

Targets and Tactics of Play Fighting: Competitive *versus* Cooperative Styles of Play in Japanese and Tonkean Macaques

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Macaques are the most geographically widespread and behaviorally diverse primate genus, and although macaque species share the same, basic social structure, they display broad interspecific variation in patterns of adult social behavior. Based on these patterns, macaque species have been arranged along a 4-grade scale for social style. At one end of the scale, there are grade 1 species (e.g., Japanese macaques) that have highly hierarchical and despotic social systems, and at the other end, grade 4 species (e.g., Tonkean macaques) that have more relaxed and egalitarian social systems. We predicted that a species from the more despotic end of the spectrum should have more competitive play fights and that a species from the egalitarian end, more cooperative ones. A detailed analysis of videotaped sequences of juvenile play fighting in Tonkean and Japanese macaques was used to characterize the targets and tactics of attack and defense. Even though the two species have a similar behavioral repertoire, there are significant differences in how that repertoire is used and these differences are consistent with one species having more competitive interactions than the other. Contrasting multi-animal play fights versus pairs showed that the more cooperative style of the Tonkean macaques is further exaggerated. The results suggest that differences in styles of attack and defense in play fighting may be influenced by differences in the species' social systems.

Play fighting, which is observed most frequently during the juvenile stage of development (Pellis & Pellis, 1998a), is a non-aggressive form of competitive interaction involving gaining some advantage over the partner (Aldis, 1975). For many species of mammals, from diverse groups including carnivores, primates, rodents and ungulates, the most common advantage competed over is to bite or

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otherwise contact a species-typical body target (Aldis, 1975; Biben, 1998; Fagen, 1981; Fox, 1969; Pellis, 1988; Pellis & Pellis, 1997; Rushen & Pajor, 1987; Symons, 1978). Species differences can, to a large extent, be accounted for by differences in the location of the species-typical targets (Aldis, 1975) and with the species-specific differences in the tactics available for attack and defense (Pellis & Pellis, 1998a), which are greatly influenced by idiosyncratic features of body morphology and maneuverability (Meaney, Stewart, & Beatty, 1985). For example, monkeys such as patas monkeys (Pellis & Pellis, 1997) and rhesus macaques (Symons, 1978) concentrate their bites around the upper body and neck, whereas spider monkeys bite more randomly (Pellis & Pellis, 1997). These species differences in target location influence how the animals maneuver to gain or avoid access to those targets (Pellis, 1988). Sometimes, even when the same target is competed over, there are species differences in the tactics most commonly used. For example, both montane and prairie voles compete to nuzzle the nape of the neck, but whereas the most likely defensive maneuver for the montane vole is to rear up on its hind legs and push its partner with its forepaws, the most common tactic by a defending prairie vole is to roll over on to its back and push its partner with its forepaws (Pellis, Pellis, & Dewsbury, 1989). Furthermore, the “weapons” available to different species can modify the kinds of tactics they use. For example, for species of rodents and primates, the paws and hands can be used for grasping, pushing or restraining the partner. This limb use can lead to complex patterns of playful grappling and wrestling (Aldis, 1975; Pellis, 1988) that are not possible for species such as pigs, which need to restrict the use of their limbs for postural support when attacking or fending off an attack (Rushen & Pajor, 1987). Even more complicated options are available for some species such as the spider monkey, where the tail is prehensile and is used as a fifth hand (Pellis & Pellis, 1997). But play fighting for most species is not just a low-intensity form of aggression - rather, it is a distinct form of interaction with peculiar rules for how tactics may be employed to attack and defend body targets (Biben, 1998; Pellis & Pellis, 1998b).

Computer simulations of play fighting based on game theory show that the further play fights deviate from both partners having an equal chance to win, the more likely the encounter will escalate into serious fighting (Dugatkin & Bekoff, 2003). To achieve the restraint necessary for play fighting to be reciprocal, some kind of cooperative self-handicapping is thought to be common to all species that engage in play fighting (Bekoff, 2004; Biben, 1998; Fagen, 1981; Kipper & Todt, 2002; Palagi, 2006; Pellis & Pellis, 1998b; Pellis, Pellis, & Reinhart, 2010). This unique feature of play fighting is best understood by contrasting how attacks are launched during play fighting as opposed to serious fighting. When lunging to bite the species-typical play target, animals as diverse as rats, monkeys and lemurs do not incorporate a defensive action into their attack, thus facilitating the recipient’s ability to both defend itself and launch a counterattack (Pellis & Pellis, 1987; 1997). This is quite unlike serious fighting in which animals as diverse as species of ungulates (e.g., Barrette, 1986; Geist, 1978), carnivores (e.g., Blanchard, Blanchard, Takahasi, & Suzuki, 1979; Leyhausen, 1979) and rodents (e.g.,

Blanchard, Blanchard, Takahashi, & Kelley, 1977; Pellis, 1997) have been shown to incorporate defensive maneuvers into their attacks to offset the retaliatory capability of their opponents. For some species, there is no restraint in the execution of fighting tactics during play fighting and this can lead to the impression that the animals are 'playing to win' (Thompson, 1998), but for some such cases it has been shown that the restraint comes after winning. For example, in degus (*Octodon degu*), a South American rodent, rearing up, holding the opponent and kicking with the hind legs occurs both during serious and playful fighting, and in both cases, defensive maneuvers are integrated into the attack. The difference between serious and playful fighting emerges after delivering a successful kick, which leads to the opponent being thrown onto its back. In serious fights, the attacker takes the opportunity to lunge and deliver a bite to its disadvantaged opponent, whereas in play fighting, the attacker refrains from taking such advantage (Pellis et al., 2010). Thus, not only does play fighting involve competition, but it also involves cooperation.

The above considerations suggest that differences in the play fighting of species can arise from many sources. For competition, there can be variation in the targets attacked, the tactics used to attack and defend, and the weapons available to employ for attack and defense. For cooperation, there can be qualitative differences among species with regard to the type of restraint used (during the execution of an attack, as in rats and monkeys, or after the execution of a successful attack, as in degus) and quantitative differences in how much restraint is used. The latter has been well documented for both dogs and rats, where playful pairings of different partners has revealed that, with some pair mates, the win-to-loss ratio can deviate markedly from parity and still the play fighting will remain playful (Bauer & Smuts, 2007; Pellis, Pellis, & McKenna, 1993). For rats, at least, this quantitative deviation in restraint during play fighting is associated with dominance relationships, whereby the subordinate tolerates less restraint from the dominant than vice versa (Pellis, 2002). To study how and why the rules for cooperation during play fighting vary across species, it is advantageous to use closely related species that are likely to share the same targets and tactics and have comparable capacity for maneuvering during fast-paced interactions. Furthermore, given the important role for dominance identified in the play fighting of rats, a closely related group of species that differ in the strength of their dominance hierarchies could be especially useful.

Macaques (genus *Macaca*) provide a good model, from within primates, to explore the issue of how cooperation during play fighting is attained and how it can vary across species. This genus comprises about 20 species that cluster into patterns of social organization, ranging from despotic to egalitarian (Matsumura, 1999; Thierry, 2000). Furthermore, these differences in social styles reflect species differences in temperament that influence a wide range of behaviors, including dominance relationships (Thierry, 2000, 2004). Thus, while all these species are female philopatric, with female dominance hierarchies within and between matriline, and a separate dominance hierarchy for the males, there is considerable variation in how rigidly these hierarchies are enforced. For example, in the more

despotic species, within troop disputes are more likely to lead to biting by the more dominant partner, whereas for the more egalitarian species, not only is biting less frequent, but it also is more likely to be reciprocated by the recipient (Thierry, 1985). In this paper, a detailed comparison of play fighting in two species of macaques, the Japanese macaque (*Macaca fuscata*) - from the despotic end of the social spectrum - and the Tonkean macaque (*M. tonkeana*) - from the egalitarian end of the spectrum - are compared. Because species from the extreme ends of the spectrum are being compared, we will use the egalitarian and despotic descriptive terms to contrast these species, but it should be borne in mind that the 20 species fall on a gradient ranging from more tolerant (egalitarian) to more intolerant (despotic) that likely reflect small changes in traits rather than there being distinct categories (Thierry, 2007).

With regard to play fighting, previous studies have reported both quantitative and qualitative differences in the play fighting of macaques (Caine & Mitchell, 1979), and some of these differences are consistent with differences in degree of social tolerance among the species (Petit, Bertrand, & Thierry, 2008; Thierry, Iwaniuk, & Pellis, 2000). What is uncertain from these earlier studies is whether the differences arise from differences in the targets and tactics used, in how they cooperate during play fighting, or some combination of both. In this study, we test two hypotheses about the similarities and differences in the play fighting of juvenile Japanese and Tonkean macaques.

The first hypothesis is that dyadic play fighting in these two species of macaques, despite their differences in sociality, should be comparable - it should involve attack and defense of the same body target, which if contacted, is bitten (albeit, usually gently), and the same defensive tactics to avoid such contact. Given previous studies, not only of other macaques (Symons, 1978), but also, of other Old World monkeys, such as the patas monkey (Pellis & Pellis, 1997), and of apes, such as the gorilla (Schaller, 1963), we predict that the shoulder area is likely to be the modal target competed over during play fighting in both Japanese and Tonkean macaques. Similarly, based on these previous studies, we predict that both species of macaques have defensive tactics that involve either rolling over to supine or remaining standing, likely in a bipedal position (see Aldis, 1975 for many other primates).

The second hypothesis to be tested is that the degree of cooperation shown by the two species in their play should vary in relationship to the differences in their species' social styles. Thus, the more egalitarian Tonkean macaque should modify its patterns of attack and defense in a way that tolerates greater variation in attack and defense, and engage in more prolonged interactions than the more despotic Japanese macaque. Specific predictions arise from this hypothesis. First, in dyadic interactions, Tonkean macaques should be more likely to bite body targets and use defensive strategies that are more likely to prolong continued bodily contact (i.e., less bites to the face relative to the shoulder and more supine defense relative to standing defense) (Pellis & Pellis, 1998a, 1998b). Second, these species differences in dyadic play fights should be exaggerated when additional partners join in the interaction.

As is typical for most species studied (Fagen, 1981), both species of macaques engage in classic dyadic play fights, where each partner has to contend with the moves of the other, but, in addition, they also engage in polyadic play fights, where the actions of multiple partners need to be dealt with simultaneously (Pellis, 1984; Pellis & Pellis, 1998b). There is evidence that when multiple animals are involved, mistakes are more likely. To understand this evidence, we must consider play signals, which are considered to be gestures given during play to inform one's partner that the actions performed are playful (Pellis & Pellis, 1996). During dyadic encounters, play signals, such as the open mouth play face of primates (van Hoof, 1972) and the play bow of canids, are more frequently delivered just prior to grabbing or biting a partner (Bekoff, 1995; Pellis & Pellis, 1997) than at other times during the play fight. This implies that play signals are more frequently used when there is potential ambiguity in the encounter. Bonobos have been reported to emit more play signals during polyadic interactions than during dyadic ones (Palagi, 2008), suggesting that the former are more unpredictable than the latter. Sustaining many multiple animal encounters should greatly tax the cooperativeness of play fighting, as animals are more likely to receive unexpected contacts. Therefore, we predict that if the modifications in the targets and tactics of play fighting are only subtle in Tonkean compared to Japanese macaques during dyadic play fighting, they will be greatly exaggerated during polyadic play fights. For example, biting in polyadic play fights should be less focused on the modal play target in Tonkean macaques than in Japanese macaques.

