genus level difference could be explained by a different mechanism. Engaging in play fighting is highly rewarding (Siviy, 2016; Vanderschuren, Acterberg, & Trezza, 2016). However, although partners compete to contact their partners' play targets (Aldis, 1975; Biben, 1998), simply gaining access to the target without there being any competition appears to be less rewarding that having to physically overcome the partner's defenses to gain access (Pellis & McKenna, 1995; Pellis & Pellis, 2017). The greater competition involved in the pattern of play fighting in the *Mandrillus* species may thus reflect that in some species, competing for access to a target may be more rewarding than actually gaining access to the target. The high frequency of noncontact

play fighting in mandrills may be an exaggeration of this quest to experience competition.

What makes this hypothesis less likely is that, in the *Mandrillus* species, when partners are highly asymmetrical in body size, the animal with the size advantage does not refrain from pinning the smaller animal to the ground and maintaining prolonged bodily contact and long bouts of biting. That is, if the opportunity arises, mandrills and drills are not averse to making close-quarters body contact or to maintaining prolonged biting. This strongly suggests that it is the risk of retaliatory bites that inhibits a more baboon-like pattern of play fighting in *Mandrillus*. Sustaining prolonged body contact and bites and adopting defensive tactics that are less capable of blocking successful attacks by a partner are indicators of a more cooperative form of play (Palagi, 2006; Reinhart et al., 2010). Moreover, while self-handicapping is often thought of in terms of explicit maneuvers by which larger, older, or more dominant animals solicit playful contact from a partner (e.g., Biben, 1986, 1989; Hayaki, 1985; LeResche, 1976 Owens, 1975b; Pereira & Preisser, 1998; Shimada, 2006; Tanner & Byrne, 2010), it is a much more prevalent phenomenon in play fighting, even among evenly matched partners. Unlike serious fighting, in some species during play fighting, partners may act more slowly in executing a defensive maneuver and, when attacking, may fail to incorporate the defensive elements needed to block counterattacks by their partner (Pellis & Pellis, 1998). Such self-handicapping during play fighting facilitates turn-taking (Pellis, Pellis, & Foroud, 2005; Pellis, Pellis, & Reinhart, 2010) and has been identified to occur in several species of primates (Pellis & Pellis, 1997; Pellis et al., 2014; Reinhart et al., 2010). The greater ease with which baboons succeed in gaining and maintaining bites suggests that they incorporate more self-handicapping when executing attack and defense than is the case for the *Mandrillus* species. If this is so, this makes the play fighting of baboons more cooperative and that of the *Mandrillus* species more competitive. But why do these genus-level differences in play fighting exist?

**Play Fighting, Cooperation, and Social Style**

As pointed out in the *Introduction*, an explicit comparison between variation in the pattern of play fighting with an index of sociality based on social organization and mating system failed to find an association (Pellis & Iwaniuk, 1999). A more promising avenue is to consider a third factor of sociality – social structure – the pattern of relationships and interactions among group members (Kappeller & van Schaik, 2002). The genus *Macaca* provides a model for how this aspect of sociality may influence species-typical patterns of play fighting. Despite an overall similarity in social organization and mating system, less tolerant, despotic species are more rigid in their maintenance of dominance relationships than are more tolerant, egalitarian species (Balasubramaniam et al., 2012; Thierry, 2007). More tolerant species engage in play fighting that is more cooperative than less tolerant species, which have more competitive play fighting (Ciani et al., 2012; Petit et al., 2008; Reinhart et al., 2010). Similar differences in play fighting and social style are evident in chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) (Palagi, 2006; Palagi & Cordoni, 2012). The same may apply to the species of *Mandrillus* and *Papio* studied in this paper. Even

though all four species have a basic similarity in social organization – centered around one male harems (Barton, 2000; Swedell, 2011) – there may be differences in the degree of tolerance in the rigidity of their dominance hierarchies, and these may account for the more cooperative play in *Papio* and the more competitive play in *Mandrillus*. Although for this branch of the papionins there is not the same detailed comparative information on social style as that which exists for macaques (Thierry, 2011), there are some suggestive clues.