By revealing how the play fighting of different species are grossly similar, and how subtle differences may reflect broader species difference in sociality, the present study has implications for conducting more extensive comparative studies of primates that would test the relationship between sociality and play fighting.

Method

Given that captive or free-living, but provisioned troops, were used, two methodological strategies were adopted to ensure that the comparisons made truly reflect similarities and differences between species rather than merely troop differences. First, for a detailed analysis of the content of play fighting, one troop from each species was selected. These two troops were matched as closely as possible for group demographics and physical environment. Second, three other troops for each species - which ranged widely with regard to demographics and physical environment - were used to test whether the measures that were shown to conform to the predicted outcomes in the first analysis were consistent across other troops of the same species.

Part 1 – Comparison of the Two Focal Troops

Subjects

Juvenile play fighting was examined in two groups of captive macaques. These groups were matched as closely as possible in terms of their housing conditions, group size and composition, their geographic location, as well as in the timing of the data collection, for which both the time of year and the time of day for making observations were considered (see below). Because many of the potential, confounding environmental variables were controlled for, it was likely that behavioral differences would reflect species-typical dispositions (de Waal & Luttrell, 1989).

Tonkean macaques are found in the central region of the island of Sulawesi, Indonesia (Thierry, Anderson, Demaria, Desportes, & Petit, 1994). A group of Tonkean macaques was imported into France (to the Landskron Château in Southern Alsace) in 1972, and were released into an area of about 0.81 hectares, with the intention of establishing a new population from eight reproducers (Herrenschmidt, 1977). In 1978, the newly founded breeding population at the Landskron Château was divided into two groups, with one group maintained at the Primate Research Centre of the Université Louis Pasteur in Strasbourg, France (Thierry et al., 1994). Since 1982, the other group has been maintained at the Orangerie Zoo of Strasbourg, and this was the group observed for this part of the study. The group was housed in a 120m² outdoor enclosure that is connected to a 13m² indoor shelter. The walls of the outdoor portion of the enclosure are 4m high and the indoor portion, which was cleaned in the morning, 2 times per week, has 1.8m walls. Monkey pellets were provided twice daily and water was available *ad libitum*. At the time of the study, the group contained 20 individuals: 3 adult males (8 - 14 years old), 4 adult females (8 - 17 years old), 6 juvenile males (one 5 year old, one 4 year old, two 3 year olds and two 2 year olds), 4 juvenile females (one 4 year old, two 3 year olds and one 2 year old), and 3 infant females (1 year or less of age). The ten juveniles were included in the study.

Japanese macaques are indigenous to the Japanese islands. In 1985, 10 Japanese macaques (3 males, 7 females) were imported from the Nagatoro Monkey Park, Japan, and a captive group was established at the Parc Zoologique de Paris in Paris, France. The group was housed in a 300m² outdoor enclosure that is connected to a 20m² indoor shelter, where the animals were kept at night. Monkey pellets were provided each day and water was available *ad libitum*. At the time of the study, the group contained 20 individuals: 5 adult males (9 - 21 years old), 6 adult females (7 - 18 years old), 1 adolescent female (5 years old), 3 juvenile males (one 3 year old and two 2 year olds), 3 juvenile females (one 3 year old and two 2 year olds), and two infants (one male and one female both between 1 - 2 years old). Eight individuals, including all 6 juveniles and the two older infants, were included in the study.

Observation protocols

The group of Tonkean macaques was observed over a period of 3 months from June to August, 2005. The group of Japanese macaques was observed over a period of 2 weeks in August, 1997. Data were collected between 0900 and 1800. All play fights involving juvenile members of the group were filmed using a Sony Digital Video Camera (model no. DCR-PC9). When two or more interactions began simultaneously, the one involving the individuals less frequently sampled was chosen for filming (de Waal & Yoshihara, 1983; Thierry, Gauthier, & Peignot, 1990). The animals were filmed only in the outdoor enclosure. Approximately 18h of video were obtained for the Tonkean macaques and 6h for the Japanese macaques.

Behavioral measures for play fighting

After the videos were collected, the digital cassettes were converted to VHS format and a time code (1/30th of a second) was added using a Horita TRG-50 time encoder (Horita, Mission Viejo, CA). To maintain consistency in the scores among animals, all interactions were viewed at normal speed, in slow motion, and frame-by-frame by the same observer (CR), although once the analysis was completed, measures of play that were found to be consistent across the various troops studied were identified, and a sample of the same videos were re-scored by another researcher (SP) to ensure that the scores were consistent across scorers (see below). Bearing in mind that the movements observed during play fighting are often functionally organized around gaining access to, and protecting, a particular area of the body (i.e., biting a specific body target without being bitten) (Aldis, 1975; Pellis, 1988; Symons, 1978), 200 play fights, including both dyadic and polyadic interactions, were scored to determine what region(s) of the body juvenile macaques were targeting (i.e., play-biting). Note that, given the differences in total video available between the species, the first 200 play fights that met the appropriate criteria (see below) were used to ensure an unbiased and comparable sample for comparison between the species. Prior to the formal scoring, about 30 interactions from each of the two species were observed in detail, noting the movements of one

partner relative to the other. As unsuccessful bite attempts by one animal may be due to the defensive actions performed by the other, frame-by-frame analysis of the movements of both partners can often reveal the target being aimed at in an attack. The actual bite delivered may represent a deviation from the targeted attack (Pellis & Pellis, 1988, 1997). Nonetheless, the targeted body area should be the one receiving the modal number of bites (Pellis, MacDonald, & Michener, 1996). Therefore, the initial qualitative analysis to identify the apparent target(s) was followed up by a quantitative analysis to determine if the inferred target was indeed the one most likely attacked. For the quantitative analysis, only interactions meeting more stringent criteria (see below) were used so as to avoid errors in cross-species comparison (Pellis & Pellis, 1997).

Only play fights that met the following criteria were included in the quantitative analysis: (1) the interaction had to have occurred on a relatively flat surface within the enclosure (as opposed to tree branches, ropes, or other hanging structures), (2) the initiation and termination of the interaction had to be clearly visible, (3) at least one bite had to be delivered or an obvious bite had to be attempted during the interaction, (4) all participants had to be identifiable, (5) no adult participation could occur during the play fight, and (6) the interaction could not revolve around competition for an object (e.g., a stick or large rock). When scoring play bites, the body was divided into the following 5 regions (similar to Pellis & Pellis, 1997): (1) Head/Face (H/F), (2) Neck/Shoulder/Upper Arm (N/S/UA), the upper arm being above the elbow, (3) Body (B), including the dorsal, ventral and lateral areas, (4) Lower Arm/Hand (LA/H), the lower arm being below the elbow, and (5) Leg/Foot (L/Ft). Of course, when responding to a playful bite, the recipient could deliver a retaliatory bite. Because previous analyses have revealed that the targeting of retaliatory, or defensive bites can differ from the targeting of initiating, or offensive, bites (Pellis & Pellis, 1997), offensive and defensive bites were recorded separately. The number of offensive and defensive bites directed to these regions of the body was totaled, and offensive and defensive bite distributions were calculated.

In addition to scoring playful bites, the duration, the initiator and the terminator of each play fight were also noted. A play fight was considered to have begun when the animals approached one another, with the first animal to deliver a bite or lunge with an open mouth being considered the initiating play partner. A play fight was considered to have terminated when one of the participants either evaded the interaction, or began engaging in a different solitary or social activity. Duration of play fights was scored from the frame of first body contact to the frame when the animals ceased interacting.

One limitation of scoring play fights that have, at the outset, varying approach orientations and participant postures, is that it can be difficult to determine whether individuals are biting a preferred play target or are opportunistically biting a region of the body in response to their own and/or their partner's position, relative to one another. For example, if one individual were to approach and attack another individual from behind, both partners are limited in that the attacker can only access and bite a sub-set of the defender's body regions. The defender, on the other hand, is limited in making a response to the bite because of the attacker's approach angle. Thus, the outcomes of such an encounter can be very different from one in which the attacker approaches from a different orientation. If species differences involve preferences for different attacking orientations, then differences in targets may not be due to species preferences for biting particular areas of the body. Therefore, a subset of play fights was extracted for subsequent analyses in which the animals were in the same orientation: face-to-face (F-to-F).

In these play fights, the play partners were facing each other and were in a sitting, standing or rearing position, but not laying down. In this situation, as both play partners would be vertically oriented, they are relatively equal in terms of their opportunities to make offensive playful attacks and defensive movements in response to attacks. The F-to-F context that was used for these analyses could occur at either the beginning of the play fight (i.e., the initial approach and attack), or at any point within an ongoing play fight. Thus, several F-to-F contexts could be achieved within a single play bout. From the 200 play fights sampled from each species, a total of 252 F-to-F contexts were analyzed for Tonkean macaques and 179 for Japanese macaques.

Because play fighting is a dynamic interaction between individuals, the movements of one animal can influence those of the other. Therefore, it is critical that when making quantitative measurements of the maneuvers used, the animals are in a standardized configuration. For example, if

defensive maneuvers following a bite attempt by one partner are scored, but no further constraints on the configuration is prescribed, a finding such as 'species A leaps away more frequently than species B, and, in turn, species B rolls over onto its back more frequently', even if statistically significant, would not be interpretable. A closer analysis may reveal that, for species A, most of the defenses scored arise from bites to the rump from a rear orientation, whereas for species B, most of the defenses scored arise from bites to the shoulder from a frontal orientation. To determine if the species do indeed have different preferences in their use of tactics, the comparison must be from the same bite target and partner orientation (Pellis, 1989; Pellis & Pellis, 1992). Therefore, the defensive responses used in the F-to-F contexts when a bite was delivered to the modal target, were analyzed. The 30 interactions for each species that were analyzed qualitatively provided the description of the types of defensive tactics used (see *Results*). The quantitative analysis of the F-to-F encounters yielded 166 interactions in the Tonkean macaques and 85 in the Japanese macaques.

Statistical Analyses

Given that the data were mostly categorical and often involved relatively small sample sizes (e.g., n of 7 or 8), non-parametric tests were used in most analyses. To avoid potential problems with small sample sizes, exact methods were used to calculate the test statistics (Mundry & Fischer, 1998). Similarly, tied scores were corrected for where necessary, and for pair wise comparisons following significant non-parametric analyses of variance (see below), appropriate Bonferroni corrections were used to adjust for the number of comparisons (Siegel & Castellan, 1988). Wherever possible, multiple techniques were used to ensure that the significant patterns discerned were unlikely to have arisen by chance. Significance was set at $p < 0.05$, but wherever possible, actual p values are given.

Dyadic play fights

Targets: Bite distributions. The 252 and 179 F-to-F contexts that were scored involved 10 juvenile Tonkean macaques and 8 juvenile Japanese macaques. As mentioned previously, the number of offensive and defensive bites directed to the various regions of the body was totaled and bite distributions were calculated for each species. Chi-square analyses of the pooled raw scores for each species were performed to test whether the offensive and defensive bites found for each species were randomly distributed. Given the unequal contribution of individual group members to the pooled score, this distribution may not represent the group as a whole, but instead, may result from the effect of some outlier. Therefore, a sub-set of the scored F-to-F contexts was used to calculate offensive and defensive bite distributions for individual animals. To be included in the analyses, an individual had to have been involved in 10 interactions in the F-to-F context, with no more than 5 out of these 10 interactions being with the same play partner. To ensure an unbiased sample from each individual, the first 10 interactions recorded were used, unless an interaction had to be omitted for not meeting the criteria mentioned above. For example, when compiling animal A's sample of 10 interactions, if animal A already had 5 interactions with animal B, then the 6th interaction between A and B could not be included in A's sample, and another interaction involving a different play partner had to be found. Consequently, 8 Tonkean and 7 Japanese macaques were included in the subsequent within and between species analyses for bite distributions.

Although Chi-square analyses are generally inappropriate for pooled data, such analyses were valuable for two reasons. First, it enabled us to use the entire data set to determine whether an overall pattern existed. Second, as will be elaborated on in the *Discussion*, the finding that the pooled data yielded the same results as when using individualized data, helps support the argument that the group differences found represent robust species differences. Conversely, significant Chi-squares based on pooled data not supported by analyses of individualized data should be given little weight other than as guides for future studies.

Tactics: Defensive responses. The 166 and 85 defensive responses that were scored involved 10 juvenile Tonkean and 8 juvenile Japanese macaques, respectively. Chi-square analyses of the pooled raw scores for each species were performed to test whether the defensive responses reported for each species were randomly distributed. For the reasons given above, additional analyses

involving individual data were conducted. To be included in the analyses, an individual had to have performed a minimum of 5 defensive responses in the F-to-F context. Where possible, a maximum of 10 responses was used for an individual, ensuring that no more than 50% of that individual's responses came from interactions with the same play partner. Therefore, the interactions used to make up each individual's sample were the first 5 - 10 recorded for that individual, unless a response had to be omitted for not meeting the criteria mentioned above (in which case, another interaction involving a different play partner was found). Consequently, 77 responses from 8 Tonkean macaques, and 60 responses from 7 Japanese macaques were included in the subsequent within and between species analyses for defensive response distributions.

To analyze the data derived from individuals for both bite targets and defensive actions, a Friedman ranked-scores analysis of variance was used. For cases where the analysis of variance indicated a significant deviation from random, appropriate follow-up tests were used that corrected for the number of comparisons (Siegel & Castellan, 1988). For cross species comparisons of specific bite locations and defensive tactics that were found to be significant in the within species comparisons, Mann-Whitney U tests were used.

Play fight durations. From the 200 play fights for each species all instances in which the beginning and end of encounters could be determined were used to calculate the mean duration and 95% confidence intervals. Although the sample sizes were sufficiently large to offset likely distribution errors, because the data involved pooling durations from multiple animals, another method was used to compare durations with equal contributions from each individual. To avoid selection bias, the first 14 recorded play fights for each individual were used to calculate that individual's mean score. Again, only 50% of the scored durations came from interactions with the same partner, so if the first 14 encounters did not fulfill this requirement, additional bouts of play fighting were used. A Mann-Whitney U test was used to compare species.

Polyadic play fights

Of the 200 play fights scored, 18 of those in Japanese macaques involved more than two partners, whereas in Tonkean macaques, 62 involved polyadic interactions. Because about half of the polyadic play fights by Tonkean macaques involved more than three individuals, and all of those in Japanese macaques only involved triads, an additional 208 play fights for the latter species were scored so that we had at least some examples of polyadic play fights involving more than three partners. Three types of analyses were performed. First, the frequency distribution for the number of individuals involved in play fights were scored. Second, the location of bites, both offensive and defensive, was scored. Third, the duration of polyadic interactions was scored. Because of the paucity of interactions involving more than three animals in the Japanese macaques, only triadic interactions were scored and compared for bite distributions and play fight durations between the species. Also, for reasons that will become evident in the *Results*, comparison of the tactics of defense in multiple partner interactions in the two species was not possible, so a quantitative analysis was not attempted.

Targets: Bite distributions. The number of offensive and defensive bites directed to the various regions of the body was totaled, and bite distributions were calculated for each species. Chi-square analyses were performed on the pooled raw scores for each species. Unlike dyadic play fights, scores for individual participants could not be obtained for polyadic play fights, as these involved a shifting number of participants. For example, a play fight could begin with individuals A and B, be joined by C, and then D could join and B could leave. Given the changing membership of a play fight, bites by any individual - even A in the above example, who remained in the encounter from beginning to end - could not be recorded in a consistent context. For this reason, it was not possible to extract data for individuals to confirm the results from the pooled data. Therefore, a different analytical approach was used to test the data so as to avoid undue influence of potential outliers and to increase confidence in the patterns observed. It should also be noted that as is the case for bites in dyadic interactions, offensive bites are 2-3 times more frequent than defensive bites (present study, and, for other species, see Pellis & Pellis, 1997; Symons, 1978). Given the difference in numbers available for the two types of bites, the quantitative analyses needed to be slightly different.

The data for each species, for both offensive and defensive bites, were grouped into 'bins'. For example, the first 20 offensive bites for Tonkean macaques were placed into bin #1, the next 20

bites were placed into bin #2, and so on, until no more bins could be filled with 20 bites. The defensive bites were organized in the same manner, except that each bin contained only 10 bites because the total number of defensive bites available for analysis was substantially smaller. So as to only use bins containing equal numbers of bites, bites that were in excess of the requisite number for the final bins were discarded from further analysis. In total, there were 9 offensive bins and 4 defensive bins for Tonkean macaques, and 8 offensive bins and 6 defensive bins for Japanese macaques. In a sense, bins substituted for individual scores. These were then compared using a Friedman ranked-scores analysis of variance. For cases in which the analysis of variance indicated a significant deviation from random, appropriate follow-up tests were used that corrected for the number of comparisons (Siegel & Castellan, 1988). Mann-Whitney U tests were used for cross species comparisons of specific bite locations.

To compare polyadic bite distributions with dyadic ones, Chi-square analyses of the pooled raw scores for each species were performed to test whether or not the distributions of offensive and defensive bites observed in polyadic play fights could be predicted from the bite distributions derived from the analysis of dyadic play fights.

Play fight durations. Given that for the first 200 play fights only 18 clear-cut examples of polyadic play fighting were available for Japanese macaques, the first 18 examples of polyadic play fighting from the Tonkean macaques were used to make species comparisons. These 18 data points for each species were used to calculate the mean duration and 95% confidence intervals. However, because of the potential distortion due to unequal contributions from individual animals, a method to randomize the data was developed. Each species' sample of 18 polyadic play fights was assigned a number (1-18), and using a random number generator, three bins of six scores each were constructed. A Kruskal-Wallis one-way analysis of variance was then used to test, within species, whether there were significant differences between bins. The procedure was repeated 10 times, and in no case was there a within species difference among bins ($p > 0.05$). Therefore, the 18 samples from each species were treated as separate scores for the purpose of comparing between species using a Mann-Whitney U.

In order to compare dyadic with polyadic interactions, a sample of the first 18 dyadic play fight durations recorded for each species were used, randomly assigned to bins and tested with Kruskal-Wallis tests as described above. Again, there were no within species differences ($p > 0.05$), and so the data were combined for cross-species comparisons using Mann-Whitney U tests.

Part 2 – Multiple Troop Comparisons

Subjects

Another six troops (three per species) were videotaped, with play fights recorded opportunistically as they occurred during the observation period. Details on these troops can be found in the literature (Huffman, 1991; Nahallage & Huffman, 2007; Reinhart, 2008; Thierry et al., 1994), so only the information pertinent to the comparisons being made is presented.

Tonkean macaques

Over a period of two weeks in July 1996, a troop housed at the Primate Research Centre (PRC) in Strasbourg was filmed (T1). The troop was derived from the same stock as the troop filmed at the Orangerie Zoo (see above) and was housed in a 2-acre wooded enclosure containing an indoor shelter, surrounded by a fence electrified at the top (Thierry et al., 1994). The troop contained 24 individuals: 2 adult males, 9 adult females, 7 juvenile males, 1 juvenile female, 2 infant males, and 3 infant females.

A new troop was constituted at PRC in the 2-acre park in December 2002 (T2). The adult male came from the Orangerie Zoo to join four adult females and one infant from the initial PRC troop. The troop contained 13 individuals: 1 adult male, 4 adult females, 3 juvenile males, 1 juvenile female (not filmed), 2 infant males, and 2 infant females. This troop was filmed over a period of four weeks from April - May, 2006.

The third troop of Tonkean macaques (T3) was also housed at the PRC and contained five juveniles (2 males, 3 females). All five individuals were removed, simultaneously, from their home group at PRC on April 6, 2006, to constitute a new group. The individuals were between 17 - 22 months of age when they were removed from their home group and ranged in age from 19 - 25 months during the data collection period. The troop was housed in a 14.4m² outdoor wire-mesh enclosure containing a 4m² indoor shelter. This troop was filmed over a period of five weeks from May to June 2006.

Japanese macaques

Two troops were filmed at the Primate Research Institute, Kyoto University. The first troop (J1) was derived from animals taken from Takahama in Fukui Prefecture, Japan, in 1970 and 1971. The troop was maintained in a 960-m² open-air enclosure surrounded by a 5m high concrete wall topped with an electric fence. The troop contained 51 individuals: 7 adult males, 14 adult females, 9 juvenile males, 9 juvenile females, 3 infant males, and 9 infant females. The troop was filmed over a period of 10 days in November 2007.

The second troop (J2) was derived from subjects taken in Tottori Prefecture in 1974. The troop was maintained in a 524-m² open-air enclosure surrounded by a concrete wall topped with an electric fence. The troop contained 37 individuals: 2 adult males, 14 adult females, 3 juvenile males, 6 juvenile females, 4 infant males, and 8 infant females. The troop was filmed over a period of 12 days in November, 2007.

The third troop (J3) comprised the provisioned, free-ranging Arashiyama troop which ranges in the mountains on the northwest outskirts of Kyoto, Japan (Huffman, 1991). The troop consisted of 171 individuals, containing many juveniles (21 males, 18 females) ranging in age from 1 - 5 years of age. This troop was filmed over a period of 10 weeks (September - December) in 2007 (Vasey, VanderLaan, Rains, Duckworth, & Kovacovsky, 2008).

Analyses

Following the procedures of Part 1, 50-100 play fights per troop were analyzed. From these, 32-54 examples of play occurring when the monkeys were restricted to the F-to-F configuration and 6-18 examples of triadic play were analyzed for each troop. The selection procedures for choosing play fights were the same as those for Part 1. The one exception was that, for some troops, the identity of individuals could not be determined in each case. Nonetheless, wherever possible, the contribution of different individuals was balanced by bypassing play fights involving frequently scored individuals and instead, scoring the next available play fight involving other individuals. Videos were viewed and every play fight that occurred which met the criteria was scored. For some troops, all the available encounters meeting the criteria were used and in others, scoring ceased once the first hundred encounters were scored.

To increase both the number of troops for statistical comparison and also by way of testing whether repeated measures from the same troops yield comparable findings, 50 previously unanalyzed play fights in each of the two focal troops were scored. These scores began from the end of the taped material scored for Part 1. As for the additional six troops, any consecutive play fight meeting the criteria was used, thus reducing the risk of a biased sample.

Predictions from the two main hypotheses were tested. Criteria were established for the predictions that were confirmed by multiple analyses of the focal troops in Part 1 and each of the eight troops were scored for whether they conformed to those criteria or not. Given the various ways in which different troops differed from one another and that scores could not be provided for all individual animals, a nonparametric analysis was used. A table showing whether troops were consistent (+) or inconsistent (-) with the predictions was created and tested using a sign test (Siegel & Castellan, 1988). The predictions and the criteria developed to meet those predictions will be described once the analyses for Part 1 are presented.