*Mandrillus* spp. exhibit greater sexual dimorphism than *Papio* spp., which may be indicative of greater inter-male aggression (Cords, 2012), a possibility supported by higher circulating testosterone levels in male mandrills compared with male hamadryas baboons (Whitten, 2000). Increased likelihood of counter-aggression (Thierry, 1985) and reconciliation following agonistic interactions is a major hallmark of more egalitarian species of macaques (Thierry et al., 2008). Both mandrills and hamadryas baboons engage in redirected aggression and post-conflict reconciliation (e.g., Colmenares & Silveira, 2008; Romero, Colmenares & Aureli, 2009; Schino & Marini, 2011, 2014), but systematic cross-species comparisons are not available to ascertain whether there are quantitative differences between the species. That there may be variation in these parameters is suggested by a comparative study showing that Guinea baboons are intermediate for these measures between crested macaques (*Macaca nigra*), a highly egalitarian species, and Japanese macaques, a highly despotic species (Petit, Abegg, & Thierry, 1997).

Another clue is that another one male harem species, the gelada baboon, engages in more contact play and less upright maneuvers than do mandrills (Emory, 1975). Also, as in more egalitarian species of macaques (Ciani et al., 2012), adult-adult play is common in gelada baboons (Mancini & Palagi, 2009) but has not been reported in mandrills (Pellis & Iwaniuk, 2000). Again, it may be that a more egalitarian social style in gelada baboons is associated with more cooperative patterns of play fighting. These hints point to the possibility that the more cooperative play in *Papio* versus the more competitive play in *Mandrillus* characterized in the present paper reflects genus-level differences in social style, with the latter being less tolerant than the former.

Given that in macaques, the association among the traits that reflect species differences in social style are strongly constrained by phylogenetic relationships (Thierry, 2004; Thierry, Iwaniuk, & Pellis, 2000; Thierry et al., 2008), it is possible that the differences between the *Mandrillus* and *Papio* species are due to inherited shared genus-level traits rather than to socioecological factors. As there are only two species of *Mandrillus* that are limited in their geographical distribution and very similar in their socioecology (Cords, 2012; Swedell, 2011), this is a poor genus with which to explore variation in social style with relatedness. In contrast, *Papio* includes five species that are widely distributed across Africa and into the Western Arabian peninsula (Swedell, 2011). Also, baboons are quite variable in social organization, with some, like the hamadryas baboon, being built around one male units, others, like olive baboons (*P. anubis*), forming multi-male/multi-female groups, and still others, like chacma baboons (*P. ursinus*), shifting between one system or the other depending on local ecological conditions (e.g., Henzi & Barrett, 2003, 2005). The greater variability in the social

organization and mating systems of *Papio* make it a useful genus with which to compare the potential variation in the pattern of play fighting. If the pattern of social relationships is the same across all types of social organization, then it should be the case that the degree of cooperation in play fighting should be the same across all members of the genus. In contrast, if social relationships vary independently, then the degree of cooperation in play fighting should also vary accordingly.

## Conclusion

Irrespective of the mechanisms and the evolutionary origins of these species differences in play fighting, the present study shows that even closely related species that share many social and ecological features in common can have idiosyncratic styles of playing. Thus, in primates, as among rodents (Pellis & Pellis, 2009), simple measures regarding the frequency of play may not be sufficient for comparative studies. Attention needs also to be paid to the targets of competition, the tactics used, and how cooperation is achieved. Given the importance of self-handicapping in producing some of the important benefits derived from play in the juvenile period (Pellis, Pellis, & Bell, 2010; Špinka, Newberry, & Bekoff, 2001), the manner in which behavior during play is modified to achieve cooperation is important to understand. This is especially so because not all forms of play are able to produce the same functional outcomes either in the juvenile period or in adulthood (e.g., Marks, Vizconde, Gibson, Rodriguez, & Nunes, 2017; Palagi, 2011; Pellis, 2002; Pellis et al., 2019). It is important to identify the components that are essential for particular functions (Pellis & Pellis, 2017). Characterizing variations in tactics and modes of cooperation in play fighting can be difficult if the targets of competition also differ across species. The present study adds to a growing list of cercopithecine species that compete for the same body targets during play fighting. If this remains true across a wider range of species, then this subfamily would provide an excellent taxon for comparative analyses of social style and level of cooperation in play fighting.

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