Results

Part 1 – Comparison of the Two Focal Troops

Dyadic play fights

The dynamic nature of the interactions and the primary body target around which these competitive interactions were organized is illustrated in Figure 1, which shows a play sequence in Japanese macaques, starting from the F-to-F orientation (A). The smaller individual (on the left) attacks by jumping up into the air and twisting his body (B) while orienting to the side of the defender's neck (C). As the attacker moves through the air, the defender rotates to face the attacker and delivers a retaliatory bite to its neck (C – F). As the original attacker lands on the ground, the defender continues to bite the back of the attacker's neck (F) until the attacker swerves away (G). Detailed qualitative analyses of play fights in both species indicated that the play target for macaques is the neck/shoulder/upper arm (N/S/UA). Bites to other locations were mostly in response to the actions of one's partner. For example, when one macaque grabbed another animal's arm or head, the recipient could bite at its partner's hand or lower arm (see Pellis & Pellis, 1997). In other cases, the defender's evasive actions did not permit the attacker to gain access to the N/S/UA, and so a bite was delivered at some distance from this area (see Pellis & Pellis, 1988). Nonetheless, it was predicted that, despite these variations due to the partner's maneuvers, the area of the body most often bitten should be the N/S/UA. This prediction was confirmed by quantitative analyses of the bite distributions.

Targets: Bite distributions. The pooled F-to-F data for each group showed that the modal offensive play target for both species is the N/S/UA region of the body (Figure 2A). Chi-square analyses for each species showed that the distribution of offensive bites delivered to the different regions of the body were not random (Tonkean: $X^2(4, 278) = 345.7, p < 0.001$; Japanese: $X^2(4, 210) = 160.8, p < 0.001$). From a total of 278 offensive bites, Tonkean macaques bit the N/S/UA 61.9% of the time, and out of 210 offensive bites delivered by Japanese macaques, the N/S/UA was bitten 46.7% of the time. When bite distributions were calculated for individual animals, a within species Friedman ranked-scores analysis of variance showed that each species differed from a random distribution (Tonkean: $X_r^2(4, 8) = 159.4, p < 0.001$; Japanese: $X_r^2(4, 7) = 140.4, p < 0.001$). Based on z values corrected for number of comparisons (Tonkean: $z = 7.33$; Japanese: $z = 5.92$), follow-up pair wise comparisons showed that, in both species, the N/S/UA was bitten significantly more than all other regions of the body ($p < 0.05$). Between species comparisons of the offensive bite distributions using Mann-Whitney U tests indicated that there were no significant differences ($p > 0.05$) between species in terms of the frequency with which the N/S/UA was bitten. That is, Tonkean and Japanese macaques do not differ in their modal offensive target.

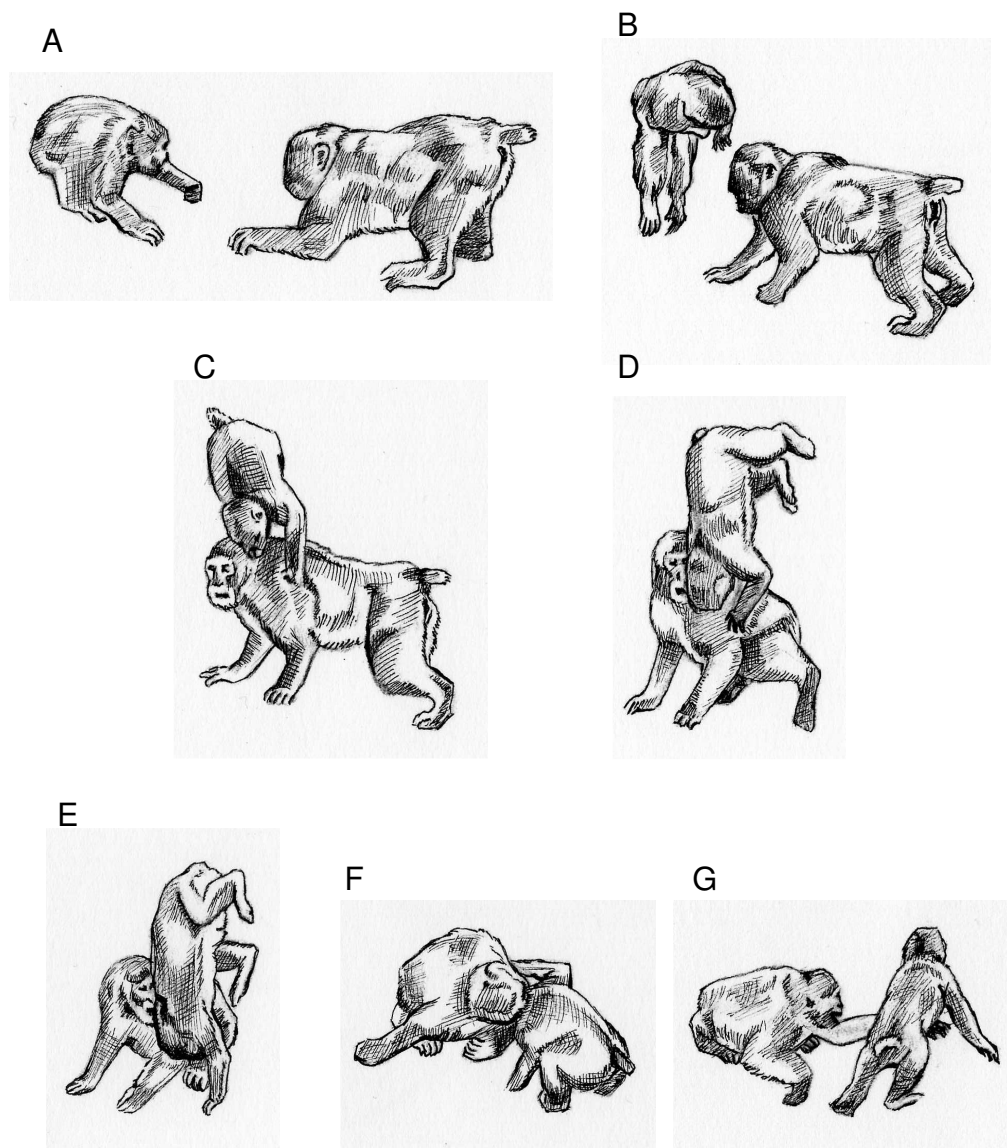


Figure 1. A sequence of play fighting by two juvenile Japanese macaques drawn from videotaped records shows a complete encounter starting from the F-to-F orientation. Note that both the attacker and defender are targeting the neck/shoulder/upper arm (N/S/UA) region of the body. See text for description.

For retaliatory bites, the pooled F-to-F play fight data for each group showed that the modal defensive play target for both species is the N/S/UA region

of the body (Figure 2B), which further reinforces the view that the N/S/UA is the play target for macaques. Chi-square analyses for each species showed that the distributions of defensive bites delivered to the different regions of the body were not random (Tonkean: $X^2(4, 142) = 271.1, p < 0.001$; Japanese: $X^2(4, 154) = 172.0, p < 0.001$). From a total of 142 defensive bites, Tonkean macaques bit the N/S/UA 74.6% of the time, and out of 154 defensive bites delivered by Japanese macaques, the N/S/UA was bitten 49.4% of the time. Based on individual bite distributions, a within species Friedman ranked-scores analysis of variance showed that for each species, defensive bites differed from a random distribution (Tonkean: $X_r^2(4, 8) = 154.7, p < 0.001$; Japanese: $X_r^2(4, 7) = 139.7, p < 0.001$). Corrected follow-up analyses for Tonkean macaques (using the corrected $z = 7.33$) showed that the N/S/UA is bitten significantly more than all other regions of the body ($p < 0.05$). For Japanese macaques (using a corrected $z = 5.92$), not only is the N/S/UA bitten significantly more than other regions of the body ($p < 0.05$), but also the head/face ($p < 0.05$). However, the N/S/UA and H/F were not significantly different from each other ($p > 0.05$). Between species comparisons using Mann-Whitney U tests indicated that there were significant between species differences for: (1) N/S/UA bites ($U(7, 8) = 7.5, p < 0.01$), with Tonkean macaques biting this region more than Japanese macaques, and (2) H/F bites ($U(7, 8) = 5.5, p < 0.01$), with Japanese macaques biting the H/F region more than Tonkean macaques.

Tactics: Defensive responses. The detailed qualitative analyses of complete play fight sequences indicated that when responding to a bite to the modal play target (N/S/UA), the animals of both species react in a manner that enables them to maintain the F-to-F orientation. That is, a defender typically makes movements that rotate its upper body to face its attacker, rather than turning its body away from its attacker or not responding. Based on the patterns that emerged from the sequences analyzed qualitatively, frame-by-frame (see above), five different configurations were consistently identified for the defending monkey: (1) horizontal rotation (HR): the defending individual rotates its body to face the attacker while rolling onto its side or back, (2) the defending individual rotates its body to face its attacker while maintaining a vertical body orientation, remaining at eye level with the attacker, and delivering a retaliatory/defensive bite (VSELB), (3) the defending individual rotates its body to face its attacker while maintaining a vertical body orientation, remaining at eye level with the attacker, and pushing the attacker away or moving backwards, away from its attacker (VSELPA), (4) the defending individual rotates its body to face its attacker while maintaining a vertical body orientation, and changes its eye level relative to the attacker by lowering its head and forequarters to the ground (VCELS), and (5) the defending individual rotates its body to face the attacker while maintaining a vertical body orientation, and changes its eye level relative to the attacker by raising its head and forequarters higher than when the playful bite was delivered by the attacker (VCELT). Figure 3 illustrates three of these tactics (HR, VSELB, VSELPA).

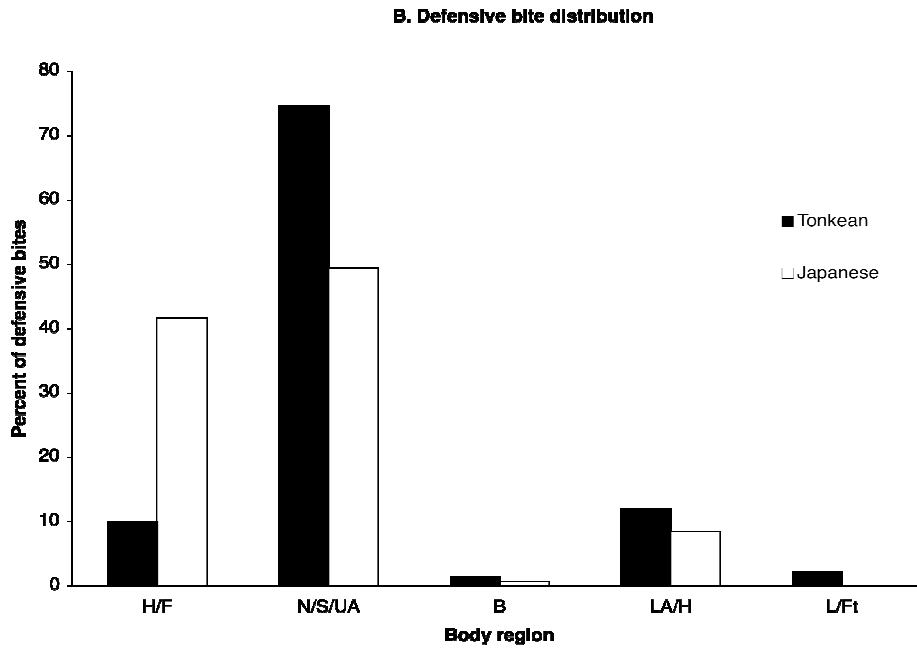
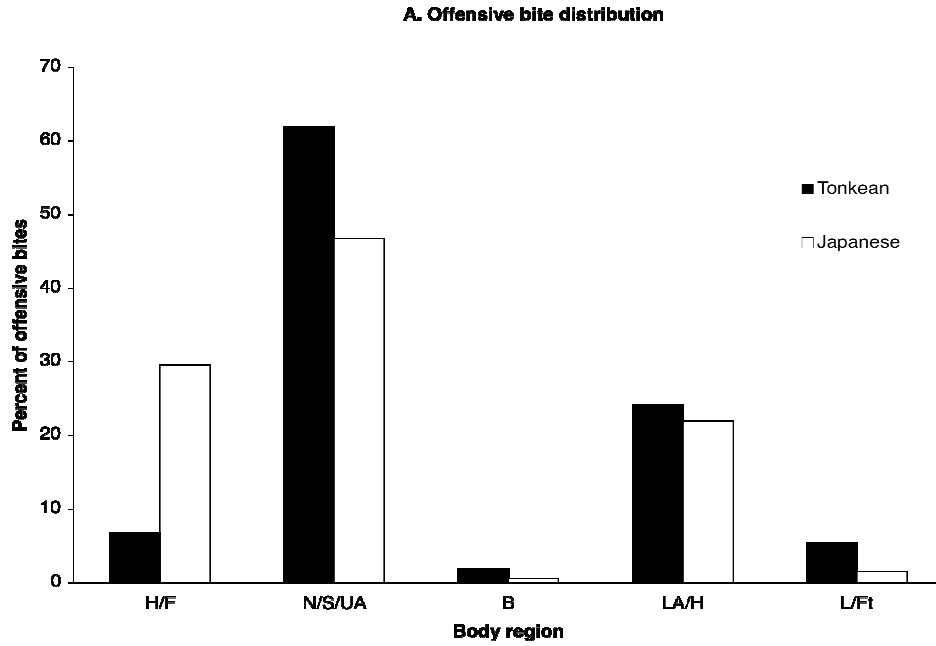


Figure 2. A) Offensive and B) defensive bite distributions during play fighting in F-to-F contexts. Body regions: Head/Face (H/F), Neck/Shoulder/Upper Arm (N/S/UA), Body (B), Lower Arm/Hand (LA/H), Leg/Foot (L/Ft).

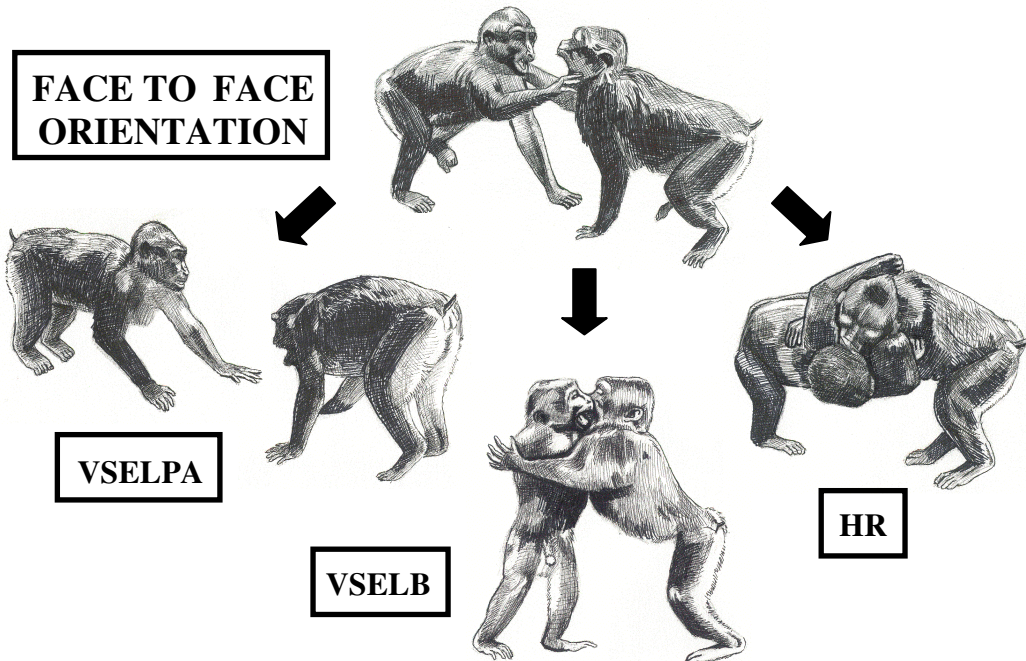


Figure 3. Some of the main defensive responses during play fighting in a F-to-F orientation are shown for Tonkean macaques (drawn from videotaped records): VSELPA–vertical, stay eye level, push/pull away; VSELB–vertical, stay eye level, bite; HR – horizontal, roll to back/side.

Quantitative analyses show that for both species, the modal response to receiving an N/S/UA bite is VSELB (Figure 4). Chi-square analyses of the pooled defensive response data for each species showed that the distributions of defensive responses were not random (Tonkean: $X^2(4, 153) = 45.3, p < 0.001$; Japanese: $X^2(4, 85) = 111.5, p < 0.001$), with VSELB being significantly more frequent than all the other tactics (Tonkean: $X^2(1, 153) = 15.8, p < 0.001$; Japanese: $X^2(1, 85) = 50.4, p < 0.001$). From a total of 153 facing defensive responses, Tonkean macaques used the VSELB tactic 39.9% of the time, and out of the 85 responses exhibited by Japanese macaques, VSELB was used 64.7% of the time. When defensive response distributions were calculated for individual animals, a within species Friedman ranked-scores analysis of variance showed that each species differed from a random distribution for the defensive tactics used (Tonkean: $X_r^2(4, 8) = 146.1, p < 0.001$; Japanese: $X_r^2(4, 7) = 138.3, p < 0.001$). Corrected follow-up comparisons showed that for both Tonkean ($z = 7.33$) and Japanese ($z = 5.92$) macaques, VSELB was used significantly more often than any of the other tactics ($p < 0.05$).

Although both species share the same modal tactic of defense (i.e., VSELB), Mann-Whitney U tests revealed that there were significant species differences with Tonkean macaques using the following tactics more frequently than Japanese macaques: HR ($U(7, 8) = 4, p < 0.01$), and Change eye level (VCELS + VCELT) ($U(7, 8) = 9.5, p < 0.05$). In contrast, Japanese macaques use the following more frequently: VSELB ($U(7, 8) = 13, p < 0.05$), VSELPA ($U(7,$

8) = 13.5, $p < 0.05$), Vertical (all defenses except HR) ($U(7, 8) = 4$, $p < 0.01$), and Stay eye level (VSELB + VSELPA) ($U(7, 8) = 6$, $p < 0.01$). To summarize, after being bitten, Japanese macaques are more likely than Tonkean macaques to maintain vertically-oriented defensive postures as opposed to relatively vulnerable horizontal positions, and they are also more likely to remain at eye level with their attackers, rather than dropping their heads to ‘become shorter’ or rearing up to ‘become taller’ than their play partners.

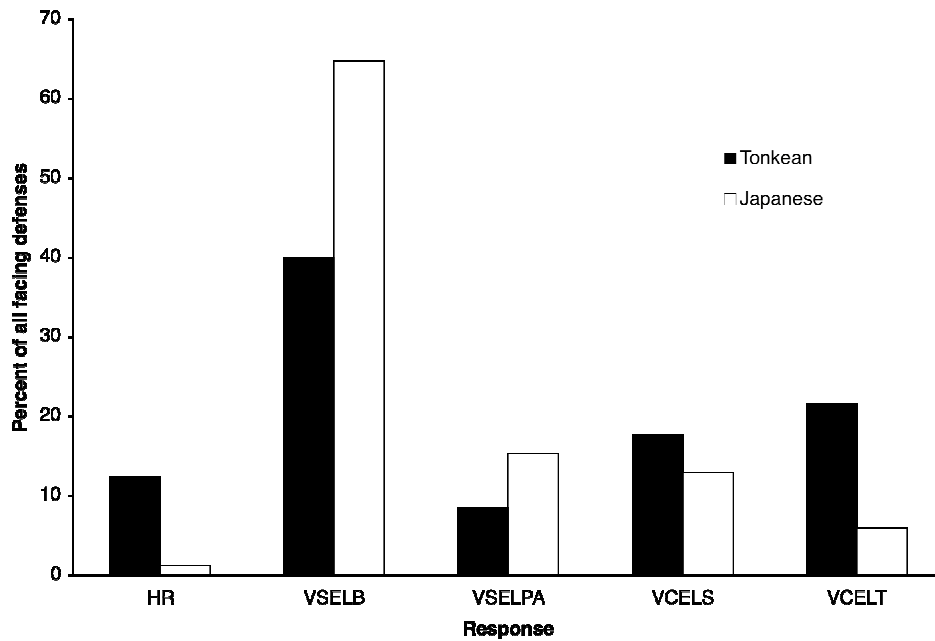


Figure 4. Distribution of facing defensive responses to N/S/UA bites delivered in F-to-F contexts. Responses: HR – horizontal, roll to back/side; VSELB – vertical, stay eye level, bite; VSELPA – vertical, stay eye level, push/pull away; VCELS – vertical, change eye level, move downward (‘become shorter’); VCELT – vertical, change eye level, move upward (‘become taller’).

Not only did 100% of the attacks received by Japanese macaques result in a facing defense compared to 92% for Tonkean macaques, they were also more likely to couple their defense with a retaliatory bite. Mann-Whitney U tests on the individualized data of the percentages of defensive responses that had an associated bite revealed that Japanese macaques were significantly more likely to deliver a retaliatory bite when defending against an N/S/UA bite in the F-to-F context ($U(7, 8) = 7.5$, $p < 0.01$).

Play fight durations. The data on the duration of dyadic play fights taken from the pooled data from each group revealed a species difference. Tonkean

macaques have longer lasting dyadic play fights (Mean \pm 95% confidence intervals: Tonkean macaques ($N = 138$): 22.4 s \pm 2.5 than do Japanese macaques ($N = 182$): 11.6 s \pm 1.8). When dyadic play fight durations were calculated for individual animals, a Mann-Whitney U test confirmed that dyadic play fights are significantly longer in Tonkean macaques ($U(7, 8) = 0, p < 0.001$). That is, the play fights of Tonkean macaques were, on average, about twice as long as those of Japanese macaques, which suggest that the Tonkean macaques sustained more prolonged, close bodily contact.

Polyadic play fights

Number of play partners. For Tonkean macaques, 36.5% of all play fights were polyadic, whereas for Japanese macaques, only 11.1% were polyadic. Furthermore, while about half of the polyadic play fights involved more than three partners in Tonkean macaques, virtually all polyadic play fights in Japanese macaques involved only three individuals (Figure 5).

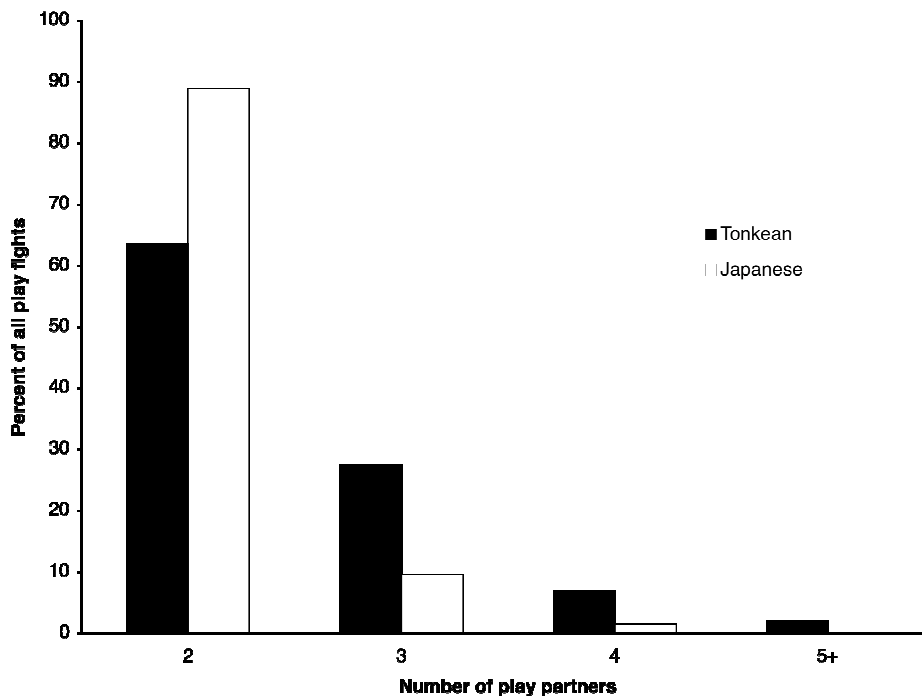


Figure 5. Percentage of play fights involving different number of play partners in Tonkean and Japanese macaques.

There is not only a species difference in the frequency of polyadic play fights, but they also differ in their organization. For Japanese macaques, polyadic interactions are relatively transient compared to that of Tonkean macaques. In

Japanese macaques, the original dyad would often break apart and a new dyad would form with the third partner, or the third individual would be involved with the original dyad for only a brief moment. The animals in the triad would continue to target the N/S/UA area of one of the other partners and avoid such bites by using the same suite of tactics evident in the dyadic encounters.

In contrast, for Tonkean macaques, polyadic interactions were completely unlike dyadic ones. Typically, a third partner joining in would throw itself on top of the other two, grabbing at whatever body part was available and biting it. These three could be joined by another, which would do the same, until, as was observed on several occasions, all the juveniles in the group were piled on top of one another! As the number of animals involved increased, it became harder and harder to distinguish which arms and legs belonged to which individuals. The monkeys could remain as a writhing mass for minutes, all the while delivering playful bites on whatever body part, of whatever animal, was accessible. In these situations, the animals did not use any - or, at least, not in an obvious manner - of the defensive tactics present in the dyadic interactions. Rather, if an animal had its arm bitten, in its defense, it would simply pull it away. Therefore, it was not possible to make an objective comparison of the tactics of defense used in the polyadic interactions between the two species. Nonetheless, it was possible to reveal the species differences in polyadic play fights by comparing bite distributions and play fight durations, even when the comparison was limited to triads.

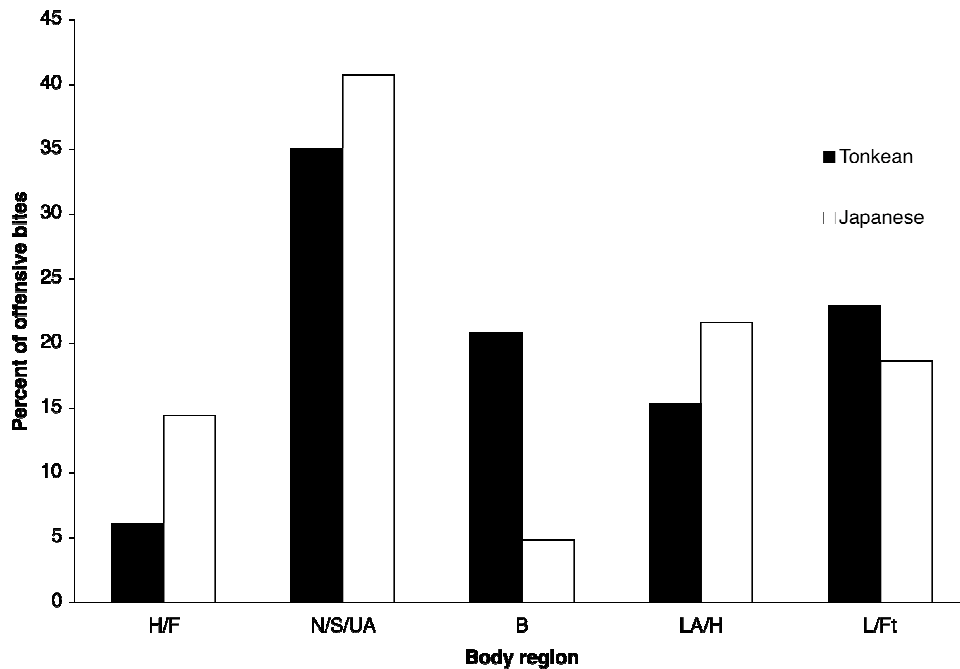
Targets: Bite distributions. Chi-square analyses of the pooled raw scores for each species showed that the distributions of offensive and defensive bites delivered to the different regions of the body were not random (Tonkean offensive: $X^2(4, 183) = 41.3, p < 0.001$; Tonkean defensive: $X^2(4, 41) = 15.5, p < 0.001$; Japanese offensive: $X^2(4, 167) = 58.1, p < 0.001$; Japanese defensive: $X^2(4, 66) = 43.3, p < 0.001$). As with dyadic interactions (see Figure 2), the modal target body area for triadic interactions was the N/S/UA (Figure 6). However, there did appear to be some differences. Using the percentage bite distribution from the dyadic interactions as a means of calculating the expected values for the bite distribution in triadic interactions revealed some differences when more than two animals are involved and between the two species. Chi square analyses showed that, for both species, the bite distributions differed significantly from those expected from dyadic interactions (Tonkean offensive: $X^2(4, 183) = 904.9, p < 0.001$; Tonkean defensive: $X^2(4, 41) = 69.9, p < 0.001$; Japanese offensive: $X^2(4, 167) = 281.9, p < 0.001$; Japanese defensive: $X^2(4, 66) = 15.6, p < 0.001$). In Tonkean macaques, for both offense and defense, the frequency of bites to N/S/UA decreased and bites to B and L/Ft increased ($p < 0.05$), whereas in Japanese macaques for offense, H/F bites decreased and B, LA/H and L/Ft bites increased ($p < 0.05$), and for defense, H/F and L/Ft increased ($p < 0.05$).

Play fight durations. The data on the duration of polyadic play fights taken from the pooled data from each group revealed a species difference. Tonkean macaques have longer lasting polyadic play fights (Mean \pm 95% confidence intervals: Tonkean (N = 62): 41.2s \pm 6.7) than do Japanese macaques (N = 18): 16.8s \pm 3.5). As mentioned in the *Methods*, a different analysis was needed for the

polyadic encounters. Kruskal-Wallis one-way analysis of variance tests on the binned data for 18 durations from each species showed that there were no within species differences ($p > 0.05$). A Mann-Whitney U test, using the entire 18 durations for each species, showed that Tonkean macaques have longer polyadic play fights than do Japanese macaques ($U(18, 18) = 45.5, p < 0.001$).

To compare polyadic play fights with dyadic ones, a sample of 18 dyadic durations from each species were binned and evaluated using the Kruskal-Wallis one-way analysis of variance tests, revealing no within species differences ($p > 0.05$). That being the case, all 18 durations from both species were used to compare polyadic with dyadic interactions using Mann-Whitney U tests. The polyadic play fights are significantly longer than dyadic play fights in Tonkean macaques ($U(18, 18) = 78.5, p < 0.01$), but there was no difference in the durations of dyadic and polyadic play fights for Japanese macaques ($p > 0.05$). That is, not only did polyadic play fights last longer in Tonkean macaques than in Japanese macaques, but while polyadic play fights were on average about twice as long as dyadic ones in Tonkean macaques, the duration of the play fights did not significantly increase in Japanese macaques when an additional partner joined in the interaction.

A. Offensive bite distribution



B. Defensive bite distribution

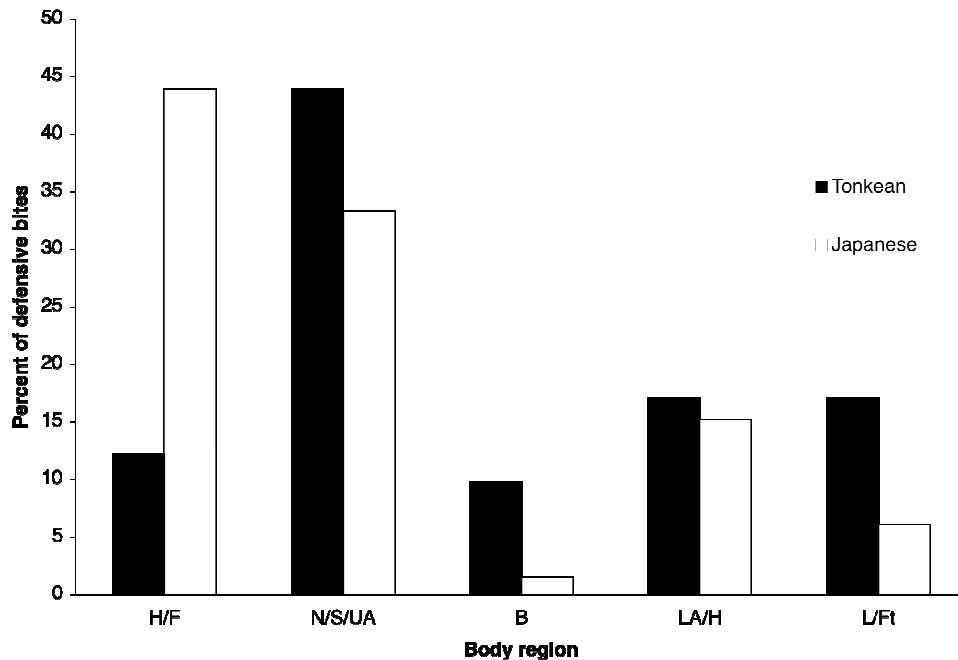


Figure 6. A) Offensive and B) defensive bite distributions during polyadic play fights. Body regions: Head/Face (H/F), Neck/Shoulder/Upper Arm (N/S/UA), Body (B), Lower Arm/Hand (LA/H), Leg/Foot (L/Ft). (Total number of offensive bites: Tonkean 183, Japanese 167; defensive bites: Tonkean 41, Japanese 66.)

Part 2 – Multiple Troop Comparisons

Using data derived from eight troops, two predictions from hypothesis 1 and seven predictions from hypothesis 2 were tested. The sole issue tested in this analysis was whether different samples from different troops conformed to the pattern predicted from the similarities and differences established in the analyses of the two troops in Part 1. The predictions were as follows:

(H1/P1) Hypothesis 1: Prediction 1. During dyadic play fighting, for all troops, the modal target area bitten should be the N/S/UA.

(H1/P2) Hypothesis 1: Prediction 2. During dyadic play fighting, all troops should use all the tactics of defense, including those involving standing and turning to supine.

(H2/P1) Hypothesis 2: Prediction 1. During dyadic play fighting, the main difference between the two focal troops for offensive bites was that there were relatively more bites directed toward the side of the head relative to the modal target (N/S/UA) in Japanese macaques and less in Tonkean macaques. Therefore, for Tonkean macaques, the proportion of head bites relative to bites to the N/S/UA

should be 20% or less, whereas, for Japanese macaques, it should be more than 20%.

(H2/P2) Hypothesis 2: Prediction 2. During dyadic play fighting, the main difference between the two focal troops for defensive bites was that there were relatively more bites directed toward the side of the head relative to the modal target (N/S/UA) in Japanese macaques and less in Tonkean macaques. Therefore, for Tonkean macaques, the proportion of head bites relative to other bites should be 20% or less, whereas, for Japanese macaques, it should be more than 20%.

(H2/P3) Hypothesis 2: Prediction 3. During dyadic play fighting, the main difference between the two focal troops for defensive tactics was that there were relatively more horizontal tactics (HR) related to remaining vertical (VSELB) in Tonkean macaques compared to Japanese macaques. Therefore, for Tonkean macaques, the proportion of horizontal tactics relative to vertical ones should be 20% or more, whereas, for Japanese macaques, it should be less than 20%.

(H2/P4) Hypothesis 2: Prediction 4. For duration of dyadic play fighting, the main difference between the two focal troops was that interactions lasted twice as long in the Tonkean macaques (22.4 s vs. 11.6 s). Therefore, for Tonkean macaques, the duration of dyadic play fights should be 20 s or greater, whereas, for Japanese macaques, less than 20 s.

(H5/P5) Hypothesis 2: Prediction 5. For the duration of triadic play fighting, the main difference between the two focal troops was that interactions increased markedly in Tonkean macaques but only marginally in Japanese macaques (41.2 s vs. 16.8 s). Therefore, for Tonkean macaques, the duration of triadic play fights should be 40 s or greater, whereas, for Japanese macaques, it should remain under 20 s.

(H2/P6) Hypothesis 2: Prediction 6. In triadic play fighting versus dyadic play fighting, the main difference between the two focal troops for bite specificity was that while in Japanese macaques a similar proportion of bites to the N/S/UA were retained in both types of interactions, the proportion of bites to the N/S/UA dropped markedly in the triadic interactions of Tonkean macaques. Therefore, for Tonkean macaques, the proportion of bites to the N/S/UA should be reduced by 20% or more in triadic interactions compared to dyadic ones, but remain within 10% of the value in Japanese macaques.

(H2/P7) Hypothesis 2: Prediction 7. In triadic play fighting, the main difference between the two focal troops for tactics of attack and defense was that while Japanese macaques retained the same pattern as that present in dyadic ones, for Tonkean macaques, the pattern was not the same. Therefore, all the Japanese troops should retain the dyadic-like pattern, but Tonkean macaques should not.

The data were entered and analyzed with regard to whether each troop met the species-typical criteria established by the focal troop analyses (Part 1) as yes (+) or no (-) (Table 1). Except for the two solely qualitative predictions (H1P1 and H2P7), modal values are shown for predictions about targets and tactics (%) and mean values for play fight durations are shown in seconds (s). The actual values used to decide on whether the troops conformed to the predicted pattern are shown so as to provide a sense of the variation in behavior evident across troops. Both

predictions from the first hypothesis and five from the second were confirmed (Table 1). For the measures involving targets and tactics, only three troops deviated from the expected pattern, and then, for only one measure each. In part, these deviations could have resulted from the random selection of each play fight that fit the criteria, irrespective of matching for similarities between contestants. Such factors may have been particularly important for troops with a limited pool of play partners, where younger (smaller) individuals were constrained to interact with older (larger) partners (e.g., T2 and J2). Another factor could be that by using cut-offs for species-typical values rather than continuous scores, the degree of closeness of match to the species-typical pattern is underestimated (e.g., for relative face bites during offense, Jf scored 19.2%, just under the cut-off of 20%). Nonetheless, given these potential sources for error, across troops, all the measures involving aspects of attack and defense significantly conformed to the species-typical pattern as established by the detailed analyses of the focal troops.

In contrast to the measures derived from targets and tactics, the measures of duration deviated across multiple troops and so there was no significant effect. Three of the troops of Tonkean macaques had values close to those of the Japanese macaques in either dyadic or polyadic interactions. For two troops of Japanese macaques, the duration of polyadic interactions increased above twenty seconds, but in both of these cases, the duration was under 26 s, values that were close to that of the dyadic play fights of the focal troop of Tonkean macaques (see Part 1). Even though the measures of play fight duration were the least consistent across troops, only troops of Tonkean macaques ever exceeded durations of 40s in polyadic interactions.

Once the most robust measures of play fighting were identified, samples of video sequences analyzed for the two focal troops in Part 1 were re-analyzed by another person to evaluate inter-observer reliability. This was important so as to determine the replicability of these measures. Three of the most useful, and the most difficult measures were re-scored: modal offensive biting target, relative use of head versus shoulder target in defense, and the relative use of horizontal versus upright defensive tactics. The same sequences, for both species, that were scored by CR were re-scored by SP without pre-training. Sequences from the juveniles of both species were used yielding 15 individuals (see Part 1). Spearman's rank correlations revealed a significant association between raters for all three measures (offensive bites: $r_s = 0.82$, $p < 0.01$; defensive bites: $r_s = 0.89$; defensive tactics: $r_s = 0.73$, $p < 0.01$). With practice, reliability should be even greater, especially for the tactics of defense that involve dynamic movements by both partners, requiring subtle judgments as to the most appropriate video frame to use for scoring.

Table 1

A qualitative comparison is shown for whether the various troops tested conformed to the predictions arising from the hypotheses (see text)

Troops	H1/P1	H1/P2	H2/P1	H2/P2	H2/P3	H2/P4	H2/P5	H2/P6	H2/P7
Tf [#]	+	+	+	+	+	-	-	+	+
	(81.3%)		(11.8%)	(15.0%)	(80.3%)	(19.0s)	(18.8s)	(53.7%)	
T1	+	+	+	+	+	-	-	+	+
	(69.4%)		(12.7%)	(6.7%)	(31.5%)	(14.5s)	(24.3s)	(40.5%)	
T2	+	+	+	+	+	+	+	+	+
	(56.1%)		(17.5%)	(11.8%)	(28.6%)	(25.2s)	(41.4s)	(34.1%)	
T3	+	+	+	+	+	-	-	+	+
	(75.9%)		(19.5%)	(21.3%)	(33.4%)	(9.5s)	(14.8s)	(42.6%)	
Jf [#]	+	+	-	+	+	+	+	+	+
	(63.7%)		(19.2%)	(96.3%)	(16.0%)	(12.9s)	(18.3s)	(58.1%)	
J1	+	+	+	+	+	+	-	+	+
	(58.1%)		(22.2%)	(71.3%)	(10.6%)	(14.2s)	(25.6s)	(61.6%)	
J2	+	+	+	+	-	+	-	+	+
	(51.4%)		(20.4%)	(45.4%)	(74.9%)	(12.6s)	(25.6s)	(61.6%)	
J3	+	+	+	+	+	+	+	+	+
	(66.7%)		(29.6%)	(73.1%)	(18.8%)	(4.7s)	(7.5s)	(55.5%)	
Sign test	**	**	*	*	*	ns	ns	**	**

Note: Cases where the troop conforms to the predicted value are shown as +, and cases where it does not are shown as -, and where appropriate, the numerical values used are shown in parentheses. The level of significance is given at $p < 0.05$ (*) or $p < 0.01$ (**). #Tf and Jf represent the additional samples taken from the two focal troops used in Part 1.

Discussion

The videotaped play interactions of the two species of macaques were used to test two hypotheses: (1) that both species compete for the same body targets and use the same tactics to defend against such contact, and (2) that the more egalitarian species, the Tonkean macaque, uses patterns of biting and tactics of defense that promote and prolong playful interactions. Both hypotheses were supported by the analyses of the two focal troops and most of the predictions arising from these hypothesized similarities and differences were confirmed by the analyses of additional troops.

Qualitative analyses of videotaped play fights suggested that the play target for both groups of macaques was the confluence of the side of the neck, shoulder and upper arm (N/S/UA). Quantitative analyses confirmed that this was the area to which bites were most often directed in all troops of both species. Therefore, play fights can be conceptualized as involving attack and defense of the N/S/UA. This is also consistent with the findings from studies of other macaques (Symons, 1978), other Old World Monkeys (Pellis & Pellis, 1997) and apes (Schaller, 1963). Similarly, all troops of both species used the same suite of defensive tactics to avoid or break free from bites to the shoulders, and again, the tactics that we discerned are comparable to the ones described for other Old World Monkeys (Pellis & Pellis, 1997; Symons, 1978). Therefore, consistent with hypothesis 1, in dyadic play fights, the two species of macaques studied used the

same targets and tactics. However, consistent with hypothesis 2, there were subtle species differences in how those targets and tactics were implemented.

Targets of attack and defense

Japanese macaques are more likely to direct bites to the side of the face than are Tonkean macaques, especially when launching defensive bites - that is, those launched in retaliation to a bite from a partner. Consistent with the present findings, studies of play fighting in other species of primates have also shown that defensive bites are often directed to the side of the face (Pellis & Pellis, 1997; Owens, 1975a; Symons, 1978). Given that in these species of primates play fighting appears to mimic serious fighting (Aldis, 1975; Owens, 1975b; Symons, 1978), it is reasonable to suppose that similar targets are attacked and defended. Indeed, several studies on captive and free-living macaques have reported data on wounds presumably derived from intra-specific aggression, and these reveal a preponderance of lesions and scars on the upper body and head, especially the face (Bernstein & Gordon, 1974; Hausfater, 1972; Hori, Tokura, & Tadaki, 1972; Ruehlmann, Bernstein, Gordon, & Balcaen, 1988; Whitten & Smith, 1984; Zhao, 1994). If our supposition is correct, then the modal offensive target during play fighting - the upper arms, shoulder and neck region - should be the primary target of agonistic offense, and the bites to the sides of the face should be equivalent to the defensive, retaliatory bites. Studies of the targets and tactics used in both play fighting and serious fighting are rare for primates, but where the data are available, this pattern for offense and defense is supported (Owens, 1975b). Detailed studies of agonistic interactions in rodents further support this view.

In most fights, both opponents are engaged in both attack and defense, but for territorial rodents, placing an unfamiliar intruder into the home cage of a resident leads to the resident initiating most of the attacking and the intruder most of the defending (Blanchard & Blanchard, 1990). In this context, the defending intruder delivers most of the bites to the side of the face, and the attacking resident delivers most of the bites to the lower flanks and dorsum. These differences are also consistent with wounds recorded for both captive and free-living data for rats and other species (Blanchard et al., 1977, Blanchard, Blanchard, Pank, & Fellows, 1985; Pellis, 1997; Pellis & Pellis, 1988, 1992). In cases where both animals attack and defend, such as at the border of two territories, there can be a combination of bites directed at the species-typical offensive target and bites directed at the defensive target, usually to the side of the face (Pellis et al., 1996). Given that, in both serious fighting and play fighting, offense and defense are likely regulated by different neural, endocrinological and genetic mechanisms (Adams, 1980; Blanchard & Blanchard, 1994; Pellis & Pellis, 1991), the relative balance of offensive and defensive bites launched can be an index for how defensive an animal is during combat (Pellis, 1997).

Detailed studies of rodents have revealed that, during play fighting, some species are more likely to retaliate with bites to the play target, while others are more likely to retaliate with bites to the side of the face. Those that retaliate against

the side of the face are more likely to break contact and terminate the playful encounter. Conversely, those that primarily retaliate against the species-typical play target are also the ones that have the most complex and prolonged playful interactions (Pellis & Pellis, 1987, 1998a; Pellis et al., 1989).

If directing retaliatory bites to the species-typical play target facilitates the continuation of play fighting, then such targeting may be considered cooperative. In contrast, if directing retaliatory bites to the side of the face inhibits further playful contact, then such targeting may be considered competitive. If this schema for different targets is correct, then the greater likelihood that both retaliatory and non-retaliatory bites by Japanese macaques are directed to the side of the face suggests that, with respect to body targets, Japanese macaques are more competitive in their play fighting than are Tonkean macaques. That the dyadic play fights of Tonkean macaques could be twice as long as those of Japanese macaques, supports the hypothesis that play fights in the Tonkean macaques are more cooperative and the play fights of Japanese macaques are more competitive.

Defensive tactics and play fighting

For our most detailed analyses, we deliberately chose to use a particular configuration between attacker and defender (face-to-face) with one partner directing a bite to the other's play target in order to evaluate species differences in tactics of defense. We did so to ensure that any species differences found were not due to confounds such as species differences in attack behavior (Pellis, 1989). From this position, it was found that individuals from both species were most likely to use a maneuver whereby the defender maintained a standing posture and remained at eye level with the attacker. However, unlike Japanese macaques when using the standing defensive maneuver, Tonkean macaques were more likely to alter their eye level to below or above that of their partner. Furthermore, Tonkean macaques were more likely to rotate around the longitudinal axis of their bodies, which often led them to lie on their sides or their backs (see Figure 3 for drawings illustrating these defensive maneuvers). Using rotatory and standing types of defense has also been described in the play fighting of other primates (Emory, 1975; Owens, 1975a; Pellis & Pellis, 1997; Symons, 1978), as they have in rodents for which detailed comparisons across species provide a framework within which to interpret these species differences (Pellis & Pellis, 1998a).

For those species of rodents where play fighting is prolonged and complex, turning to supine is more frequently used than standing (Pellis & Pellis, 1987, 1988; Pellis et al., 1989). Similarly, for any given species, such as the laboratory rat, age-related changes in defensive tactics occur, with play fighting being most frequent, prolonged and complex at the age when the turning to supine tactic is used most often (Pellis & Pellis, 1987). Turning to supine reduces the defender's ability to retaliate and limits its ability to control the actions of the partner standing on top (Pellis & Pellis, 1998b; Pellis, Pellis, & Foroud, 2005), and for this reason, appears to be the defensive tactic most likely to facilitate prolonged bodily contact. Reducing one's own control over the situation necessarily means that the

advantage is transferred to the partner (Pellis et al., 2010). In this respect, a supine defense, as opposed to a standing defense, may be viewed as being a more cooperative action. Thus, the greater use of rotatory tactics by Tonkean macaques suggests that their playful defense is more cooperative than that of the Japanese macaques.

Polyadic versus dyadic play fights

Taken together, the greater frequency of retaliatory bites to the side of the face in Japanese macaques and the greater use of rotatory defense in Tonkean macaques, support the hypothesis that Japanese macaques are more competitive in their play fighting and Tonkean macaques more cooperative. If this is correct, then play fights involving more than two animals should exaggerate this intergroup difference, and this is what was found. It should also be pointed out that the rarity of polyadic play fights in Japanese macaques is consistent with earlier studies (e.g., Koyama, 1985; Petit et al., 2008), and the greater frequency of such interactions in the Tonkean macaques may be common to other Sulawesi macaques as well (Petit et al., 2008). Polyadic play fights in Japanese macaques are similar to dyadic ones. Indeed, when another animal joins a pair that is play fighting, the polyadic phase seems transitory, since the play fight will typically revert to two individuals. With regard to body locations bitten, there is little difference between two or three animals playing - the shoulder area is still the primary play target and retaliatory bites to the side of the face are still frequent. Similarly, the standing tactics remain the most common, with others occurring at a similar frequency to how they are used during dyadic interactions.

Polyadic play fights in Tonkean macaques contrast with their dyadic play fights in that bites are delivered more opportunistically over partners' bodies, and individuals no longer use any particular tactics to defend themselves. Rather, Tonkean macaques cluster into writhing masses of bodies, with individuals grabbing and biting whatever body part of another macaque is accessible. The reduced structure in play fighting involving multiple animals is revealed by the higher frequency of bites delivered all over the body including the extremities. Given that during polyadic play fights individuals are most likely to roll over to supine on the ground or on top of other animals, the opportunity to use defensive tactics that can regain control over the situation is diminished. That polyadic play fights in Tonkean macaques are different to dyadic ones is further reinforced by the finding that polyadic play fights could last twice as long as dyadic ones. Indeed, the longest lasting of any of the play fights observed in any of the eight troops scored were for Tonkean macaques engaged in polyadic interactions. The comparative literature again provides a guide in how to interpret these results.

The analyses of dyadic and polyadic play fights in Japanese and Tonkean macaques support our predictions that, even though these species have a common play target and use a common suite of defensive tactics, the pattern of play fighting is more cooperative in Tonkean macaques and more competitive in Japanese macaques. Moreover, these differences, as predicted, are more pronounced in

polyadic play fights. Indeed, irrespective of whether any particular troop deviated from the expected species-typical pattern seen in dyadic interactions, all troops exhibited the species-typical pattern of attack and defense during polyadic interactions (Table 1).

Some caveats

Since significant intraspecific variation can exist among troops of the same species (de Waal & Luttrell, 1989), caution should be exercised in drawing conclusions about species-level differences from any one study (Petit et al., 2008). To reduce the role of such variation in this study, we used two approaches. First, we matched the two focal troops studied for as many variables as possible, and then we used a variety of analytical approaches to compare different aspects of the troops dyadic and polyadic play fights. Irrespective of the analytical approach, there were persistent troop differences. Second, to confirm that these were species differences, rather than merely troop differences, the most robust findings in the two-troop analyses were tested on a broader set of troops with different histories, locations, physical living conditions and demographics. Again, despite these inter-troop differences, the analyses supported the general conclusion that play fighting of Japanese macaque juveniles was more competitive and that of the Tonkean macaque juveniles was more cooperative. Even when deviating on one measure or another, for each troop scored, the overwhelming number of measures conformed to that predicted from the detailed analyses of the focal troops (*Results*, Part 1). That is, no troop deviated from the predicted behavior in more than one measure of targets and tactics (Table 1). Measures of duration seemed the most labile when comparing across and within troops, but even so, interactions of a longer duration were found in Tonkean macaques. Therefore, we are confident that the differences reported here, especially those associated with patterns of attack and defense, reflect differences at the species level.

Studies have shown that several traits of the social repertoire, such as conciliatory tendency, are consistently found to have a narrow range of variation across populations of the same species (e.g., Judge & de Waal, 1997; Kutsukake & Castles, 2001; Thierry, Aureli, Nunn, Petit, Abegg, & de Waal, 2008). Therefore, play fighting, like some other social traits, may be robust in exhibiting species-typical features across a range of contexts and populations. For example, studies of species, ranging from kangaroos to ground squirrels to squirrel monkeys, indicate that although there may be differences in the frequency of play fighting between captive and free-living populations, the targets and tactics used do not differ (Biben, 1998; Pasztor, Smith, MacDonald, Michener, & Pellis, 2001; Watson, 1998). However, these consistencies across species and contexts must be weighed carefully against the specific questions being asked. For example, in our case, we wanted to know if, when they did play, whether the behavior patterns used (bite targets and defensive tactics) were similar between the two species, and if the variation in these features of play between the two species was reflected in their species differences in social style (i.e., despotic versus egalitarian). The measures

characterized and compared in this study seem adequate to address these issues (see above). Nonetheless, collecting data from the different troops of the two species did take different amounts of time, suggesting that the frequency of play varied. Such variation may reflect important contextual factors, such as climactic, demographic and resource differences, that impinge on how much time particular troops devote to play (e.g., Baldwin & Baldwin, 1976; Barrett & Dunbar, 1992; Stone, 2008). The data we extracted from the present study do not address such concerns.

From a methodological perspective, the cross troop variations we did find indicate that there may be two types of measurements for comparing play fighting across species: those such as duration, that appear relatively labile and those derived from targets and tactics, that appear relatively robust. The more labile measures may only be usefully compared for closely matched samples, whereas the more robust ones may be useful even when comparing troops that are not closely matched. Even so, the current study supports using multiple measurements for comparing troops of different species, rather than relying on any one measure (Thierry et al., 2000), and wherever possible, patterns of behavior that appear typical of a species should be confirmed by observations made across multiple troops (Pellis & Iwaniuk, 2000).

Of particular value for species-level comparisons are playful situations that tax the emotional and cognitive capabilities of the participants, such as play fighting which involves multiple animals (Palagi, 2008). While we found that polyadic play was more rare in some troops than others, even within the same species, it was the case that when they did play with multiple partners, Tonkean macaques, from all troops and unlike any of the troops of Japanese macaques, interacted in a manner that increased cooperation. These findings suggest that in more demanding and extreme situations, Tonkean macaques can achieve a level of cooperation in their play fighting that far exceeds that of Japanese macaques.

Play fighting and sociality

Given that all macaque species derive from a common ancestor, it is not surprising that both species of macaque have a similar behavioral repertoire (Capitani, 2004). However, even though both species compete for the same play targets and use the same tactics of defense, there are stylistic differences in the organization of their play fighting. Furthermore, the species differences in play fighting appear to be consistent with the species differences in sociality. More egalitarian species, such as Tonkean macaques, appear to have a temperament that makes them more tolerant of others, and conversely, more despotic species, such as Japanese macaques, appear to have a temperament that makes them less tolerant, and these differences in temperament are reflected across a range of social behavior (Thierry, 2004), including play fighting (Petit et al., 2008). As shown in the present study, in play fighting, these species-level differences in temperament lead to a style of interaction that is either more cooperative (Tonkean macaques) or more competitive (Japanese macaques).

The findings from the present study are consistent with those made from comparisons of more distantly related species. For example, comparisons of the play fighting of chimpanzees and bonobos show that the more egalitarian bonobo has a style of play that is more cooperative than that of the more despotic chimpanzee (Palagi, 2006, 2007). Furthermore, there have been various reports suggesting that differences in the sociality of species are somehow reflected in species differences in play fighting (e.g., Cheney, 1978; Maestriperi & Ross, 2004; Watts & Pusey, 1993; Zucker & Clarke, 1992). A methodological problem has been that of discerning what aspects of sociality and of play fighting to compare. A cross-species study of rodents failed to find a significant relationship between the association pattern of adult males and females (as a measure of sociality) and the complexity of play fighting (as a measure of play) (Pellis & Iwaniuk, 1999). Studies of macaques suggest that species differences in non-sexual social behavior may be more robustly conserved than species differences in mating behavior (Thierry, 2000, 2004), and so may be a better source from which to develop suitable measures of sociality (Thierry, 2007; Thierry et al., 2000). The present study suggests that the most promising measures for comparing patterns of play may be the ones that emphasize targets and tactics and that these should be used to develop indices of relative cooperativeness or competitiveness (Pellis et al., 2010). Armed with reliable indices of sociality and of play, and by making multi-species comparisons using appropriate statistical techniques (Pellis & Iwaniuk, 2000) and including a wide range of species of Old World Monkeys that differ markedly in both sociality and play fighting, it would be possible to test, comprehensively, the hypothesis that differences in sociality influence species differences in play fighting.

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